Quail 9: National Quail Symposium Proceedings

August 1-5, 2022 | Springfield, Missouri

QUAIL 9: NATIONAL QUAIL SYMPOSIUM PROCEEDINGS

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The cover is a photo of Stony Point Prairie Conservation Area, a remnant native grassland located in southwest Missouri, USA, that is managed with fire and grazing. Research from Missouri suggests this approach to grassland management represents the best chance for stabilizing quail populations in southwest Missouri. Also depicted, from left to right, are Montezuma quail, scaled quail, Gambel's quail, and northern bobwhite, which are some of the species reported on in these proceedings.

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FOREWORD

The National Quail Symposium Proceedings are a project of the National Bobwhite & Grassland Initiative (NBGI), the National Bobwhite Conservation Initiative Technical Committee (NBCITC, formerly known as the National Bobwhite Technical Committee, NBTC), and the NBCITC Science Subcommittee.

The Quail 8 National Quail Symposium and the 23rd Annual Meeting of NBTC were held as a joint quail conference in 2017 in Knoxville, Tennessee. Following the success of that meeting, the Missouri Department of Conservation, University of Missouri, and USDA Forest Service submitted a letter of intent to host the Quail 9 National Quail Symposium and 28th Annual Meeting of NBCITC as a joint quail conference and were awarded the opportunity in 2018. With the addition of representatives from the National Bobwhite & Grassland Initiative, National Bobwhite Conservation Initiative Technical Committee, Quail Forever/Pheasants Forever, and Clemson University, a steering committee was formed to launch the Joint Quail Conference in Springfield, Missouri, August 1–5, 2022. This is the second time the National Quail Symposium and NBCITC have met jointly.

The steering committee also committed to publishing and making available the Quail 9 Proceedings at the Joint Quail Conference, something which had been done only twice before. Like previous proceedings of the National Quail Symposia, this proceedings is published as the National Quail Symposium Proceedings in the Tennessee Research and Creative Exchange (TRACE), the University of Tennessee's Open Access repository. This publicly accessible archive features research and creative work by scholars and researchers. The Quail 9 National Quail Symposium is following the trend in scientific publishing and with this volume will publish the proceedings online only, available at <https://trace.tennessee.edu/nqsp/>. A new feature of this proceedings is that all articles and abstracts in the proceedings have a Digital Object Identifier (DOI), which is a unique and never-changing string assigned to online (journal) articles, books, and other works. DOIs make it easier to retrieve and cite articles and abstracts. Publication of the proceedings prior to the symposium required tremendous effort by the authors, associate editors, and editorial assistant. We especially thank Cynthia Moser for copyediting submissions and Kari Finkler for the publication design and layout. All manuscripts and abstracts went through a peer review and revision process prior to publication. The proceedings is an opportunity to publish contributions that may not be suitable for other scientific outlets, but nevertheless the editors want to ensure the work is presented clearly and accurately and makes appropriate inferences.

The Joint Quail Conference is a gathering of approximately 250 participants consisting of managers, researchers, and educators focused on quails, related species, and the ecosystems in which they occur. The Quail 9 National Quail Symposium includes 61 scholarly contributions presented in oral presentations or poster presentations. The plenary session focuses on the benefits of adaptive management for quail conservation with presentations by Dr. Lenny Brennan and Dr. James Martin providing a western and eastern perspective. Dr. Martin also presented on the state of the northern bobwhite in 2022. Since the conference is being held in Springfield, Missouri, there are also presentations by Kyle Hedges and Dr. Frank Thompson on the Southwest Missouri quail study, which occurred nearby. Following the plenary session, there are concurrent sessions on bobwhite restoration, translocation, western quail, bobwhite ecology, quail physiology, population estimation, and hunting. Species covered include northern bobwhite, scaled quail, Montezuma quail, masked bobwhite, and the long-tailed wood-partridge. The conference concludes with a stimulating presentation by Fidel Hernández: The Evolution of Quail Research: Trends in Themes, Cognitive Extent, and Lexical Diversity.

Many contributed to the excellence and timeliness of the proceedings. We are particularly indebted to those listed in the Acknowledgments, Editorial Committee, Reviewers, and Committee sections.

—Frank R. Thompson III, Editor in Chief and David Hoover, Steering Committee Chair

ACKNOWLEDGMENTS

The Quail 9 proceedings and symposium required many people to be successful. At this writing, 5 weeks before the symposium, some key people could be missed in the proceedings' acknowledgments, and similarly, institutional contributions in some cases will not be finalized until after Quail 9. Final formal recognition of individuals and institutional contributors will be announced at the meeting and published in the program and on the symposium website. The formal roles of many of the following recognized individuals, and their affiliations, are listed in the Joint Quail Conference Committees page.

Quail 9 is part of a series that began in 1972. The location in Missouri resulted largely from the encouragement of Dr. Thomas Dailey, Chair of the Quail 8 National Quail Symposium Technical Committee. Early on, we relied on the guidance of Tom until the Steering Committee was fully formed and operational, and we benefited greatly from the participation of returning steering committee member Penny Barnhart. Before we even agreed to host the conference, we engaged Erica Lovercamp, from the Conference Office, University of Missouri Extension; we would not have attempted this meeting without her help. Erica and her staff took care of all the meeting logistics. Dr. Mitch Weegman was an early steering committee member and Co-Editor but departed those roles because of his move to the University of Saskatchewan; we thank him for his important early efforts. The implementation of the Joint Quail Conference, including preparation and follow-up business, was made possible by a dedicated team of individuals under the leadership of the steering committee (see Committees section for details), which

included Erica Lovercamp, Lisa Potter, Jef Hodges, Casey Bergthold, Frank Loncarich, Penny Barnhart, Kyle Hedges, and Frank Thompson. The production of the proceedings and management of the editorial process in TRACE was assisted by Molly Foley. Cynthia Moser copyedited all submissions and Kari Finkler did the design and layout of the publication.

Funding for Quail 9 was procured through the efforts of many committee members. Institutional support of Quail 9 was essential to the publication of the proceedings and a high-quality experience for symposium participants. At this writing, not all contributions have been secured, so final recognition of contributors will occur at the event and be published in the program and on the symposium website. Quail 9 was built on the funding foundation provided through both in-kind contributions and cash from the Missouri Department of Conservation, University of Missouri, USDA Forest Service, National Bobwhite & Grassland Initiative, the National Bobwhite Conservation Initiative Technical Committee, and Quail Forever/Pheasants Forever. Sponsors also included Caesar Kleberg Wildlife Research Institute, Arkansas Game and Fish, National Bobwhite & Grassland Initiative, the USDA Natural Resources Conservation Service, Roundstone Seed, Truax Company, Clemson University College of Agriculture, Forestry, and Life Sciences, Missouri Prairie Foundation, Hamilton Native Outpost, Pure Air Native Seed, Bamert Seed, Bass Pro/Cabela's, Cedar Creek Farm, Lotek, Lick Skillet Seeds, Missouri Conservation Heritage Foundation, Project Upland, Larry P. O'Reilly and Family Foundation, and Family Center Farm and Home.

—Frank R. Thompson III, Editor in Chief and David Hoover, Steering Committee Chair

IN MEMORIAM

DR. DANIEL W. SPEAKE (1926-2019)

Dan Speake was born in 1926 in Decatur, Alabama, where he grew up roaming the woods hunting and "catching snakes and turtles," passions that were developed young and stayed with him throughout his life. Dr. Speake was a noted wildlife researcher and Auburn University professor who was known throughout the wildlife fraternity as an extraordinary naturalist and researcher. He was passionate about his work. His teaching and research spanned over 40 years and included major contributions on bobwhite quail, eastern wild turkey, and eastern indigo snake.

After a stint in the Navy during World War II, Dan went to Auburn University on the GI bill, eventually earning a PhD working on bobwhite quail in the Alabama piedmont. He became the Assistant Leader and later, the Unit Leader, for the Alabama Cooperative Wildlife Research Unit at Auburn from 1955-1995. In Dan's words, there was a "technology explosion" in the 1970s with the advent of radio telemetry. He was a pioneer in many ways, but certainly in the use of radio transmitters on wildlife. He and his students were the first to document double brooding in quail in 1987, as well as second brood production in eastern wild turkeys in 1991. His cutting-edge research allowed monitoring of wildlife populations as never before, leading to better management practices and resulting in the recovery of the wild turkey in Alabama, as well as other states.

His research with nongame and endangered species in the 1970s was at a time when very little research was supported for nongame wildlife. He established the first eastern indigo snake captive breeding program in the United States and continued this research into the 1980s with reintroductions throughout south Alabama and other states in efforts to re-establish a viable population of the endangered species. He developed and used one of the first cameras to be put down gopher holes, revealing for the first time the long list of animals that were dependent on this environment. He was known far and wide for his collection of live snakes, most notably "Bubba," who was a huge eastern diamondback he donated to the Montgomery Zoo when he retired. Those of us fortunate enough to have spent time with him roaming the woods of the South remember how he always travelled with a pillowcase in the event he needed a way to carry some "ready" species of snake back to Auburn.

Dan was the recipient of 19 wildlife awards, including the Special Recognition Service Award from The Wildlife Society for his leadership on wild turkey research. He received the coveted Henry S. Mosby Award in 1991, presented by the National Wild Turkey Federation, for his extraordinary accomplishments in wild turkey research. At the time of this award, he was only the fifth recipient to receive this special recognition.

Dr. Speake had a long relationship with Tall Timbers Research Station. He took his upland wildlife class on an extended field trip there for many years. He served on the Board of Trustees of Tall Timbers from 1990-1993 and several of his last graduate students did their field work there, including an award-winning study on turkey poult mortality published in 1995. He authored or co-authored numerous publications on quail including some of the earliest work on brood habitat use, effects of pen-raised birds on wild populations, hunter and covey interactions, and supplemental feeding, some of which is published in previous Quail Symposium Proceedings. Perhaps his most enduring legacy is that he along with Dr. Lee Stribling were co-founders of the Albany Quail Project in 1992.

Dr. Speake was a colorful character who enjoyed his life and life's work. When you were with him, it was impossible not to go along for the ride. He had many sayings, but some of the best remembered are that he "knew a lot more about turkeys than he could prove" and "if you don't know what your data is telling you before you analyze it, it don't mean nothing."

The twinkle in his eye never faltered and his wonderful sense of humor never left. The many wonderful stories will linger on and he will be remembered fondly by the many students and wildlife workers that he trained for the wildlife profession. They truly broke the mold when they made Dr. Speake.

—Mark Sasser, Alabama Regional Biologist, Tall Timbers Game Bird Program and D. Clay Sisson, Albany Quail Project Director, Tall Timbers Game Bird Program

ALVA GREGORY (1964–2019)

Alva Gregory worked for the Oklahoma Department of Wildlife Conservation (ODWC) for 31 years. He began his career on Beaver River Wildlife Management Area (WMA), transferred to Packsaddle WMA, and finally transferred to the ODWC office in Woodward as the Northwestern Oklahoma Habitat Coordinator. In his time in Woodward he built relationships with landowners that allowed for the improvement of habitat for numerous species including bobwhite quail, scaled quail, and lesser prairie chickens. Alva worked tirelessly to promote reconnecting upland bird species to the landscape in agricultural and cattle production areas. Northwestern Oklahoma is known by many as true quail country, and without the influence of Alva Gregory, I am not sure that would be the case. I often tell people if you see a property in northwestern Oklahoma that has no cedar trees, you have Alva to thank for it.

In 2018 alone Alva met with more than 37 landowners in 16 counties impacting more than 45,414 acres. He also gave presentations to the Natural Resources Conservation Service, U.S. Fish and Wildlife Service, National Wild Turkey Federation, Dewey County Commissioners, and NW Cattlemen's Association, and assisted with 4 field days by Oklahoma State University's Extension Office.

Alva was previously recognized as Wildlife Technician of the year in 2007, Habitat Coordinator of the year in 2013, and recipient of the Oklahoma Chapter of the Wildlife Society's Oklahoma award for his outstanding contributions to wildlife management in 2018. He received the NBCI Firebird award posthumously in 2019. His special interests included hunting, fishing, watching and playing sports, raising and training horses, working with cattle on his favorite horse, Chigger, and cutting down and milling cedar trees. He was also a member of the American Quarter Horse Association, the board of the Oklahoma Prescribed Burn Association, and president of the Vici Rodeo Club.

On May 1st, 2019 northwestern Oklahoma lost one of its greatest wildlife warriors. Alva passed away at the age of 55.

—Tell Judkins, Upland Game Biologist, Oklahoma Department of Wildlife Conservation

RUSSELL STEVENS (1964–2021)

Russell worked as a Wildlife/Range Consultant for the Noble Research Institute for 32 years. He was a member of the Society for Range Management, Wildlife Society, Oklahoma Prescribed Burn Association, and the Oklahoma Wildlife Management Association. Russell was a published author for several range management articles. He published The Feral Hog of Oklahoma and co-authored two publications with Chuck Coffey: Trees, Shrubs and Woody Vines: A Pictorial Guide and Grasses of Southern Oklahoma. In 2015, he received the Outstanding Alumnus Award from the Agriculture Department at Angelo State University. Russell's faith was exemplified through all of his vocations and was the driving factor for all he did. Russell was an advocate for all wildlife and their management, helping landowners bridge the gap between ranching and conservation.

He passed away Wednesday, June 23, 2021 at the age of 57 surrounded by his family.

—Tell Judkins, Upland Game Biologist, Oklahoma Department of Wildlife Conservation

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ADAPTIVE MANAGEMENT AND QUAIL CONSERVATION ON RANGELANDS IN THE AMERICAN WEST

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ABSTRACT

Adaptive management has been and is being practiced with the goal of sustaining populations of wild quails on large areas of rangelands in the American West. Because the current land use practices throughout most of the eastern two-thirds of the United States largely do not promote early-successional vegetation communities, rangelands contain the largest remaining blocks of contiguous (unfragmented) habitat for the northern bobwhite (*Colinus virginianus*) and the other 5 species of quails found in the western states. Many wildlife professionals on both private and public rangelands are practicing a diverse array of quail habitat and population management actions that could be considered a form of adaptive management—an iterative process used to make decisions in the context of uncertainty. Though this "learning by doing" approach is not always formally labeled adaptive management, these wildlife professionals intuitively recognize the value of the process in sustaining populations of wild quails. We support our assertions about adaptive management with 4 case study examples of adaptive management projects that promote quail conservation—including quail hunting—on both private and public rangelands in the American West. By discussing these scenarios within an adaptive management framework, we hope to highlight current and future opportunities for adaptive management in quail conservation on rangelands and to discuss where adaptive management may be improved or no longer be appropriate.

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Key words: adaptive management, *Colinus virginianus,* mountain quail, northern bobwhite, *Oreortyx pictus*, sustainable harvest, rangelands, uncertainty

Adaptive management is a structured, iterative process used to make decisions about how to manage renewable natural resources in the context of uncertainty (Walters and Holling 1990). Though commonly thought of as trial and error, adaptive management is a definitive and structured process that assesses specific resource problems, identifies and carefully implements management options, collects data to evaluate outcomes, and adjusts management based on what was learned before repeating the process (Figure 1). When followed, the process of adaptive management can halt an endless cycle of trial and error, increasing knowledge and leading to more effective management. This common-sense approach of "learning by doing" is popular in natural resource management, though learning varies with the rigor of the approach (Figure 1) and is not appropriate for every resource problem (Figure 2).

Rangelands are areas where the native vegetation is predominantly grasses and grass-like plants and forbs (broad-leaved annual and perennial plants that have fleshy stems and produce seeds, many of which are eaten by quail). In many cases rangelands also contain extensive areas of shrubs or dispersed trees (Pellant et al. 2020). Not only are the greatest opportunities for quail conservation in America on rangelands, the most widespread opportunities for hunting wild quails today are on rangelands (Brennan and Hernández, in press). These quail hunting opportunities are predominantly on privately

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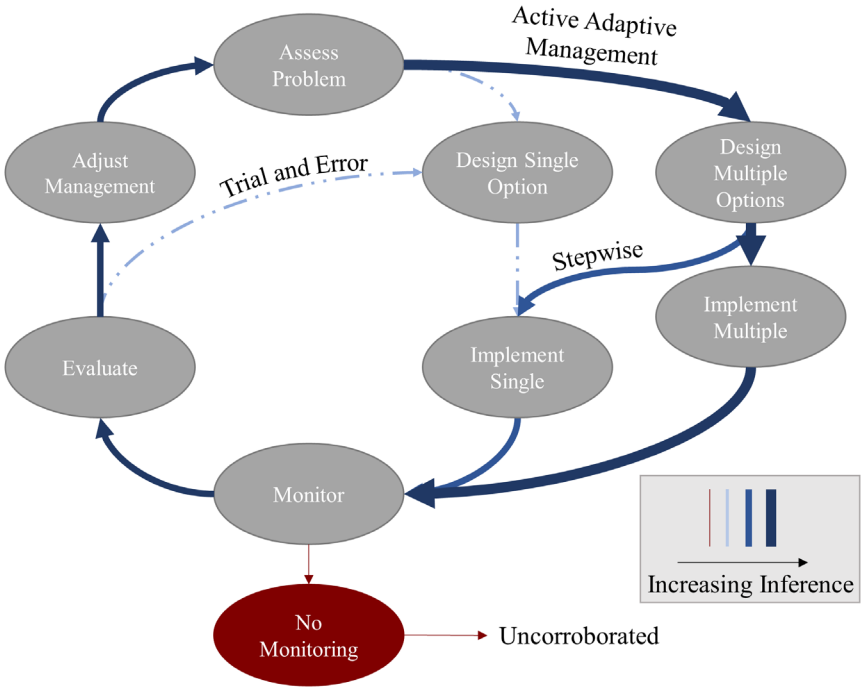

Fig. 1. Adaptive management is a structured, iterative process used to make decisions about how to manage natural resources when there is uncertainty. The potential for learning and inference improves as the approach becomes more robust, from little or none in uncorroborated learning to more through trial and error, even more in a stepwise approach, and finally maximizing learning and inference through active adaptive management (adapted from Allen et al. 2011).

owned rangelands, such as in Texas, USA and Oklahoma, USA, as well as on publicly owned rangelands managed by resource agencies across many states in the American West (defined here as the area of the conterminous United States west of the eastern borders of North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, and Texas) and on some state agency wildlife management areas. Approximately two-thirds of rangelands in the contiguous 48 states are privately owned, with the remaining third in the public trust (USDA NRCS 2020). Rangelands make up about 30 percent of the land area, or roughly 312 million hectares, in the 48 states (Reeves and Mitchell 2011).

In temperate North America, rangelands support all 6 species of native quails with the American West serving as a stronghold for most quail populations (Sauer et al. 2013). In general, rangeland management typically involves ecological methods such as replacing large-scale disturbances through grazing or fires (i.e., pyric herbivory [Fuhlendorf et al. 2009]) or a combination thereof rather than agronomic methods such as cropping and silviculture. The disturbance elements of general livestock-based rangeland management are used—with certain modifications—for quail management. For example, modulating grazing pressure to maintain residual grass cover for nesting quail, and forbs that produce arthropod and seed foods, is an essential component of quail management for all species of quails on rangelands. Mechanical soil disturbance from disking or aeration (or both) is also a key quail habitat management tactic in many rangeland circumstances. Applications of prescribed fire are extremely important for maintaining quail habitat on rangelands. Restoration of native vegetation on disturbance corridors from oil and gas extraction activity, or on pastures with nonnative grasses, is also a key element of rangeland management applied to quail conservation.

Adaptive management for quail conservation on rangelands is often conducted by people who do not realize that they are practicing adaptive management or may know it by another name. This statement is not intended to be ironic. It simply means that adaptive management for quail conservation on rangelands of the American West is a phenomenon that is often underappreciated or overlooked, possibly because investigation of the life history of quail first began in the southeastern pine forests by Herbert Stoddard (1931) nearly a century ago. Following Stoddard, Walter Rosene (1969) focused on the life history and management of northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) in the southeastern Coastal Plains and the pine forests that once supported legions of bobwhite coveys. Quail population research slowly marched west to cropland landscapes in the Midwest in the work of ecologists such as Errington (1945), and Roseberry and Klimstra (1984). The numerous references to bobwhites in the central and southeastern states by Leopold (1933) also cemented the concept where the forest and cropland landscape matrix still dominates a great deal of quail conservation thinking—especially for bobwhites—today.

Val Lehmann started working as a professional wildlife biologist for the King Ranch in South Texas during the 1940s. The nearly 4 decades it took to publish his landmark book

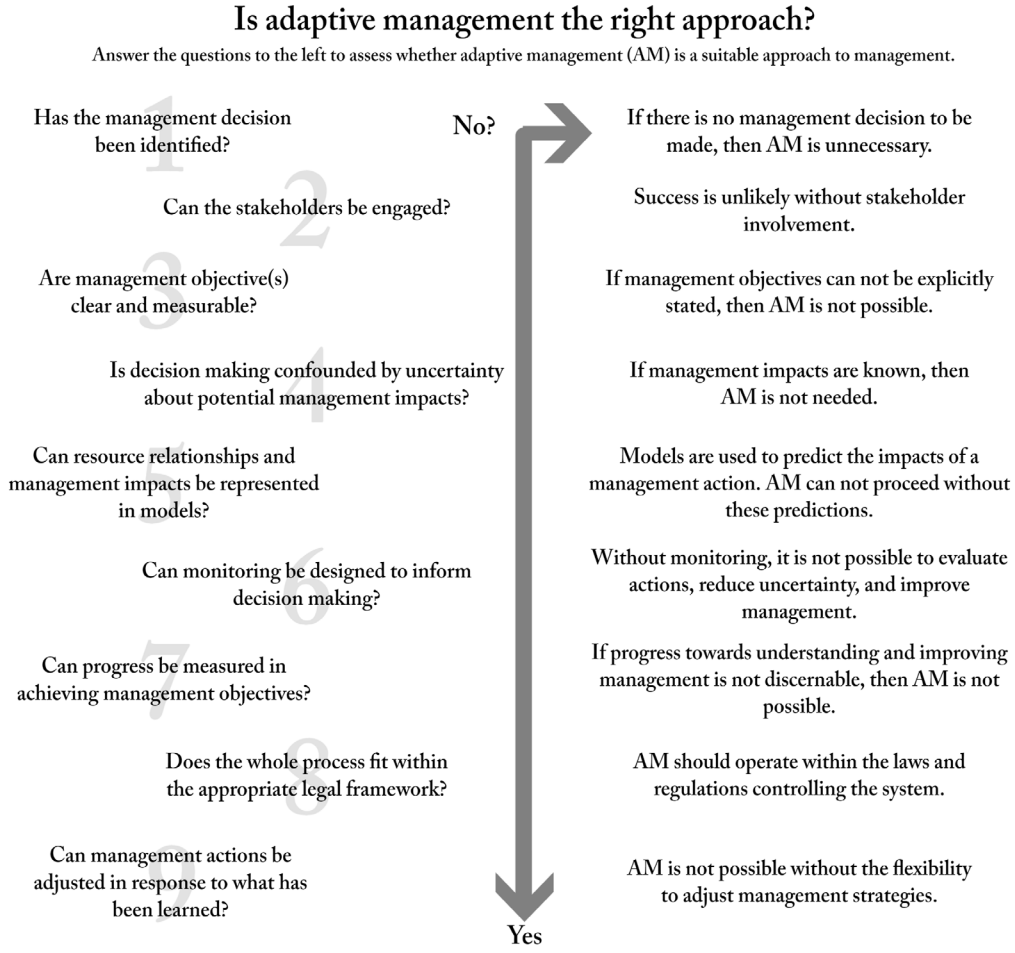

Fig. 2. This key can be used to determine whether adaptive management is an appropriate approach to decision-making in the context of management problem(s) (adapted from Williams et al. 2009).

(Lehmann 1984) was probably one factor responsible for the relative lack of appreciation for the ability of rangelands to sustain abundant populations of wild quail, and by extension, excellent opportunities for quail hunting, especially during years of relatively abundant rainfall.

Bobwhite populations are now essentially locally or regionally extinct in the croplands or forest lands of the southeastern and Midwest United States, which were once the core of the bobwhite's distribution (Chapman et al. 2020). These landscape changes have brought to light the important role of rangelands in bobwhite conservation, and with improved understanding of these systems, an increase in appreciation for these rangelands. A body of peer-reviewed scientific literature and books from major academic presses sharpened our understanding and appreciation of the importance of rangelands for quail. The first and second editions of "Beef, Brush and Bobwhites*"* (Guthery 1986, Hernández and Guthery 2012, respectively) and the book "Texas Quails: Ecology and Management*"* (Brennan 2007), along with the scores of peer-reviewed publications from university wildlife programs—especially in Oklahoma and Texas—have done a great deal to support the idea that rangelands are critically important to sustaining, and in many cases elevating, populations of wild quails.

Though in this introduction we have highlighted a plethora of advances in knowledge of rangeland management for bobwhites, fewer studies and literature sources exist for the 5 other species considered here. Because adaptive management helps to address uncertainty, it may be that the opportunity for future use of adaptive management is greatest for these less studied quail species (Figure 3). Moreover, rangelands are inherently heterogeneous and defined in part by stochastic processes (Fuhlendorf et al. 2001) over space and time, further emphasizing the benefits that adaptive management may present when managing quail under uncertainty. Given the pressure dynamics such as climate change will add to uncertainty in rangeland conditions (Brown and Thorpe 2008) in future decades, we argue that highlighting the adaptive

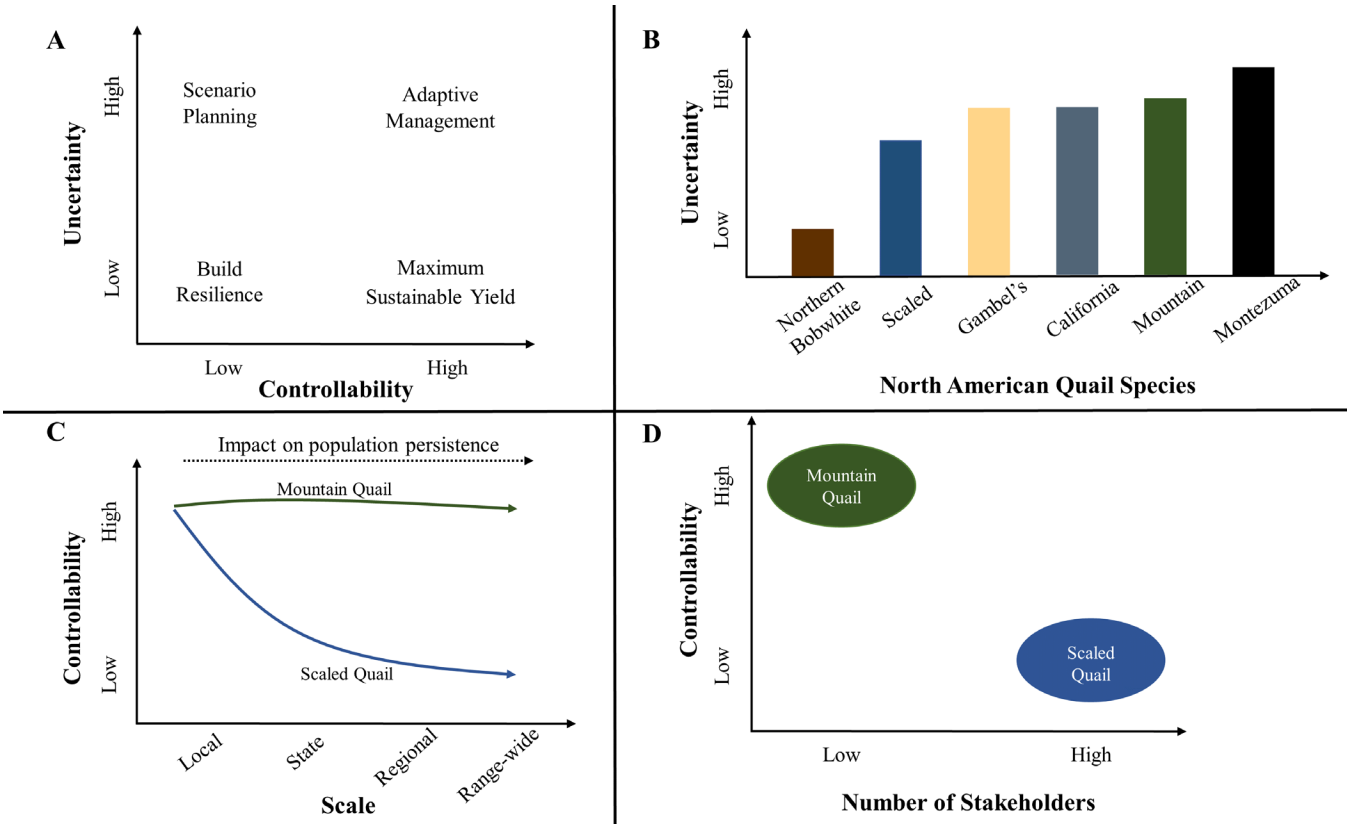

Fig. 3. Adaptive management is most useful when there are high levels of uncertainty in a system where management actions can be controlled (A, adapted from Peterson et al. 2003 and Allen et al. 2011). Uncertainty, or gaps in scientific knowledge, varies across different species of western quails, and therefore the potential utility of adaptive management varies as well. Where uncertainty is low (northern bobwhite), adaptive management may not be necessary (B). Controllability also varies across different species of western quails, largely depending on the scale of interest (C) and the number of stakeholders within each scale (D). Controllability may be highest at local scales where a single manager has authority, but may diminish at larger scales when it becomes necessary to coordinate across many decision-makers.

management process for North America quail conservation on western rangelands is critical, though perhaps not always feasible. It is our hope that by addressing these scenarios, future quail research and management will be designed to utilize adaptive management to reduce uncertainty and guide decision-making.

ADAPTIVE MANAGEMENT CASE STUDIES

We present 4 case studies of adaptive management approaches for quail conservation on rangelands: Joint Ventures, Habitat Management, Population Management, and Restoration Management. When taken together, the participants in these case studies represent a mix of stakeholders, government natural resource agencies, non-governmental organizations, and academia in some form or another. The application of adaptive management for quail conservation on rangelands is the common theme that connects these case studies.

Cooperative Joint Ventures

Joint Ventures are public-private partnership-based programs that deliver specific bird conservation objectives (Brennan et al. 2017:240). Joint Ventures were originally designed to implement national and international bird conservation plans for waterfowl (North American Waterfowl Management Plan 2004), and land birds (Rich et al. 2004), water birds, and shore birds (Brown et al. 2001, Kushlan et al. 2002) respectively. Joint Ventures are designed to "step down" large, continental-scale wildlife population goals and link them to regional or landscape habitat goals. Implementing these step-down plans then allows the cooperators in a Joint Venture to "roll up" these regional and landscape accomplishments to national and international planning groups (Giocomo et al. 2012).

Joint Ventures can be instrumental in working with partners who are management decision-makers. Within adaptive management, organizations such as Joint Ventures serve as "bridging organizations," facilitating communication and cooperation across stakeholders and even ecosystems (Allen et al. 2011). For example, state and federal agencies,

non-governmental organizations, foundations, corporations, and university partners of the Oaks and Prairies Joint Venture cooperate and collaborate to build successful habitat delivery and enhancement initiatives such as the Grassland Restoration Incentive Program (GRIP 2013), which was then adopted by other Joint Ventures. DeMaso et al. (in press) provide extensive details about 5 Joint Ventures in Texas (Figure 4), which are briefly summarized in this case study. All 5 of these Joint Ventures use Strategic Habitat Conservation (Figure 5), which serves as an example of a type of adaptive management known as adaptive governance (Folke et al. 2005). In this example, joint-venture science and planning partners are building a vision and framework to achieve shared goals, while land management joint-venture collaborators are providing the management to achieve this vision. This approach allows adaptive management to move forward at larger ecological scales while providing support and cohesion to a diverse array of stakeholders who collectively learn, adjust, and manage a valued natural resource together for the benefit of all.

Cooperative partnerships are common in the wildlife conservation world. Joint Ventures represent a unique type of cooperative partnership because all partners invest significant resources in conservation activities, which means every member organization in a Joint Venture shares risks and costs but also receives rewards and credit if a specific initiative or project is successful. Sharing of resources and responsibilities is a critical component of the success of adaptive governance, as it promotes participation and encourages collaboration (Folke et al. 2005).

Three Texas Joint Ventures (Gulf Coast Joint Venture, Lower Mississippi Valley Joint Venture, and Playa Lakes Joint Venture) were established in the late 1980s to deliver habitat for breeding and wintering waterfowl. The development of continental plans for land birds, shore birds, and water birds, starting in 1990, resulted in the three Joint Ventures expanding the scope of the species being addressed and the addition of two more Joint Ventures by 2008 (Oaks and Prairies Joint Venture and the Rio Grande Joint Venture). While there are differences in operations, geographic scale, numbers of staff members, areas of conservation focus, management board structure, and membership, each of the 5 joint ventures has identified one or more species of quail for conservation planning and delivery.

In one project, the Gulf Coast Joint Venture spent a considerable sum (nearly $100,000) to identify bird species of conservation concern for this geographic region. The data from this project indicated that long-term (>40 years of counts) data could reliably estimate population trends of land birds that have high conservation priority such as brown-headed nuthatch (*Sitta pusilla*), northern bobwhite, Swainson's warbler (*Limnothlypis swainsonii*), and wood thrush (*Hylocichla mustelina*; Sands et al. 2017). Population trends for these and other species of high conservation concern were then linked to long-term changes in land cover across the Gulf Coast (Sands et al. 2018). Based on these findings, the Gulf Coast Joint Venture developed the Coastal Grassland Restoration Program (C-GRIP), which provided landowner subsidies as an incentive to implement the delivery of quail and land bird habitat conservation activities such as prescribed fire, brush management, and removal and reduction of nonnative invasive plants. At the time of this writing (February 2022), 4 of these Joint Ventures (Gulf Coast, Lower Mississippi Valley, Oaks and Prairies, and Rio Grande) have delivered nearly 83,000 hectares of improved or restored habitat for quail and grassland birds.

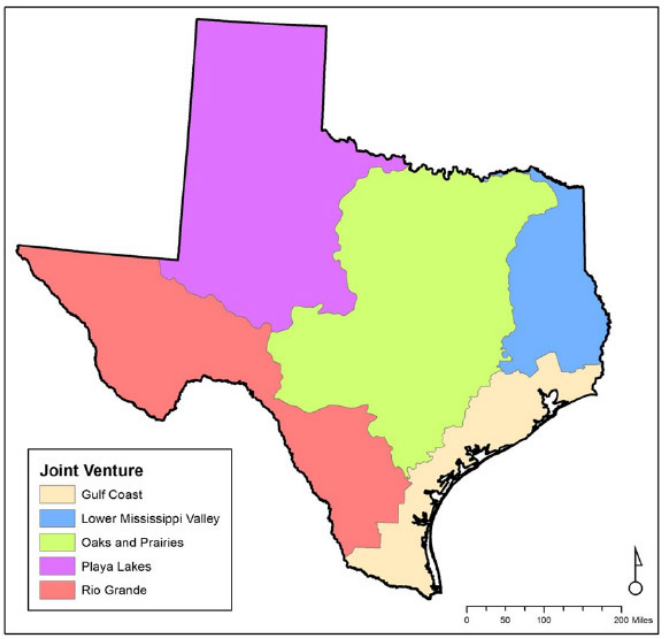

Fig. 4. Distribution of Joint Ventures across Texas, USA (Courtesy Mark Parr, Gulf Coast Joint Venture, U.S. Fish and Wildlife Service).

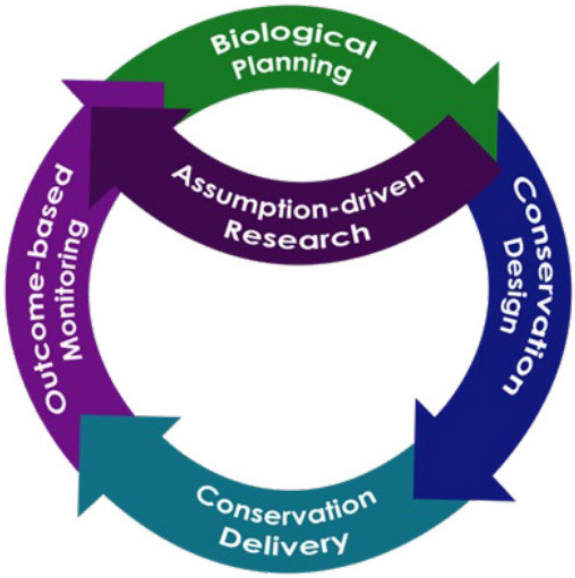

Fig. 5. Conceptual model of strategic habitat conservation (adaptive management) for delivering conservation. From DeMaso et al. (in press).

Adaptive Habitat Management

With around 4 million hectares of mostly contiguous vegetation on a landscape that grows millions of quail—when it rains—South Texas is the last great place when it comes to habitat for the bobwhite. An industry of fee-lease hunting, as well as private ownership, has emerged around upland game hunting in South Texas (Dodd et al. 2013). Howard (2007) was the first wildlife professional to document the logistics of running a South Texas quail hunting operation in an academic publication. A subsequent chapter by Howard and Rauch (in press) added to the concepts and examples in the original chapter by Howard (2007). The clear message to the readers of both of these chapters is that habitat management, in many different forms, is the backbone of running a successful South Texas quail hunting operation. Outside of quail hunting season, the bulk of employee hours are spent doing things like brush sculpting, strip-disking, prescribed burning, maintaining fencing to manage cattle, and so on.

Similar to the material in the recent book by Palmer and Sisson (2017), Howard and Rauch (in press) present a classic case study of intensive quail habitat management on private lands. Unlike our Joint Venture colleagues, the idea of adaptive management is not likely to be on the radar for wildlife professionals such as Rauch and Howard, nor their peers. They are focused more on ranch and pasture. These are highly practical wildlife professionals who seldom, if ever, get caught up with management activities that they think are not practical or simply will not work.

Understanding and dealing with plant succession is the key to successful quail habitat management in any environment. For instance, in the Piney Woods of the humid southeastern Coastal Plain, there is the need to reset the plant succession clock for "early" successional stages of vegetation using prescribed fire, selective uneven-aged forest harvest, and midstory brush and tree control. A short (≤ 3 years) return interval for prescribed fire is essential for maintaining grasses and forbs and keeping excessive woody cover under control in the humid southeastern Coastal Plains. In contrast to this short-return disturbance interval, in rangelands, the return intervals for various habitat management disturbances are much more dynamic than in the Coastal Plains. This is largely because there is a recurring pattern of extensive multiyear droughts that are punctuated by periods of relatively abundant rainfall across the rangelands of the American West.

By keeping track of covey flushes in a pasture, a manager can identify the areas in that pasture where quail were not flushed or seen (Figure 6A). After implementation of some patches of prescribed fire and a network of disked strips (Figure 6B), areas that were once void of bobwhites were subsequently used by them (Figure 6C; Howard and Rauch, in press). By implementing multiple types of management, monitoring quail responses, assessing results, and adjusting accordingly, an entire ranch may become usable space for bobwhites over time (Figure 7). The outcome is purposeful, adaptive habitat management (Larson et al. 2010, Hernández and Guthery 2012) that benefits bobwhites and many other species of grassland birds (Crosby et al. 2015). Moreover, the iterative process of identifying problems (low population or disproportionate use), applying management, monitoring responses, and assessing results reduces uncertainty in future management decision-making, resulting in the efficient use of resources and the more immediate realization of success. Though perhaps a less structured and simpler approach to adaptive management than that taken by Joint Ventures, adaptive management applied in this way is no less useful. In fact, it may be easier to use on private lands where controllability over the process is high as few decision-makers need to be engaged and those decision-makers have few barriers between them and implementing management and monitoring (Figure 3).

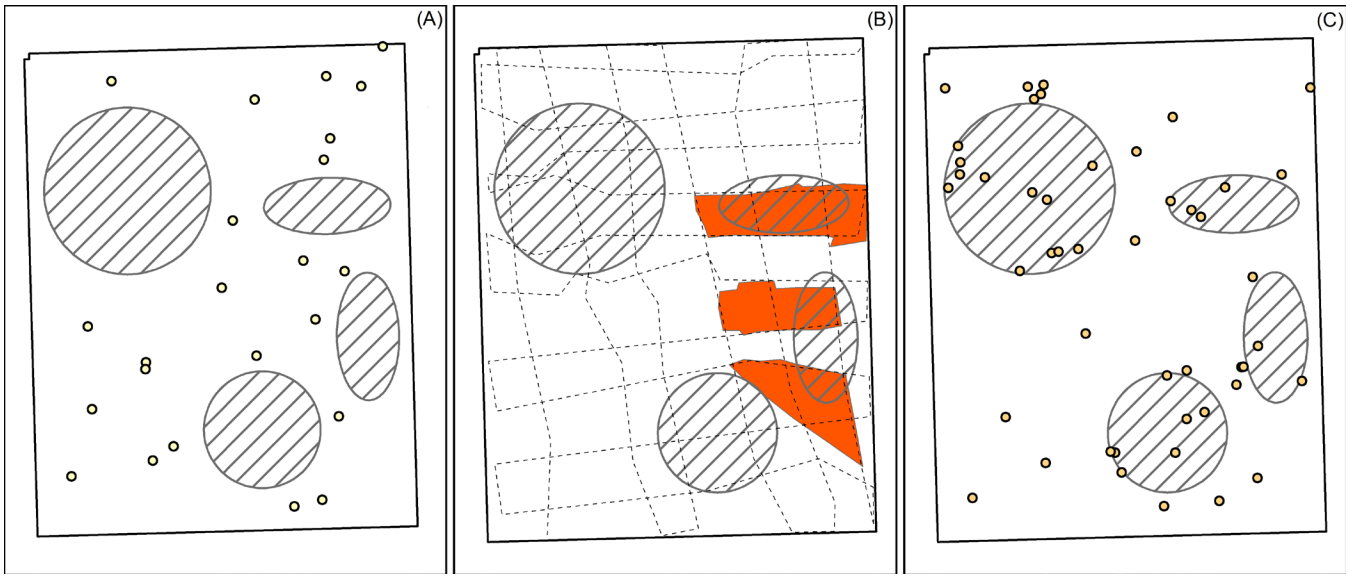

Fig. 6. Three panel maps of total coveys (yellow dots [A]), voids or areas where no coveys were found (diagonal lines within areas), management (prescribed fire [orange areas] and disk strips [dashed lines] [B]), and covey locations during the following year (orange dots [C]). Graphic by W. Rauch and H. Perotto-Baldivieso. From Howard and Rauch (in press).

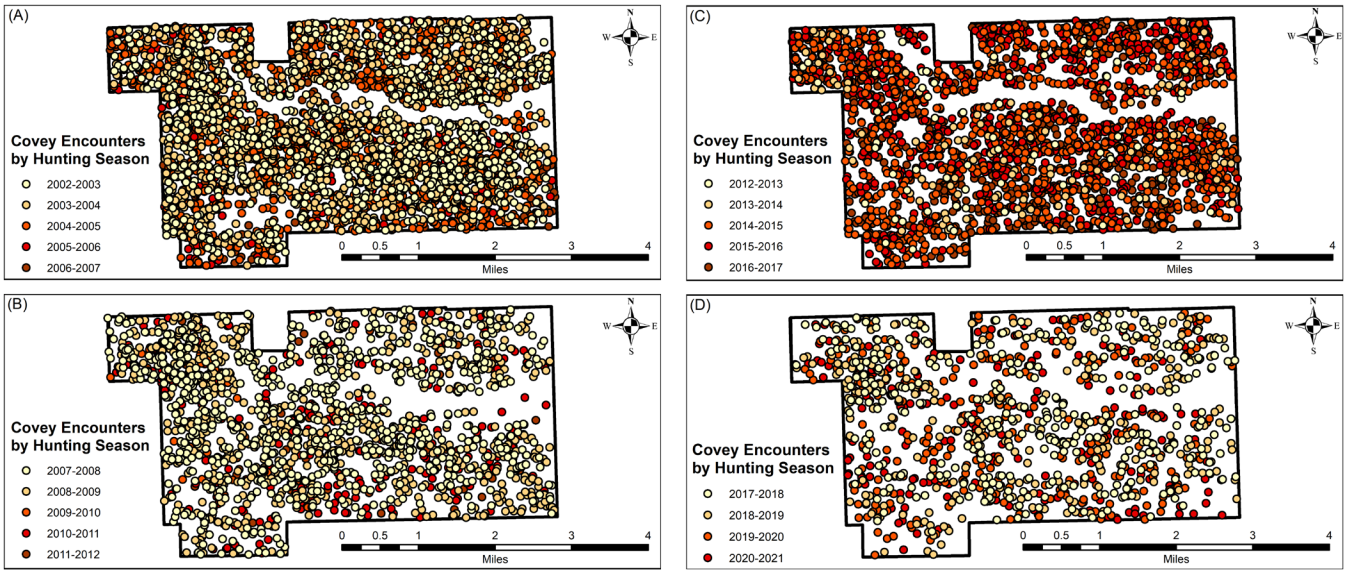

Fig. 7. Moving windows of quail covey locations on Elizita Ranch from the 2002–2003 through 2020–2021 hunting seasons. Graphic by W. Rauch and H. Perotto-Baldivieso. From Howard and Rauch (in press).

Adaptive Population Management

Adaptive Population Management can be considered in the context of adaptive harvest regulations and policies. The central concept of a successful Adaptive Population Management effort is to "adapt" the particular timing of species-specific hunting (season) and harvest (bag limit) based on a meaningful estimate of density (animals per unit area) on or before the opening of an annual hunting season. While the basic concept of tailoring or prescribing an annual harvest according to the level of abundance of a game species is theoretically a great idea, applications of wildlife harvest prescriptions are fraught with uncertainty (Connelly et al. 2020). For example, uncertainty about population dynamics and how these dynamics are structured, has caused a great deal of debate about how wildlife harvests and the timing of wildlife harvests (Dahlgren et al. 2021) should be managed. Furthermore, the uncertainty of whether hunting is additive or compensatory, and the uncertainty of density dependence on both annual production and overwinter survival are central to all upland game birds, including the bobwhite (DeMaso et al. 2013). Tomeček et al. (2015) concluded that species such as quail are characterized by limited dispersal and therefore are at risk for localized overharvest. However, before we discuss how many birds we can take, we first must have an idea of how many birds are present on a given area at the beginning of the hunting season.

How many bobwhites do I have?—On South Texas rangelands, helicopters are a platform for implementing distance sampling to estimate bobwhite population density (Smith et al., this volume; Montalvo et al., in press). This allows managers to fly surveys that use the number of coveys flushed along transects during the fall (November or early December) to estimate population density and set the annual harvest quota for a pasture or even an entire ranch. By knowing how many bobwhites are present in a given area and multiplying the number of birds by the size of the area, we then have an estimate (with a lower and upper 95% confidence interval). For example a 1,000-hectare pasture that has 1 bobwhite/hectare has approximately 1,000 bobwhites total ± the 95% confidence interval around the mean estimate of density. The smaller the confidence interval, the more confident we are of our mean estimate of density. When the spatial locations of coveys are collected during the course of flying along the transects, the density estimates can be used to create a density surface model map for the area surveyed (Figure 8).

How many bobwhites can I harvest?—Hunters are a fundamental component of bobwhite conservation (Brennan

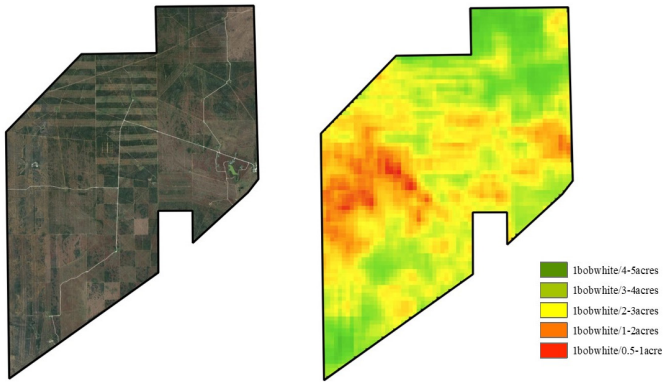

Fig. 8. Theoretical density (birds/unit area) map output from density surface model (at right) compared to aerial view of survey area. From Montalvo et al. (in press).

2015). The bobwhite is one of the most studied wild species of bird in the world, so a great deal of information is available on the metrics of its demography, such as survival, and annual productivity in nest success and egg production in relation to a large range of environmental factors such as temperature and rainfall (Guthery 2002). To understand what levels of annual bobwhite harvest may be sustainable, Sands (2010) and Sands and Tri (in press) summarized a great deal of bobwhite demographic data. These results were based on a series of simulation models that provided annual bobwhite population dynamics similar to what has been observed in South Texas (Figure 9). As a central part of this modeling effort, Sands (2010) implemented a set of simulation scenarios with 1) no harvest, 2) 10% harvest, 3) 20% harvest, 4) 30% harvest, and 5) 40% harvest. Adaptive management requires the use of models to predict the impacts of a management action and allows for the testing and refinement of multiple hypotheses simultaneously. Robust models, in this example, allowed researchers to explore the potential outcomes of different harvest scenarios and enabled them to make a more informed decision about which hunting effort scenario they should test. The model identified scenario 2, with a 20% harvest rate, to have the greatest mean annual yield of bobwhites.

Beginning in the 2018–2019 quail hunting season, Woodard et al. (this volume) began testing the 20% harvest recommendation developed by Sands (2010; Figure 9) on a 6,000-hectare hunted ranch and a comparable nonhunted ranch (4,800 hectares) approximately 16 km from the hunted ranch. Prior to the beginning of quail hunting season, Woodard et al. (this volume) used helicopters to fly transects to collect data to derive density estimates, and a subsequent 20% harvest prescription that included estimates of crippling loss. Based on data from 3 quail hunting seasons, they recommend using the lower 95% confidence interval (rather than the mean) of a bobwhite density estimate for calculating harvest prescriptions. Despite this controlled experimental study, uncertainty in adaptive quail population and harvest management will persist, particularly as quail face a changing environment and other stressors. Adaptive harvest management may continue to provide valuable structure to reducing uncertainty in harvest decisions.

Adaptive Population Restoration Management: Mountain Quail in Eastern Oregon

Sometime prior to the 1980s, the mountain quail (*Oreortyx pictus*) experienced regional and localized extinctions across large parts of the western Great Basin and lower Snake River watershed in Idaho, USA, Oregon, USA, and Washington, USA (Brennan 1990, 1994). The most likely reason behind these local extinctions was the deterioration of creekside-riparian vegetation caused by cattle grazing. In the arid rangelands of the Great Basin, creekside-riparian vegetation provides important habitat for nesting and food-producing for mountain quail, as well as loafing, roosting, and escape cover. These corridors of vegetation also provide pathways for mountain quail to disperse from relatively high-elevation nesting areas to lower valleys during the winter to avoid snow and cold. Additionally, dams along the lower Snake River, especially the Brownlee Reservoir impoundment, inundated large areas of low-elevation wintering habitat for mountain quail.

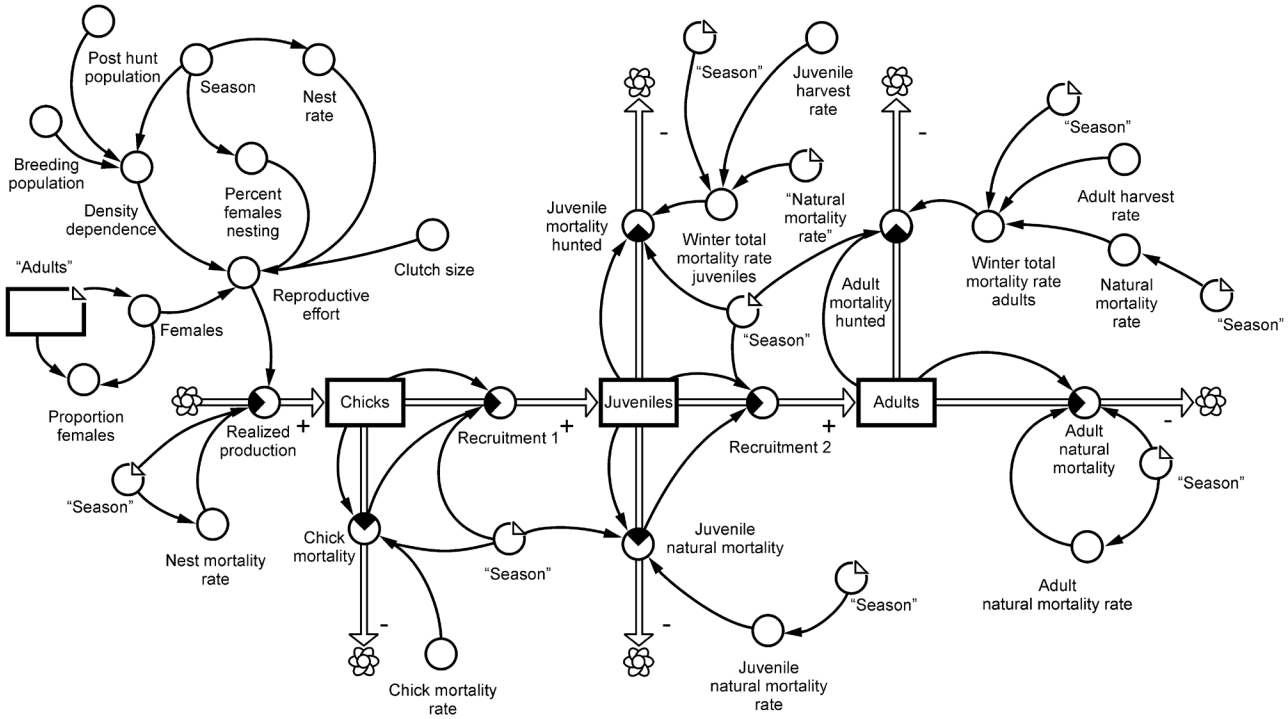

Fig. 9. Stochastic simulation model structure and parameters used to test the potential effects of different annual harvest rates on a bobwhite population in South Texas, USA. From Sands (2010).

Beginning in the late 1980s and through much of the 1990s, state wildlife agencies in Idaho, Oregon, Washington, and Nevada, USA and federal resource agencies, along with academia and stakeholder groups, worked to develop potential population restoration tactics aimed at the strategy of recovering mountain quail where they were once found in parts of the western Great Basin and the lower Snake River watershed. A key tactic of the mountain quail population restoration strategy in Oregon was to capture wild birds from the Coast Range in southwestern Oregon, where they are relatively abundant, and translocate them to places east of the Cascade Mountains where creekside-riparian vegetation was recovering from overgrazing. Mountain quail capture-relocation efforts in Oregon began in 1999 and continued through 2017 (Oregon Department of Fish and Wildlife n.d.:Table 1).

Data from radio-marked mountain quail that were captured in western Oregon and relocated to eastern Oregon from 2001 to 2010 were summarized by Budeau and Hiller (2012). Of the 1,430 translocated mountain quail, 800 were radio-marked to monitor nesting success and population persistence. The reproductive efforts of the relocated mountain quail were comparable to wild mountain quail (Pope and Crawford 2004, Budeau and Hiller 2012:354). Additionally, during subsequent years after these initial releases mountain quail that were not radio-marked were often seen in places near relocation sites, indicating that the relocated birds apparently reproduced successfully (Dave Budeau, Oregon Department of Wildlife and Fisheries, retired, personal communication).

The mountain quail relocation project in Oregon is considered to be a "remarkably successful" upland game bird population restoration project (Mikal Cline, Oregon Department of Fish and Wildlife, personal communication). Of course, not all of the specific, localized translocation efforts were successful. However, mountain quail were reestablished across sufficient areas of eastern Oregon (Figure 10), and were detected with sufficient regularity both by biologists and in reports from reputable birders that the geographic scope of mountain quail hunting was expanded from 8 to 16 counties in eastern Oregon by 2018, 1 year after restoration efforts ceased. By 2020, a 2-bird bag limit was authorized for mountain quail hunters throughout Oregon.

Adaptive management was a key to the success of the mountain quail translocation project in Oregon. Considerable efforts were made by Oregon Department of Fish and Wildlife biologists to identify release sites with vegetation that could provide mountain quail habitat. Subsequently, release sites in eastern Oregon were selected based on their similarity to

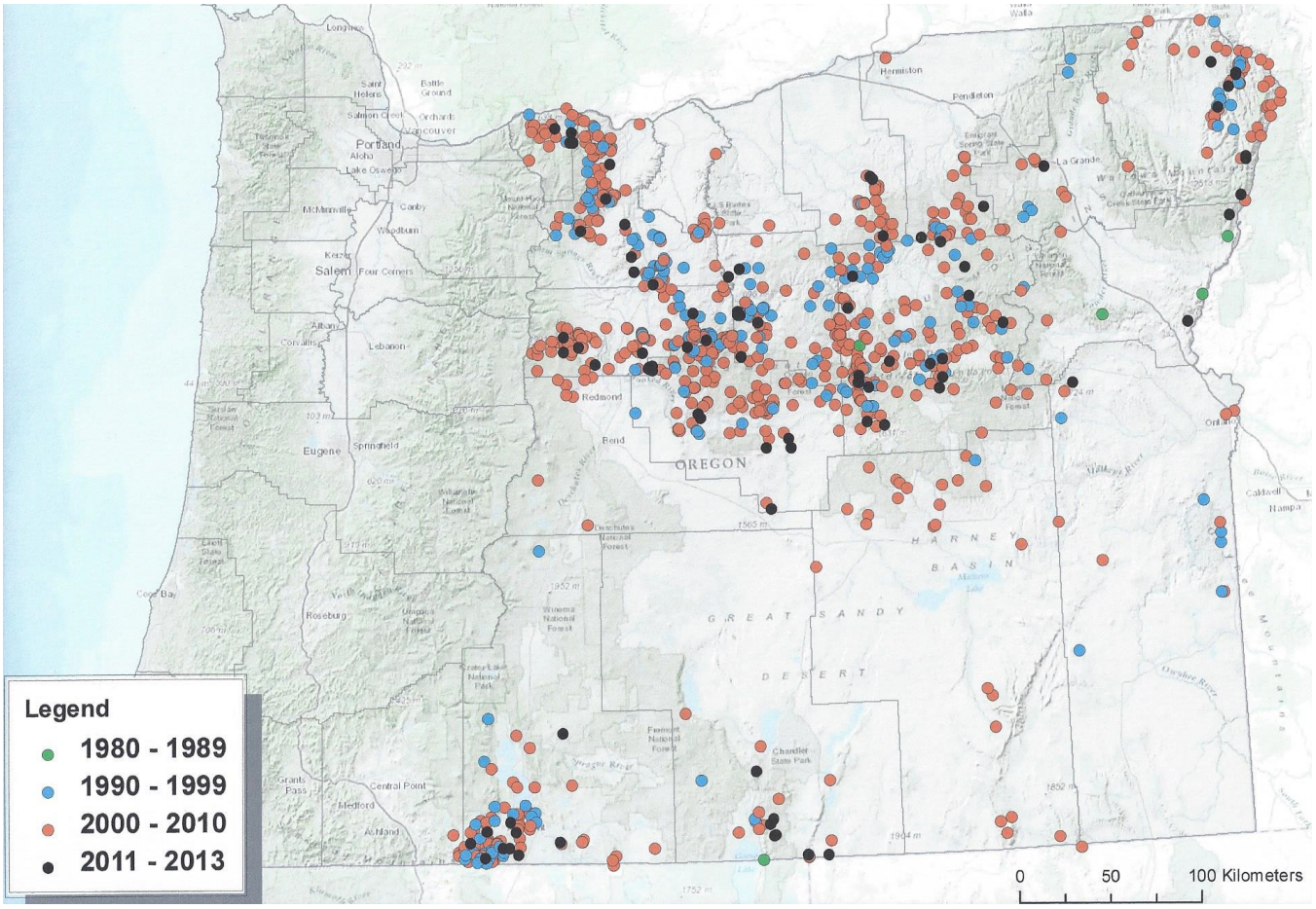

Fig. 10. Distribution of mountain quail sightings in eastern Oregon, USA, from 1980 to 2013. From Oregon Department of Fish and Wildlife.

release sites that were previously successful. This approach is an example of successful adaptive management for quail population restoration. The responsible use of state, federal, and private funds was required to make these restoration efforts successful (Mikal Cline, Oregon Department of Fish and Wildlife, personal communication).

The initial efforts to monitor the mountain quail response to relocations were based on radio-marked birds (Budeau and Hiller 2012). Since then, Oregon Department of Fish and Wildlife biologists have been monitoring the persistence of mountain quail in the translocation areas by collection of wings of hunter-harvested birds and citizen science platforms such as eBird. This story represents a contemporary case study that documents an expansion of quail hunting opportunities across nearly two-thirds of a western U.S. state, which is unique and remarkable (see the Oregon Department of Fish and Wildlife website https://www.dfw.state.or.us/resources/hunting/upland_bird/projects/mtn-quail.asp for more information).

In our experience, the mountain quail is, without a doubt, the most challenging of the 6 North American quails to hunt. Their secretive nature and preference for dense brushy vegetation that is often located in steep mountainous topography means that harvesting even 1 or 2 mountain quail in a day is a trophy-level achievement. This is in contrast to places such as South Texas, where it is possible to find and flush 30 coveys of bobwhites in a day (Valley Nature Films 2020) and easily fill a 15 bird/person/day bag limit. Nevertheless, the fact that quail hunters can now encounter and harvest mountain quail across a vast region of a western state where it was absent just a few decades ago is a testament to the importance of adaptive management for quail conservation on rangelands in the American West.

FUTURE DIRECTIONS: INTEGRATION OF TECHNOLOGY

Integration of technologies is and will continue to be a critical element towards successful implementation of adaptive management for quail populations in western rangelands. Given the highly dynamic nature of conditions and resources that exist in these systems, technological advances will help managers and scientists integrate spatio-temporal data into the adaptive management cycle to produce rapid assessments of management practices at extents that were likely not possible in the past. This is not to say that practitioners have not integrated technology into adaptive management strategies for quail on western rangelands in the past. The case studies presented earlier in this paper are a testament to this point. In this context, we aim to highlight new opportunities to provide a foundation for incorporating these data into already existing adaptive management frameworks.

Unmanned Aerial Systems

The relatively recent availability of low-cost unmanned aerial systems (UASs; or drones) has facilitated an entirely new avenue for monitoring important elements of quail management across a potentially wide range of spatial scales (Gillan et al. 2020). Rangeland inventory and monitoring data that are critical to understanding range conditions and resource availability for quail populations have historically been a labor-intensive exercise focused on sampling small portions of rangelands across a landscape to infer the health and conditions of the rangelands within the extent of management interest (Allen et al. 2017). Given the link between abiotic conditions, rangeland vegetation conditions, and quail population fluctuations, this traditional approach to rangeland inventory and analysis has been a critical tool for evaluating how quail populations respond to the interaction between environmental conditions and active management (e.g., prescribed fire, stocking rates) in rangelands. As techniques and operational workflows towards implementing UASs in rangeland monitoring continue to develop (DiMaggio et al. 2020, Gillam et al. 2020), it is clear that these tools will be a critical next step in adaptive approaches for range and habitat management (Rango et al. 2006). Given the plethora of sensors that have been developed to be fitted onto UASs to collect data, practitioners are capable of collecting data beyond just vegetation structure and composition (Pilliod et al. 2022). Thermal sensors allow observers to monitor thermal refuge (a critical component of quail habitat in rangelands [Tanner et al. 2017*a*]) and more recently potentially determine covey distributions through thermal signatures (Z. Pearson, Caesar Kleberg Wildlife Research Institute, Texas A&M University-Kingsville, personal communication). Moreover, novel adaptation of these sensors allows observers to quantify important but complex elements of rangelands such as foodscapes (Olsoy et al. 2020) or predator escape cover (Olsoy et al. 2015). With this continual need to integrate UAS technology into habitat monitoring at temporal and spatial scales not previously possible, the opportunity for managers to be formally trained in these techniques is also increasing rapidly. Online courses now exist at relatively low cost to obtain a Federal Aviation Administration (FAA) drone pilot license, while online tutorials and workshops continue to be provided so that integration of this technology becomes more obtainable for those interested.

However, challenges in integrating drone technology into adaptive management strategies for quail may exist depending on the spatial extent of the management area. Though quail populations on public lands (i.e., Bureau of Land Management [BLM] lands) or those that exist on large private ranches (i.e., South Texas [> 25,000 hectares]) may have a large enough spatial extent to implement adaptive management strategies at a population level, many lands are managed at a much smaller extent (i.e., the section level, or 259 hectares). In these situations, monitoring of conditions to provide information for adaptive management beyond the extent of the individual landowner's property may be hindered by access to adjacent lands that have direct implications for the success or failure of targeted management strategies and how data are implemented in the adaptive management cycle.

Publicly Accessible Remote Sensed Datasets

The average farm size in Oklahoma during 2020 was estimated at 180 hectares (USDA 2020). However, bobwhite covey home ranges in Oklahoma have been shown to range from 12 to 270 hectares and spring dispersal areas can range from 13 to 906 hectares (Carroll et al. 2017). These data show that bobwhites are responding to conditions and processes at a spatial extent that goes well beyond the average farm size in Oklahoma. This phenomenon clearly illustrates the need for integrating technology for data collection at a much larger scale than the average farm in Oklahoma, or practically any other state as well. With this in mind, access to new central repositories of satellite-derived or remotely sensed data across a wide range and scale of landscape conditions is providing practitioners with unprecedented ways to incorporate data about broad conditions at multiple temporal scales into adaptive management programs for quail (Oschner et al. 2019, Pilliod et al. 2022).

The recent release of the Rangeland Analysis Platform (https://rangelands.app) provides users with annual estimates of fractional cover of vegetation at a 30-m resolution across all rangelands in the United States (Allred et al. 2021). The tool also implements data on ecological resilience (Uden et al. 2019) to provide temporally and spatially dynamic data to help inform users on how management strategies are influencing vegetation dynamics and state-transitions. The Climate Engine (http://climateengine.org/) also provides users with access to global climatic conditions and vegetation data within and across years that can be integrated into the adaptive management framework to account for interactions between climate patterns, rangeland health, and management strategies. Another tools, Grass-Cast (https://grasscast.unl.edu/), provide users with predictions at a 10-km grain for above-normal, near-normal, or below-normal vegetation growth through integration of historical weather and vegetation growth data along with seasonal precipitation forecasts (Peck and Durham 2018). Such predictive data could help managers integrate flexible stocking densities and rates (Peck et al. 2019) to help buffer the variability in resources for quail that often occurs on western rangelands. Moreover, data for predicted soil moisture conditions are becoming available for western rangelands within portions of the distributions of bobwhite and scaled quail (*Callipepla squamata*) (http://soilmoisture.okstate.edu/; Ochsner et al. 2019). Such data could be integrated into assessments of range conditions or success of treatments such as herbicide applications. Here, we provide just a small number of the plethora of publicly available datasets that are available to be implemented in adaptive management strategies for quail management in western rangelands.

There Is an App for That!

One avenue of technology that can be used to bolster success of adaptive management strategies for quail management is the use of smartphone applications (apps) and citizen science programs (Teacher et al. 2013). More commonly, these 2 elements are seamlessly integrated to increase the opportunities and value that these programs may provide in the form of data for management strategies. Broadly, citizen science apps like eBird facilitate access to spatial and temporal presence data of avian species that are furnished solely through activities of citizen scientists (Sullivan et al. 2009). Recently, these data have been used to produce annual estimates of relative abundance (Fink et al. 2020), which may provide a broader view of quail population fluctuations that could be compared to local data from site-specific relative abundance monitoring efforts associated with management areas. As apps continue to become more accessible to a diverse use-base, species-specific or taxon-specific apps are becoming more common. For instance, the Gamebird Brood Observation app developed by Oklahoma State University facilitates documenting observations of gamebird broods by users to help record obervations of changes in reproduction and spatio-temporal trends in brood space use. Such an app could function as a central repository for managers interested in integrating these data into management plans intended to promote quail reproduction. Undoubtedly, the number of smartphone apps developed for quail management objectives will continue to grow, with obvious implications for adaptive management such as monitoring hunting pressure or measuring vegetation structural and compositional components related to management applications at local, regional, and rangewide scales.

Overcoming the Problem of Scale

One of the interesting aspects of adaptive management for quail conservation on rangelands is that the problem of scale works in both positive and negative ways. In a positive context, the scale of opportunities for sustaining wild and huntable populations of quails on rangelands far exceeds similar opportunities in most of the southeastern and midwestern parts of the United States, as mentioned at the beginning of this paper. In the case studies presented in this paper, positive outcomes for quail conservation projects ranged from tens of thousands of hectares (Joint Venture, Habitat Management, and Population Management Case Studies) to many thousands of square kilometers (Mountain Quail Case Study). A lesson here is that adaptive management for quail conservation can be successful on moderately large to very large scales, given that the relevant stakeholders and decision-makers can be brought together. From a negative viewpoint, the inexorable maw of urbanization and impermeable surfaces across large areas of the rangeland landscape represents a widespread and pernicious threat to virtually all rangeland quail conservation efforts. Fortunately, there are still vast areas of rangelands in the American West that support wild quail populations and the opportunity to hunt them. An inventory that compiles a reliable estimate of how many square kilometers of rangeland support wild quail populations would be a useful and interesting metric, especially if taken at 5- to 10-year intervals.

Uncertainty in a Changing Climate

Quail populations and climate and weather patterns are indisputably linked (Lusk et al. 2001, Hernández and Guthery 2012, Tanner et al. 2017*b*). A major challenge facing managers in future decades will be the uncertainty caused by rapidly changing climate patterns. For example, at the time of this writing, much of the southwestern United States within the distribution of multiple western quail species is under a megadrought—the driest period since the year 800 (Williams et al. 2022).

Drought severity, drought longevity, and increased temperatures due to climate change pose significant threats to all temperate North American quail species over future decades (Tanner et al. 2017*b*). Integrating climate scenarios into targeted management efforts and within an adaptive management framework will be a major path forward in ensuring resilience of natural resources (Peterson et al. 1997, Tompkins and Adger 2004) and subsequently quail populations under novel conditions. It is of paramount importance to understand that vulnerability will increase for some current "population strongholds" maintained under past and current climatic conditions (e.g., bobwhite in the panhandle of Oklahoma [Tanner et al. 2017*b*]), and addressing uncertainty related to climate change effects on meta-population dynamics will be critical for successful resource allocation and targeted management. There will undoubtedly be varying levels of uncertainty and disparate levels of severity to the species-specific responses to changing climate patterns (Tanner et al. 2017*b*), with both winners (Gambel's quail [*Callipepla gambelii*]) and losers (Montezuma quail [*Cyrtonyx montezumae*]) based on geographic distributions, evolutionary traits, and behavioral adaptations. Ignoring the uncertainty that changing climate patterns present to quail populations in the form of both direct (population dynamics) and indirect (increased rangeland variability) pressures will leave adaptive management strategies falling short of their goals for quail on western rangelands.

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NORTHERN BOBWHITE DEMOGRAPHICS AND RESOURCE SELECTION ARE EXPLAINED BY PRESCRIBED FIRE WITH GRAZING AND WOODY COVER IN SOUTHWEST MISSOURI

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ABSTRACT

Understanding the effects of landscape management on northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) population growth requires information about seasonal- and stage-specific demographic parameters linked across the annual cycle. We review results to date from 3 years (2016–2018) of an intensive field study evaluating drivers of bobwhite population dynamics and resource selection during the breeding and non-breeding season in southwest Missouri, USA using data from adult and juvenile bobwhite fitted with radio-transmitters. Land cover of our study sites ranged from large blocks of native grasslands maintained with prescribed fire and grazing to more traditional management resulting in small patches of grasslands interspersed with food plots, disked idle areas, and woody cover. During the breeding season, relative probability of selection by broods increased in relation to proportion of native grass managed by grazing and burning and proportion of cropland. Brood survival was also greatest on native grasslands burned and grazed within the past 2 growing seasons. During the fall and winter,

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relative probability of selection by adults increased as woody edge density increased. Fall and winter survival increased as distance from trees increased and decreased as distance to shrubs increased. Our integrated population model indicated that the number of young hatched per female and adult breeding season survival were greatest on sites with the most native grassland managed by prescribed fire with grazing. However, non-breeding season survival was greater on sites with more agriculture or food plots and woody cover. Abundance declined across all sites from 2016 to 2019. Our work suggests that native grasslands managed by prescribed fire with grazing can provide quail habitat superior to traditional management that strived for a mixture of agriculture, woody cover, and grassland. The combination of conservation grazing and fire in native grasslands interspersed with shrubs may provide the greatest chance for bobwhite populations to persist in southwest Missouri and similar landscapes.

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Key words: *Colinus virginianus*, full annual cycle, grazing, habitat management, integrated population model, native grasslands, northern bobwhite, prescribed fire, resource selection, survival

Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) have declined in abundance across their range largely due to habitat loss, fragmentation, and degradation (Brennan 1991, Williams et al. 2004, Veech 2006, Hernández et al. 2013). Bobwhite declined 80% in Missouri, USA since 1967 and the rate of decline accelerated over the past 15 years (Sauer et al. 2017). Exceptions to these declines have occurred where landscapes are purposely managed for bobwhite (McConnell et al. 2018). Declines have raised concern and generated interest in the efficacy of alternative bobwhite management strategies among conservation agencies and the public in Missouri and elsewhere. Yet in many areas of the bobwhite's range the influence of management practices on specific vital rates, and the relative influence of seasonal vital rates on changes in abundance are not well understood (Sandercock et al. 2008). This is especially true in the grassland-dominated landscapes of southwest Missouri. The National Bobwhite Conservation Initiative (NBCI 2.0; Palmer et al. 2012) and the Missouri Department of Conservation (MDC) identified this region of Missouri as having high quail restoration potential, yet bobwhite populations are declining there.

Since the 1970s, quail management in Missouri has focused on providing an interspersion of grass, food plots or cropland, disked idle areas, old fields, and woody cover with the goal of providing all essential habitat components within a 16.2-ha area; we refer to this as traditional management. Traditional management can produce usable quail habitat in agriculture-dominated landscapes (Klimstra and Roseberry 1975, Burger et al. 1995*a*) but may not be the most effective or efficient approach in expansive grassland-dominated landscapes, such as those in southwest Missouri. MDC managers historically implemented traditional management in these grass-dominated landscapes. However, in the early 2000s, managers recognized that large native grasslands maintained with prescribed burning and conservation grazing were supporting stable quail populations. Prescribed burns with grazing and mowing produce a patchy grassland mosaic which enhances species richness and structural diversity on native tallgrass prairies, mimicking fire and herbivory characteristic of historical disturbance regimes (Collins et al. 1998, Fuhlendorf et al. 2008). Heterogeneity in cover created by burning and grazing in large native grasslands is in contrast to purposeful interspersion of food plots, grass plantings, shrub, and tree cover that is more common under traditional management. We refer to these 2 different combinations of management practices and resulting land cover as grassland management and traditional management. We acknowledge grassland management and traditional management share some common management practices, but the amount of each practice and resulting land covers can vary greatly and they provide useful concepts for defining 2 ends of a gradient across sites in southwest Missouri.

Wildlife biologists began surveying for quail on selected conservation areas in southwest Missouri in 2005 and detected greater densities of quail on some grassland managed sites compared to traditionally managed sites. MDC conducted a pilot study in 2012 and radio-tagged 30 birds on Robert E. Talbot Conservation Area, which is a more traditionally managed site, and 30 birds on Stony Point Prairie, which is a grassland management area. Biologists found that birds on Stony Point Prairie (the grassland site) nested earlier and earlier nests were more successful, resulting in greater production compared to Robert E. Talbot Conservation Area (K. Hedges and F. Loncarich, MDC, personal communication).

Recent studies of bobwhite demographics using a meta-analysis (Sandercock et al. 2008), local or regional models (Gates et al. 2012, Williams et al. 2012, McConnell et al. 2018), or population viability models (Guthery et al. 2000, DeMaso et al. 2014, Rosenblatt et al. 2021) have highlighted the influence of fecundity and adult survival on population growth and viability. However, key demographic components, such as chick survival and recruitment, and their relationships to habitat management and landscape context remain largely unknown. In particular, bobwhite chick survival remains the least studied demographic rate in wild bobwhite populations, although in several recent population models (Sandercock

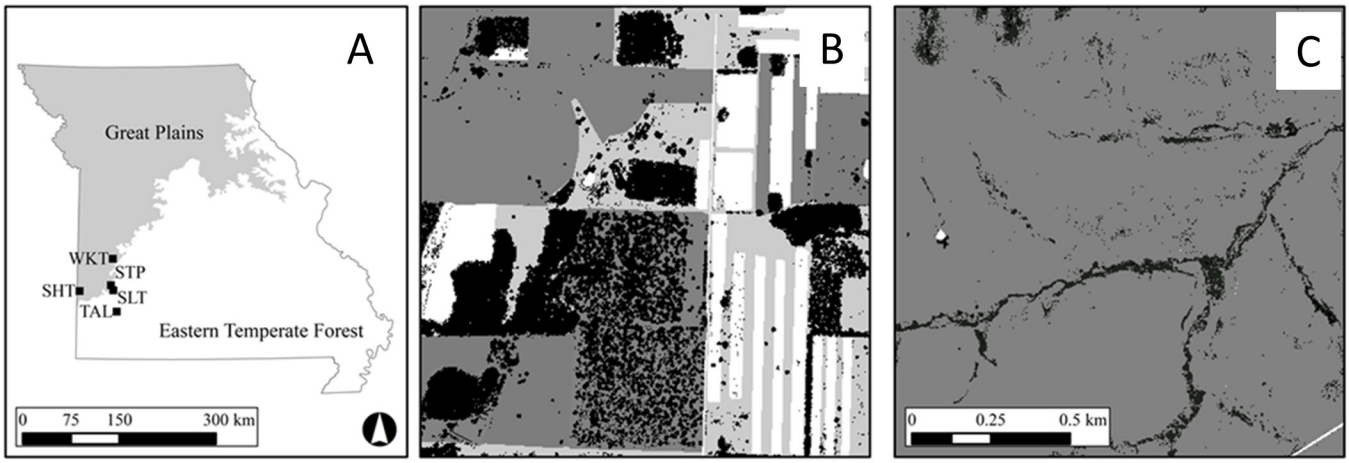

Fig. 1. A) Location of 5 study sites in southwest Missouri, USA: Shawnee Trail (SHT), Shelton (SLT), Stony Point (STP), and Talbot (TAL) Conservation Areas and Wah'Kon-Tah Prairie (WKT); B) portion of a traditionally managed site that includes food plots (white) and nonnative grass plantings (light gray), woody cover (black), and native grassland (dark gray); C) grassland managed sites were mostly native grassland with limited woody cover.

et al. 2008, Gates et al. 2012, Williams et al. 2012, Peters 2014) chick and brood survival and their contribution to annual fecundity have been identified as key demographic parameters in determining the finite rate of growth (λ) in bobwhite populations. Additionally, estimates used in these population models varied and were not necessarily based on direct estimates of survival (only 2 out of 9 were based on telemetry; Suchy and Munkel 2000, Lusk et al. 2005), but instead were based on brood counts conducted at 7 days, 14 days, and 21 days post-hatch (DeVos and Mueller 1993, Pucket et al. 1995, DeMaso et al. 1997, Mueller et al. 1999).

Based on knowledge gaps in bobwhite demographics and observations of potentially greater abundance and production under grassland management, MDC initiated a 5-year research project in 2014 to compare spring and summer adult survival, production, and resource use among sites managed by traditional management and grassland management. The study was expanded in 2016 to include juvenile survival from hatch to 100 days old and resource use across these sites. It was expanded again in 2017 to include evaluation of fall and winter juvenile and adult survival and resource use. Results from these studies have described resource selection by these cohorts (Mosloff et al. 2021, Sinnott et al. 2021*b*), survival and its relationship to management, local vegetation, and landscape factors (Mosloff 2020, Sinnott 2020, Sinnott et al. 2021*a*), and relationships between seasonal vital rates and full annual cycle population dynamics (Sinnott 2020). Our objective in this paper is to synthesize how management and land cover affect bobwhite demography and resource selection throughout the annual cycle in southwest Missouri based on these studies. While we focus on reviewing results of these studies, we also provide short descriptions of methods and analyses, and refer readers to the original publications for more details. We refer to these projects collectively as the Southwest Missouri Quail Study.

STUDY AREA

The Southwest Missouri Quail Study occurred in southwest Missouri from February 2014 to May 2019. We studied 5 sites: Shawnee Trail Conservation Area (1,471 ha; hereafter, Shawnee Trail), Robert E. Talbot Conservation Area (1,764 ha; hereafter, Talbot), Wade and June Shelton Memorial Conservation Area (130 ha; hereafter, Shelton Memorial), Stony Point Prairie Conservation Area (516 ha including 169 ha of adjacent private land; hereafter, Stony Point Prairie), and Wah'Kon-Tah Prairie (1,226 ha; Figure 1A). Shawnee Trail and Talbot Conservation Areas are at the traditional end of the management spectrum, where management focused on small units (<1–24 ha) of food plots, woody vegetation, grassland, and some larger cropland and grassland units. Management consisted of prescribed grazing, mowing, and burning of grassland units and habitat improvement practices such as planting food plots or crop fields and maintaining woody-strip cover (Figures 1B, 2A, 3). Shelton Memorial and Stony Point Prairie Conservation Areas and Wah'Kon-Tah Prairie are at the grassland end of the management spectrum. They had no food plots or cropland and were >80% native grassland managed by fire, grazing, and brush hogging, which created heterogeneity in grassland composition and structure and varying amounts of scattered shrub cover (Figures 1C, 2B, 3). Prescribed burning and conservation grazing used low-intensity grazing of 1 animal unit (454 kg of cattle)/1.6–2 ha for 90–120 days from April to August and grazing units were rested every 1–4 years depending on grazing management. One-third of a unit was burned annually or biannually with rest periods at the end or after each burn in a burning cycle. Prescribed burns occurred September–April. For additional details on study site composition and management see Mosloff et al. (2021), and Sinnott et al. (2021*a*).

Fig. 2. A) Example of traditional management on Talbot Conservation Area, Missouri, USA, including agricultural strip crops and linear wooded edges among grassland units; B) example of grassland management on Stony Point Prairie, Missouri, consisting of continuous remnant or reconstructed prairies managed with fire, grazing, and mowing (photo by David Stonner, Missouri Department of Conservation, used with permission).

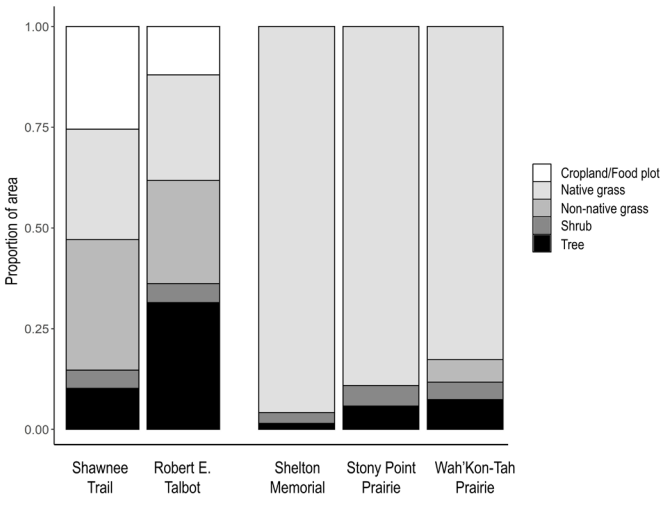

Fig. 3. Proportion of study sites in southwest Missouri, USA in different land cover types, 2016–2018.

METHODS

We conducted bobwhite spring whistle counts 15 May–1 July during 2016–2018 on Shawnee Trail (n = 16 listening stations), Shelton Memorial (n = 2), Stony Point Prairie (n = 8), Talbot (n = 16), and Wah'Kon-Tah Prairie (n = 18). We recorded the number of birds calling within 500 m during a 10-minute period between sunrise and 0900 during 1–3 visits annually to each station.

We captured and radio-tagged bobwhite to measure survival, fecundity, and resource use. Bobwhite were captured using funnel traps in February and March 2014–2018 and fitted with uniquely numbered leg bands and 6-g necklace style radio-transmitters (model AWE-QII, American Wildlife Enterprises, Monticello, FL, USA). We located birds at least 3 times/week by homing in on birds and recorded locations on a hand-held Global Positioning System to monitor adult breeding season survival and locate nests. Success of nests incubated by radio-collared birds was monitored to estimate the number of eggs hatched/adult as a measure of fecundity.

We captured broods of radio-tagged adults at approximately 20 days old and fitted them with backpack transmitters (model AWE-QC-0.8 and AWE-QC-0.65, American Wildlife Enterprises, Monticello, FL, USA) using the suture technique to estimate juvenile breeding season survival in 2016–2018 (Terhune et al. 2020). Broods were tracked on average 6 days/week and at each location we collected data on cover type, management, and woody vegetation composition using maps derived from field observations, remotely sensed land cover data, and LiDAR data (Sinnott et al. 2021*a*, *b*).

We captured bobwhite using funnel traps in September and October 2017–2018 and radio-tagged adults and juveniles for non-breeding season survival estimates and resource selection. We located birds approximately 3 times/week from 1 November to 31 January. Similar to brood locations, we collected data on cover type, management, and woody vegetation composition using maps derived from field observations, remotely sensed land cover data, and LiDAR data (see Mosloff 2020, Mosloff et al. 2021 for details).

Data Analysis

Brood resource selection.—We evaluated population-level, age-specific patterns in bobwhite brood resource selection during the juvenile development period using integrated step selection analysis within a Bayesian hierarchical modeling framework. This approach evaluated resource selection and daily movement decisions in a conditional logistic regression that included both a habitat utilization kernel and a movement kernel (Avgar et al. 2016). We sampled 10 available locations for every one used location by projecting 10 empirically sampled step lengths and randomly selected turning angles based on observed consecutive daily locations. Vegetation characteristics at end points of each used step were then compared to projected end points of each available step (Sinnott et al. 2021*b*).

Fall and winter resource selection.—We modeled bobwhite fall and winter resource selection as a function of vegetation structure, composition, and management with a multinomial logit discrete choice model in a Bayesian framework. We fit conditional multinomial logit discrete choice models to model the probability that an individual selected a location given a choice among 3 locations available at one time (i.e., forming a choice set; Cooper and Millspaugh 1999, Thomas et al. 2006, Mosloff et al. 2021).

Brood survival.—We estimated juvenile survival from hatch to 90 days and related it to cover type composition and grassland management (i.e., conservation grazing, prescribed burns, mowing and haying) at the local (50 m) and landscape (1 km) scale with a Bayesian known-fate logistic exposure model (Sinnott et al. 2021*a*).

Fall and winter survival.—We estimated fall and winter survival and its relationship with hypothesized drivers using a known-fate logistic exposure model (Shaffer 2004, Shaffer and Thompson 2007). We included covey identity and site as random effects and age (juvenile, adult) and month as fixed effects. We then examined support for various combinations of local (50 m)- and landscape (1 km)-scale cover type composition and grassland management (i.e., conservation grazing, prescribed burns, mowing and haying; Mosloff 2020).

Integrated population model.—We developed an integrated population model (IPM) that linked spring whistle counts with nest monitoring and telemetry data to estimate abundance, fecundity, and survival, in order to model population change for each site (Schaub et al. 2007, Schaub and Abadi 2011, Kéry and Schaub 2012, Zipkin and Saunders 2018). We used a 2-stage, 2-sex periodic matrix design comprising the breeding season (1 May–31 Oct) and non-breeding season (1 Nov–30 Apr) to account for differences in survival and productivity among adults and juveniles, and males and females among our sites (Burger et al. 1995*a*, Sandercock et al. 2008). We included sex-specific productivity rates because bobwhite are polygamous and both females and males contribute to fecundity (Curtis et al. 1993; Burger et al. 1995*a*, *b*). We fit our IPM in a Bayesian framework with a joint likelihood and prior probability distributions for estimates of abundance, survival, and productivity. Details on each of the component likelihoods are described further in Sinnott (2020).

RESULTS

Brood Resource Selection

Sinnott et al. (2021*b*) reported on resource selection behavior of 101 bobwhite broods for a total of 2,790 step choice-sets from 2016 to 2018. These data contained 627 steps (movements) by 80 broods ≤14 days old, 1,092 steps by 91 broods 15–35 days old, and 1,071 steps by 45 broods 36–114 days old. A model that included all proposed habitat drivers and brood age class had strong support compared to other models, including a null model. Relative probability of selection increased in relation to proportion of native grass managed by grazing and burning and proportion of cropland for all brood age classes (Figure 4). Relative probability of selection increased greatly with

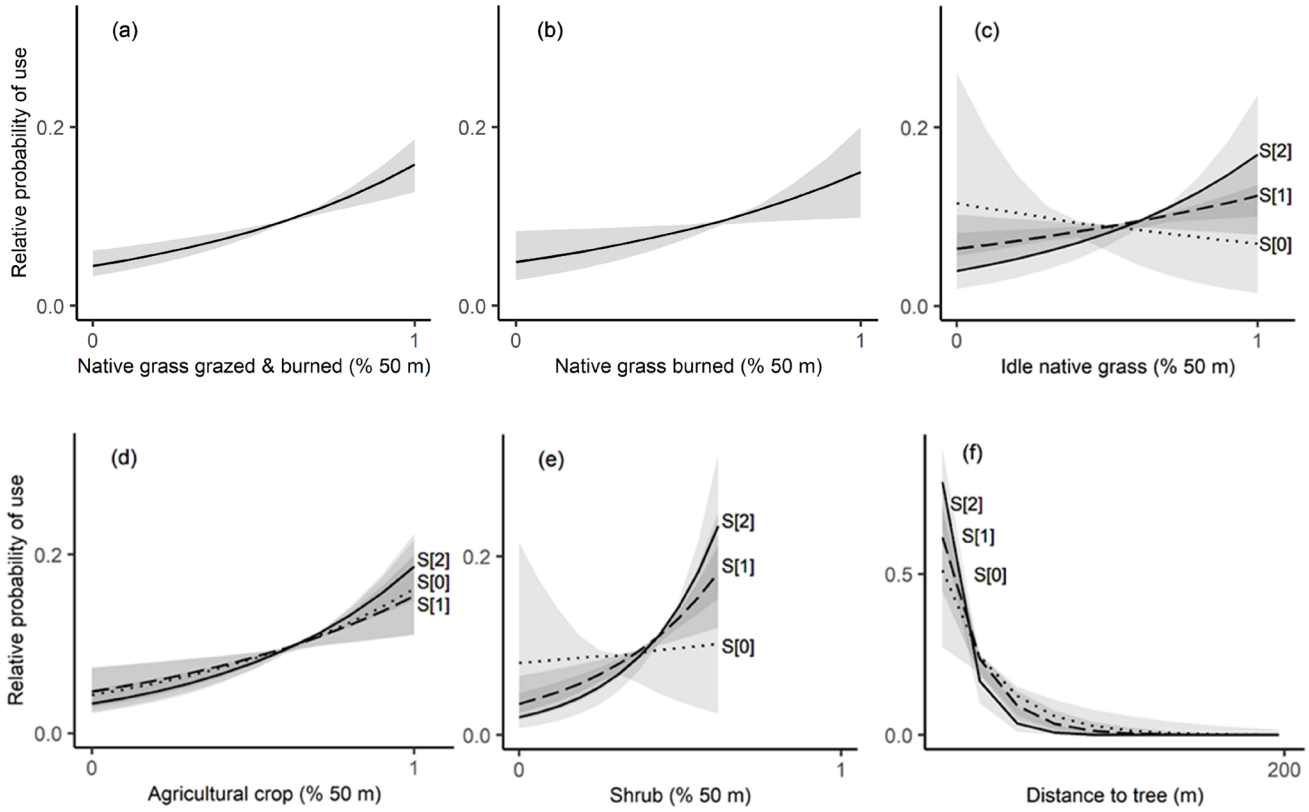

Fig. 4. Predicted relative probability of use of sites by northern bobwhite (*Colinus virginianus*) broods in southwest Missouri, 2016–2018, as a function of percent cover within 50 m of native grassland that was A) burned and grazed, or B) only burned and not grazed within the past 2 years; and stage-dependent predicted relative probability of use as a function of percent cover within 50 m of C) idle native grassland, D) agricultural crop, E) shrub cover; F) predicted relative probability of use as a function of distance to nearest tree for young flightless broods ≤14 days old (S[0]; dotted line), dependent broods 14 to 35 days old (S[1]; dashed line), and independent broods >35 days old (S[2]; solid line). Adapted from Sinnott et al. (2021*b*).

proportion of idle native grass for the older 2 age classes, but less so for the youngest broods. Relative probability of selection increased with proportion of shrub cover for the oldest 2 age classes. Counter to predictions, relative probability of selection decreased as distance to trees increased (Figure 4; Sinnott et al. 2021*b*). Broods that survived to 35 days showed stronger selection for shrub cover than broods that failed.

Fall and Winter Resource Selection

Mosloff et al. (2021) reported on resource selection based on 119 bobwhite tracked in the fall–winter of 2018–2019 and vegetation data on 650 used locations and 3 associated random locations for a total of 650 choice sets in their discrete choice analyses. We ranked competing models based on the Watanabe-Akaike Information Criterion and their null model had the least support. We summarized effects based on their top supported model and effects for which >0.85 of the posterior distribution indicated a positive or negative effect. Bobwhite selected locations closer to trees in winter but not in fall. Bobwhite also selected locations with lower percentage of grass cover at the location during fall but not winter. Bobwhite selected for locations with greater visual obstruction in winter, but not fall, and more woody stems in fall and winter. The relative probability of selection increased as woody edge density increased in fall and winter, respectively (Figure 5).

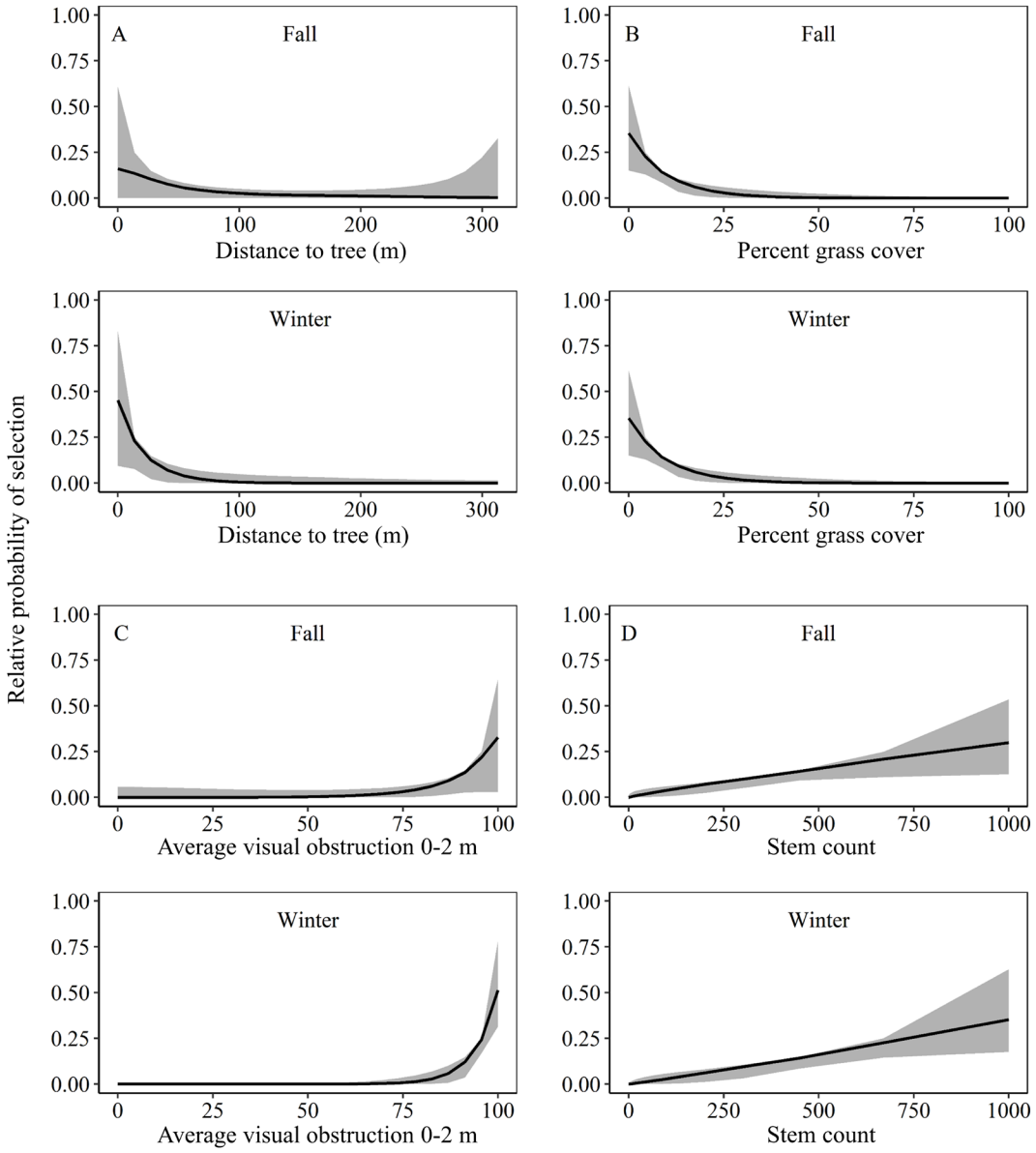

Fig. 5. Predicted relative probability of use of sites by northern bobwhite (*Colinus virginianus*) in fall and winter in southwest Missouri, USA, 2018–2019, as a function of A) distance to the nearest tree (m), B) percent grass cover measured by Daubenmire frame, C) average visual obstruction (0–2 m), and D) woody stem count in a 5-m radius. Adapter from Mosloff et al. (2021).

Brood Survival

Sinnott et al. (2021a) monitored survival of 705 individuals from 75 broods from hatch to up to 114 days old for 14,904 exposure days. Daily survival was a quadratic function of age and increased from 0.96 (95% credible interval [CrI]: 0.91–0.99) post-hatch to 1.00 (95% CrI: 0.99– 1.00) at 114 days old, for 90-day period survival of 0.33 (95% CrI: 0.18–0.46). We drew inferences on survival from the top 2 supported models which evaluated local habitat management effects and interactive effects of landscape-scale agriculture and local-scale native grassland, as well as agricultural cover on juvenile survival. Consistent with predictions, local native grasslands burned and grazed in the past 2 growing seasons had the largest positive effect on daily juvenile survival. Period survival increased from 0.21 to 0.84 as native grasslands burned and grazed within 50 m increased from 0% to 100% (Figure 6). Effects of grazed mixed grasslands were also positive and period survival increased from 0.32 to 0.81 over 0% to 100% cover. Period survival increased from 0.27 to 0.75 as percent shrub cover increased from 0% to 53%. Contrary to predictions, percent agriculture cover had a positive effect, and percent mixed grass burned had a negative effect on survival (Figure 6; see Sinnott et al. 2021a for additional details).

Fall and Winter Survival

Mosloff (2020) analyzed observations from 2,068 locations of 186 radio-tagged bobwhite from 1 November–31 January 2017–2019. She fit 10 candidate models and interpreted effects from the top 2 supported models. Based on her top model, 90-day period survival was 0.68 (95% CrI: 0.58–0.77) for juveniles and 0.78 (95% CrI: 0.61–0.89) for adults. As predicted, period survival increased from 0.67 to 0.89 as distance to trees increased from 0 m to 306 m. Period survival also decreased from 0.77 to 0.31 as distance to shrubs increased from 33 m to 160 m (Figure 7). Contrary to predictions, there was no support for a positive effect of native grasslands and vegetation managed with prescribed burning and grazing.

Integrated Population Model

Three rounds of bobwhite spring whistle counts were conducted annually on Shawnee Trail, Shelton Memorial, and Stony Point Prairie 2016–2018. Two rounds were conducted on Talbot in 2017; 3 rounds were conducted in 2016 and 2 rounds in 2017 and 2018 on Wah'Kon-Tah Prairie. We tracked 766 juveniles and 618 adults during the breeding season and monitored success of 276 nests incubated among 576 adults active on 1 May at the start of the breeding season across all years. We monitored 772 juveniles and 349 adults to estimate non-breeding season survival probabilities (see Sinnott 2020 for details).

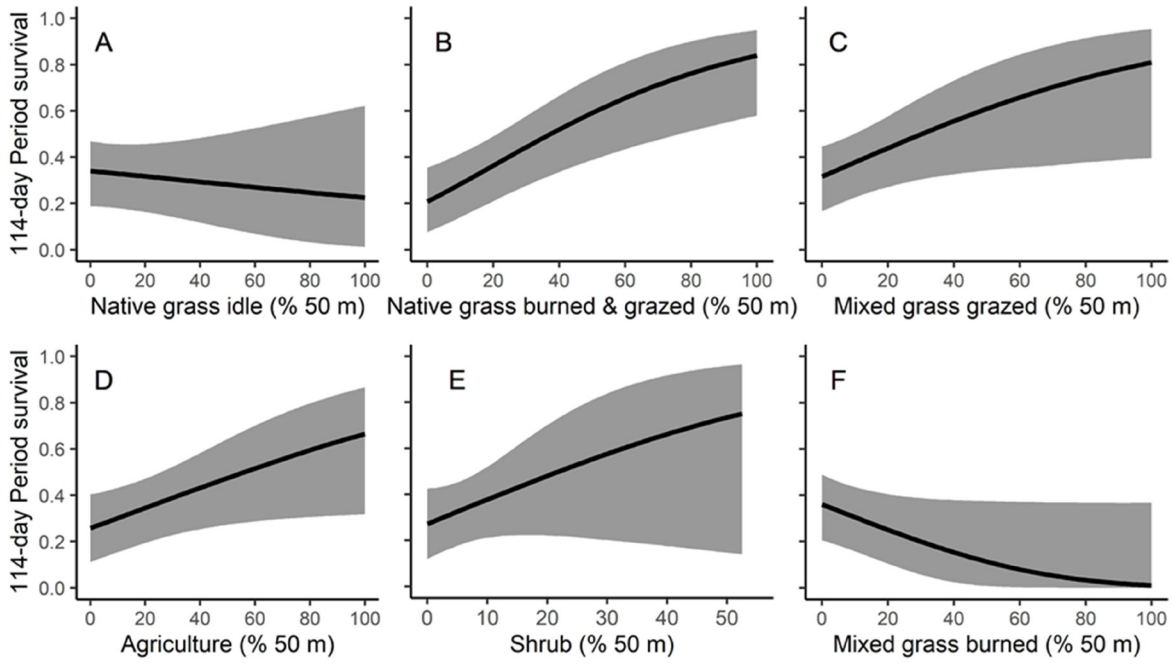

Fig. 6. Period survival estimates increased as B) proportion of native grasslands managed with fire and grazing, C) grazed mixed grasslands, D) agriculture, and E) shrub cover within 50 m of northern bobwhite (*Colinus virginianus*) juveniles increase in southwest Missouri, USA, 2016–2018. Period survival estimates decreased as (F) proportion of burned mixed grasslands within 50 m of daily locations increased and estimates did not vary with A) proportion of native grasslands left idle for at least 2 years. Mean (line) and 95% credible interval (ribbon) 90-day period survival of juvenile northern bobwhite were based on selected effects from the top-ranking cover type and management model describing percent cover composition within 50 m of daily locations.

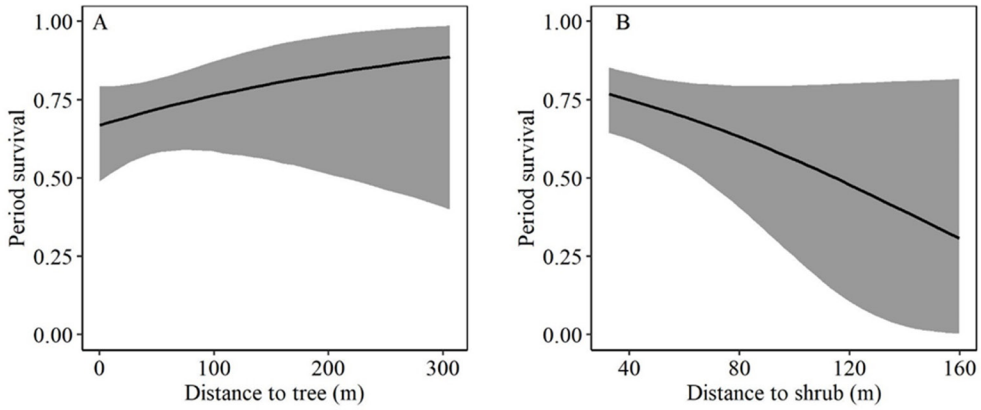

Fig. 7. Bobwhite fall and winter 90-day period survival and 95% credible interval as a function of A) distance to tree (m) and B) distance to shrub (m) in southwest Missouri, USA, November–January 2017–2019.

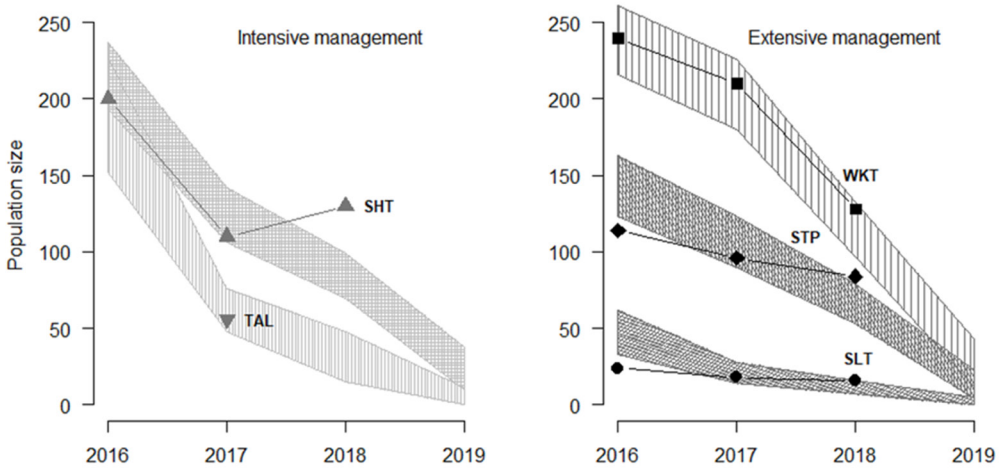

Fig. 8. Northern bobwhite (*Colinus virginianus*) population counts (points) and estimated abundances (ribbons) for (on left) 2 traditionally managed sites, Shawnee Trail (SHT) and Talbot (TAL), and (on right) 3 grassland managed sites, Shelton Memorial (SLT), Stony Point Prairie (STP), and Wah'Kon-Tah (WKT), in southwest Missouri, USA, 1 May 2016–2018.

Spring whistle counts showed declining trends for all sites with 3 consecutive years of survey data 2016–2018 (Figure 8). All spring counts were within the 95% CrI of male abundance estimates except for Shawnee Trail 2018, which was estimated low (Figure 8). Across all years, mean population growth was greater on grassland management sites ($\lambda = 0.48$, 95% CrI: 0.00–0.90) compared to traditionally managed sites ($\lambda = 0.41$, 95% CrI: 0.05–0.75) though both estimates indicated that declines had large credible intervals. Population growth was highest on the largest grassland managed site, Wah'Kon-Tah Prairie ($\lambda = 0.55$, 95% CrI: 0.13–0.94) and lowest on a traditionally managed site, Talbot ($\lambda = 0.31$, 95% CrI: 0.03–0.65).

Female fecundity was greater on grassland managed sites (4.07, 95% CrI: 2.34–6.09) than traditionally managed sites (2.38, 95% CrI: 1.11–5.62; Figure 9). Female breeding season adult survival was also greater on grassland managed sites (0.48, 95% CrI: 0.32–0.64) than traditionally managed sites (0.33, 95% CrI: 0.18–0.50; Figure 9). However, counter to expectations, non-breeding season survival was not greater on grassland managed sites (0.36, 95% CrI: 0.11–0.59) compared to traditionally managed sites (0.42, 95% CrI: 0.16–0.64; Figure 9). Non-breeding season survival varied across sites and Talbot, a traditionally managed site, had the highest mean non-breeding season survival, followed by Wah'Kon-Tah Prairie, the largest grassland managed site. The 2 smaller grassland managed sites, Stony Point Prairie and Shelton Memorial, had the lowest non-breeding season survival (Figure 9).

We compared site-level vital rate estimates to the subset of posterior samples that resulted in a population growth rate ≥ 1.0 to identify which seasonal vital rates most limited population growth at each site. Female fecundity and adult breeding season survival at traditionally managed sites were lower than rates that resulted in a stable population growth rate (Figure 8). Non-breeding season survival probability at 2 grassland managed sites, Shelton Memorial and Stony Point Prairie, were also lower than rates that resulted in stable population size (Figure 9).

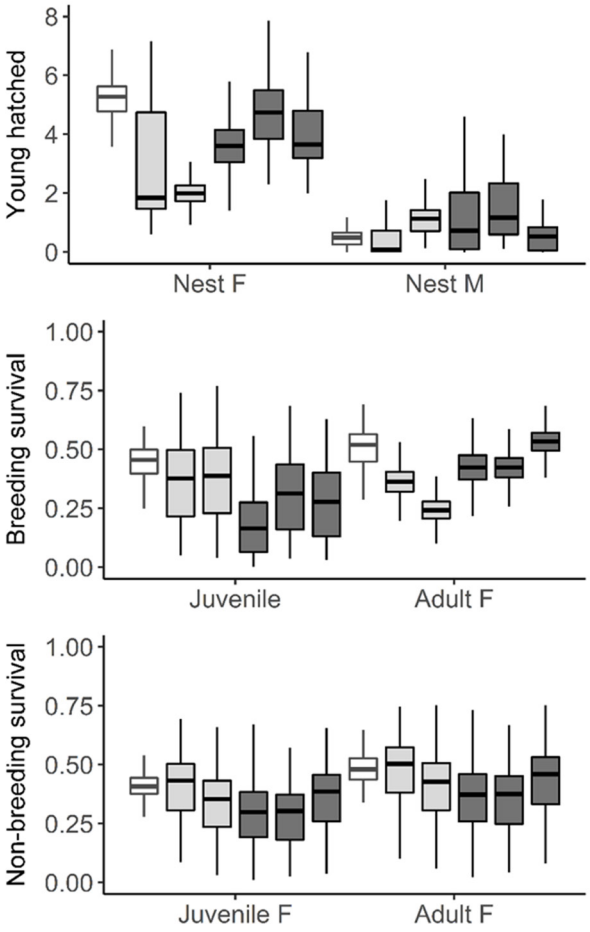

Fig. 9. Boxplots of posterior distributions of northern bobwhite (*Colinus virginianus*) seasonal vital rates in southwest Missouri, USA, 2016–2018. The first box plot for each vital rate represents a subset of posterior samples that resulted in a stable population growth rate (white; $\lambda \geq 1.00$). Observed site-level vital rates are then given in the following order for each vital rate: Shawnee Trail and Talbot (light gray, traditionally managed sites), then Shelton Memorial, Stony Point Prairie, and Wah'Kon-Tah Prairie (dark gray, grassland managed sites). Fecundity was estimated as the number of young hatched per female-incubated nest (Nest F) and male-incubated nest (Nest M). Posterior distributions of breeding and non-breeding season survival were estimated as 6-month period survival probabilities for juveniles (Juv) and adult females (Adult F). Posterior distributions of non-breeding season survival were estimated as survival probabilities for juvenile females (Juv F) and adult females (Adult F).

DISCUSSION

We synthesized 6 years of research on northern bobwhite demography and resource selection in southwest Missouri and generally found support for the idea that prescribed fire with grazing on native grasslands can provide quail habitat superior to more traditional management. Bobwhite preferred conditions created by grassland management or had greater vital rates there and these findings held among different stages of their life history. However, grassland management was not better for all stages or components of bobwhite demography. For example, bobwhite broods selected for agricultural fields and non-breeding season survival was greater on traditionally managed sites.

Resource selection by broods was strongest for native grasslands that were both burned and grazed at least once within the previous 2 years and also positive but weaker for native grasslands that were just burned or grazed the previous 2 years. Broods likely selected for burned and grazed native grasslands because these management practices provided adequate cover, open bare ground, and high invertebrate abundance for juvenile foraging, growth, mobility, and survival (Hurst 1972, Taylor et al. 1999*a*, Engle et al. 2008, Doxon and Carroll 2010, Kamps et al. 2017). Contrary to our predictions, broods also selected for row crop and idle agricultural fields. We expected row crops to provide suboptimal foraging habitat (Puckett et al. 1995, Palmer et al. 2001, Doxon and Carroll 2010, Lohr et al. 2011), but instead we found that row crops enabled broods to move easily and potentially allowed better sight of approaching ground predators, while likely providing adequate overhead cover from aerial predators. Though young broods did not select for shrub cover, older broods did. Shrubs provide protection from warm daytime temperatures and escape cover from predators (Carroll et al. 2015).

Woody cover was the primary driver of resource selection during fall and winter. As we predicted, bobwhite selected areas with greater woody edge density and more woody stems (indicative of shrub cover). Bobwhite also used areas with high woody edge density in Illinois, USA (Roseberry and Sudkamp 1998), Kansas, USA (Williams et al. 2004), Kentucky, USA (Brooke et al. 2015), and Ohio, USA (Janke and Gates 2013). Shrubs provide escape cover from predators and shelter from extreme weather (Brennan 1991, Williams et al. 2000, Sandercock et al. 2008, DeMaso et al. 2014). Contrary to our predictions, selection was negatively related to distance from trees. Trees can harbor predators such as opossums (*Didelphis virginiana*), raccoons (*Procyon lotor*), and raptors (Dijak and Thompson 2000, Byrne and Chamberlain 2011), and as discussed later, we found fall-winter survival was lower closer to trees. Bobwhite also select woodlots in other parts of their range (Lohr et al. 2011, Janke and Gates 2013). We suggest bobwhites often used shrub cover on our sites that was in close proximity to trees in more permanent woody cover such as riparian areas and fencerows, and that trees have the potential to be ecological traps.

Brood survival was greater on native grasslands managed with fire and grazing and areas with available shrub cover than in other management and vegetation types. Burning and grazing expose bare ground and allow movement and escape from predators while maintaining overhead cover (Taylor et al. 1999*a*, Harper et al. 2015, Kamps et al. 2017). These practices also can improve foraging efficiency and growth of young by removing accumulated litter and increasing insect abundance (Engle et al. 2008, Doxon and Carroll 2010, Gruchy and Harper 2014, Sinnott et al. 2021*a*). Contrary to predictions, survival was not greater on landscapes with more native grassland cover nor did mowing, local agriculture, or proximity to trees decrease survival.

As predicted, fall-winter survival was greater closer to shrub cover and farther from trees. Woody cover is often reported as an important component of winter cover (Seckinger et al. 2008, Gates et al. 2012, Janke et al. 2015). Trees, however, provide perches for raptors, and raccoons and other mammalian predators have greater movement and activity near trees and forest edges (Brown and Amadon 1968, Brown 1976, Dijak and Thompson 2000, Chamberlain et al. 2002, Seckinger et al. 2008, McClain 2017).

Results from our IPM suggest changes in bobwhite abundance were related to site-level variation and differences in seasonal vital rates between grassland and traditional management. Female fecundity and breeding season adult survival were greatest on grassland managed sites and were likely the reason population growth rate was also greater on grassland managed sites. Age- and sex-specific differences in seasonal survival and male contributions to fecundity emphasized the importance of accounting for population structure and composition in the full annual cycle demography of bobwhite. Contrary to our prediction, non-breeding season survival was not greater on grassland managed sites. Indeed, non-breeding survival was highest on a traditionally managed site and lowest on 2 small (<400 ha) grassland managed sites (Sinnott 2020). Traditionally managed sites included food plots while grassland managed sites did not, and perhaps this was a factor in winter survival. We also speculate that other contributing factors, such as hunting pressure (Roseberry 1979, Williams et al. 2000), predator community composition (Lohr et al. 2011, Atuo and O'Connell 2017), and habitat in the surrounding landscape also impacted site-level variation in bobwhite non-breeding season survival. We recommend that future research further explore these drivers to improve conservation planning and management on grassland and traditionally managed areas.

MANAGEMENT IMPLICATIONS

We suggest that overall, grassland management has provided better bobwhite habitat than traditional management in these grassland landscapes in southwest Missouri. Prescribed burning with conservation grazing was implemented on the southwest Missouri sites to promote a shifting mosaic that facilitates brood use since at least one-third to one-half of each area was disturbed each year. Coupling grazing and fire on tallgrass prairies and grasslands promotes heterogeneity in vegetation structure and composition (Fuhlendorf and Engle 2004, Veen et al. 2008), and provides fine-scale grass, forb, and shrub cover in native grasslands, which positively influences breeding season survival and fecundity. Disturbance from fire and grazing also creates more suitable structure by removing litter and reducing vegetation density. While fire is clearly beneficial to birds during the breeding and non-breeding seasons, burning at intervals >1 year may promote greater non-breeding season survival. Our work consistently showed negative effects of tree cover on bobwhite survival so reducing tree cover could result in greater survival. We believe that a management combination of fire and grazing, and landscape composition of grassland with interspersed shrubs, will provide the greatest chance for bobwhite populations to persist in southwest Missouri and similar landscapes.

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ADAPTIVE MANAGEMENT FACILITATES INCREASE IN NORTHERN BOBWHITE POPULATIONS

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ABSTRACT

Adaptive resource management (ARM) is an approach to managing that allows decision makers to learn about a system and subsequently change management actions based on new information about system processes (i.e., adapt) to better meet fundamental objectives. This is not to be confused with changing management actions when the state of the system changes. For example, changing a harvest regulation when populations decline is not ARM. This dynamic decision making may be fortuitously optimal, but if the effect of harvest is uncertain then changing regulations may be suboptimal—for example, weather may have caused the decline. Adaptive resource management can be implemented along a spectrum of passive to active to reduce system uncertainty. Active ARM is when explicit hypotheses are posited then implemented to test them, and monitoring occurs to elucidate whether the effect of the management action achieved a given result. Passive ARM uses current management practices, natural variation in the system, and monitoring to reduce uncertainty. Even though northern bobwhite (*Colinus virginianus*) have been studied for a century, uncertainty regarding optimal management strategies still exists. The Albany Quail Project (AQP) has used both modes of ARM to learn about northern bobwhite populations to better meet the hunting objectives of stakeholders. Between 1992 and 2019 the AQP radio-tagged 5,182 unique individuals and banded an additional 5,008 birds on the primary study area near Albany, Georgia, USA. Additionally, 1,724 nests have been monitored and population surveys conducted in the spring and autumn. Active ARM occurred with tests of supplemental feeding, hardwood cleanup, and predator control whereas passive ARM was used to learn about prescribed fire regimes, brood habitat preferences, small mammal cycles, and raptor migrations. We built an integrated population model (IPM) that combined known-fate survival data, nesting records, dead recoveries from harvest, and population surveys to model the system. The preliminary results of the IPM demonstrated that populations have increased during the project. The 5 most abundant autumn populations have occurred in the most recent 10 years of the project when bobwhite populations throughout their range have continued to decline. Unlike typical ARM applications, the AQP has not had an explicit model to predict consequences of future management actions; nonetheless, the essence of ARM has been followed. Since its inception uncertainty has been reduced, management actions have been changed, and bobwhite populations have responded. Improvements to AQP and similar projects could include explicit hypotheses and predictive models about the system to facilitate the transfer of knowledge to future bobwhite managers.

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Key words: *Colinus virginianus*, integrated population model, learning, long-term monitoring, northern bobwhite, uncertainty

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HABITAT WORKS: HOW PARTNERSHIPS AND HABITAT IMPROVEMENT HAVE RESTORED QUAIL POPULATIONS IN THE 2C QUAIL FOCUS AREA, MISSOURI

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ABSTRACT

The Missouri Department of Conservation (MDC) began establishing Quail Focus Areas (QFAs) on private lands in 2004. The goal of QFAs was to bring groups of landowners together to manage bobwhite habitat on a larger scale in a targeted landscape. Through a variety of state, federal, and other partnership programs, habitat improvement efforts have resulted in large increases in northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) numbers in the 2C QFA. In spring 2013, MDC staff and Quail Forever biologists began monitoring bobwhite and songbirds in a portion of the 2C QFA in Carroll County, Missouri, USA and in a control area (without habitat management for bobwhite). This effort is part of the Coordinated Implementation Plan developed by the National Bobwhite Technical Committee as a part of the National Bobwhite Conservation Initiative. The goal of the monitoring plan is to document whether quail habitat management can achieve sustainable bobwhite populations within 5–10 years. We selected a 2,100-ha portion of the 2C QFA where habitat management for quail has been conducted through efforts by landowners, MDC staff, and Quail Forever volunteers. Point-transect surveys were conducted at 48 250-m radius points in spring for bobwhite and songbirds and at 12 500-m radius points in fall for bobwhite coveys. Quail densities ranged from 0.18 quail/ha (95% credible interval [CrI] = 0.09–0.32) to 0.41 quail/ha (95% CrI = 0.30–0.57) in the focus area and from 0.04 quail/ha (95% CrI = 0.01–0.11) to 0.12 quail/ha (95% CrI = 0.06–0.20) in the control area from 2013–2019. We have also documented increases in grassland songbirds through monitoring efforts. Results show that dedicated management efforts were successful in increasing bobwhite density in the focus area.

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LANDOWNER COOPERATIVE KEY TO SUCCESS IN THE BEE RIDGE QUAIL FOCUS AREA, MISSOURI

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ABSTRACT

The Missouri Department of Conservation (MDC) began establishing Quail Focus Areas (QFAs) on private lands in 2004. The goal of QFAs is to increase and expand quail habitat management efforts around a core area. Because most (93%) of the landscape of Missouri, USA is in private ownership, habitat improvement programs on private lands have greater potential to impact quail populations than on public lands alone. A motivated group of landowners led the charge to begin habitat improvement efforts in the Bee Ridge QFA. This group was instrumental in starting earlier monitoring efforts to determine whether habitat improvements were leading to increased northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) numbers. In fall 2017, MDC staff began monitoring bobwhite and songbirds in a portion of the Bee Ridge QFA in Knox County, Missouri and in a control area (without habitat management for bobwhite). This effort is part of the Coordinated Implementation Plan developed by the National Bobwhite Technical Committee as a part of the National Bobwhite Conservation Initiative. The goal of the monitoring plan is to document whether quail habitat management can achieve sustainable bobwhite populations within 5–10 years. We selected a 2,225-ha portion of the Bee Ridge QFA where habitat management for quail has been conducted through efforts by landowners and MDC staff. Point transect surveys are conducted at 46 250-m radius points in spring for bobwhite and songbirds and at 12 500-m radius points in fall for bobwhite coveys. Bobwhite densities ranged from 0.23 bobwhite/ha (95% credible interval [CrI] = 0.14–0.35) to 0.27 bobwhite/ha (95% CrI = 0.15–0.43) in the focus area and 0.03 bobwhite/ha (95% CrI = 0.01–0.08) to 0.06 bobwhite/ha (95% CrI = 0.01–0.15) in the control area from 2013 through 2019. Landowners working together to implement recommended habitat management practices resulted in greater quail and songbird numbers in the focus area, compared to the control area.

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Key words: *Colinus virginianus,* focus area, Missouri, monitoring, northern bobwhite, point transect surveys, private land

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LESSONS LEARNED FROM THE FIRST 10 YEARS OF THE OAKS AND PRAIRIES JOINT VENTURE'S GRASSLAND RESTORATION INCENTIVE PROGRAM (GRIP)

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ABSTRACT

The Oaks and Prairies Joint Venture (OPJV) was formed in 2008 as a public-private partnership of agencies and organizations working across jurisdictional boundaries in portions of Texas and Oklahoma, USA. The OPJV's major focus is reversing declines of bird populations by supporting strategic habitat conservation (biological planning, conservation design, conservation delivery, mission-based monitoring, and assumption-driven research) for northern bobwhite (*Colinus virginianus*), grassland-obligate species, and their respective habitats. Our objective for this paper is to document and share a decade of lessons learned in developing a partnership-based native grassland conservation program to meet grassland bird conservation targets. We share lessons learned about how to manage partnership-based, large-scale habitat incentive programs to better target project locations and habitat practice types. To establish initial shared purpose, OPJV partners drew from population and habitat objectives in various state, national, and international bird conservation plans, stepped down to ecoregion levels, to establish the OPJV Grassland Bird Conservation Business Plan. The plan has 4 strategies directly contributing to the achievement of OPJV grassland bird biological objectives that are directly supported by OPJV staff or resources (or both). The overall objective for 2015–2025 was 619,978 ha (1,532,000 acres) improved within 40 focal counties, representing 1/3 of all counties in the OPJV. Our main strategy was to provide financial incentives through the OPJV Grassland Restoration Incentive Program (GRIP) to private landowners for conducting beneficial grassland bird habitat management practices. Since inception in 2013, GRIP has treated over 44,515 ha (110,000 acres) on private lands in Texas and Oklahoma, with the goal of maintaining high-quality grassland bird habitat on treated hectares for ≥5 years. In 2017, OPJV partners working with USDA Natural Resources Conservation Service, began a 5-year, $6.1 million partnership to provide additional technical and financial assistance to private landowners interested in grassland conservation through the Regional Conservation Partnership Program (RCPP). A project scoring system was designed to strategically encourage individual projects to include prescribed fire—one of the lowest cost practices per hectare—as a recurring practice to maintain program-achieved grassland improvements. Post-inception of the RCPP, the area treated with prescribed fire increased from approximately 809 ha (2,000 acres)/year to 3,237 ha (8,000 acres)/year, while maintaining average annual hectares of all other beneficial practices. Beginning in 2013, bird point count surveys were conducted annually to monitor northern bobwhite and grassland bird populations, including a subset of points under the National Bobwhite Conservation Initiative (NBCI) Coordinated Implementation Plan. To date, nearly 25,000 individual point counts have been performed in Texas (n = 20,111) and Oklahoma (n = 4,558). Working together, OPJV partners have made significant progress toward meeting grassland bird habitat and population objectives, while tracking progress and improving methods. However, there is still considerable work ahead.

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Key words: *Colinus virginianus,* Grassland Restoration Incentive Program, habitat objective, incentive program, northern bobwhite, Oaks and Prairies Joint Venture

The Oaks and Prairies Joint Venture (OPJV) was formed in 2008 as a public-private partnership of federal and state agencies, non-governmental organizations (NGOs), universities, tribes, private landowners, businesses, and other partners working across jurisdictional boundaries in portions of Texas and Oklahoma, USA within the Oaks and Prairies Bird Conservation Region (BCR) and the Edwards Plateau BCR (Figure 1). The OPJV is guided by a management board with representatives from 14 agencies and organizations and supported by a science technical team and various Local Initiative Teams (LITs) representing dozens of additional partner organizations as well as other interested individuals. The OPJV mission is "to plan for and facilitate bird habitat conservation, research, and outreach in an effort to ensure sustainable populations of priority bird species in the Edwards Plateau and Oaks and Prairies Bird Conservation Regions in Oklahoma and Texas" (OPJV 2021).

Over the past 3 decades, an entire suite of North American grassland birds has experienced significant declines (Brennan 1991; Knopf 1994; Rosenberg et al. 2016, 2019). These declines are primarily attributed to the landscape-level loss of suitable habitats that historically supported stable populations of >30 species of migratory and resident grassland birds, including northern bobwhite (*Colinus virginianus*; Brennan 1991, Williams et al. 2004, Brennan and Kuvlesky 2005, McCracken 2005, Hernández et al. 2013). It is unlikely that any single conservation action or policy will adequately address the needs of differing species, but clearly, a coordinated, strategic approach must be employed at a landscape level, and especially on private lands, to ultimately solve this crisis (Drum et al. 2015). The OPJV's major approach to stabilize and reverse declines of bird populations was the implementation of strategic habitat conservation (biological planning, conservation design, conservation delivery, mission-based monitoring, and assumption-driven research) for northern bobwhite, grassland associated bird species, and their respective habitats (NEAT 2006, USFWS 2008, Giocomo et al. 2017).

Starting in 2008, partners used existing population and habitat objectives in various state, national, and international bird conservation plans, stepped down to ecoregion levels, to establish focus areas (clusters of focal counties) to concentrate partner conservation efforts, and increase the likelihood of detecting potential population-level impacts for priority bird species. The OPJV's focus areas were developed based on a variety of factors including the National Bobwhite Conservation Initiative's (NBCI's) Biologist Ranking Index (BRI) and Breeding Bird Survey data, and were analogous to NBCI focal landscapes as described in the "tiered delivery" vision of the NBCI Coordinated Implementation Program (Figure 1; Sauer et al. 2008, OPJV 2010, Morgan et al. 2014). The objectives of this paper are to document a decade of lessons learned in developing a partnership-based native grassland conservation program to meet grassland bird conservation targets, and share some lessons learned about how to manage partnership-based, large-scale habitat incentive programs to better target project locations and habitat practice types.

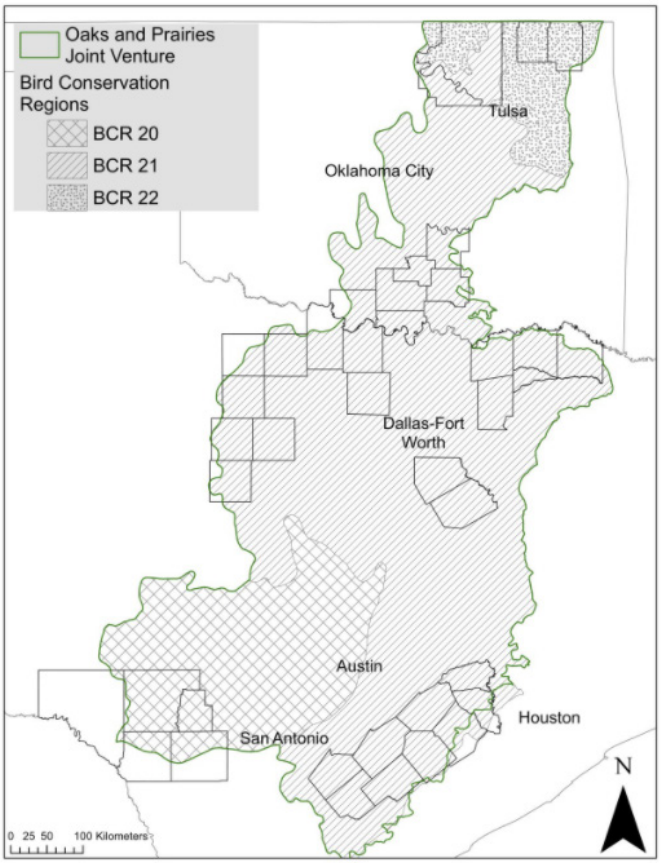

Fig. 1. The location of the Oaks and Prairies Joint Venture in Oklahoma and Texas, USA. The geography encompasses Bird Conservation Regions 20 (Edwards Plateau), 21 (Oaks and Prairies), and portions of 22 (Eastern Tallgrass Prairie). The counties shown are focal counties for the Grassland Restoration Incentive Program (GRIP), which were determined based on the Northern Bobwhite Conservation Initiative's Biologist Ranking Index and Breeding Bird Survey data as well as other factors.

OPJV partners established the OPJV Grassland Bird Conservation Business Plan with 4 strategies directly contributing to the achievement of OPJV grassland bird biological objectives that are directly supported by OPJV staff or resources (or both). These strategies were 1) providing financial incentives through the OPJV Grassland Restoration Incentive Program (GRIP) to private landowners for conducting beneficial grassland bird habitat management practices, 2) supporting local landowner cooperative conservation efforts, 3) developing market-based conservation delivery strategies, and 4) implementing a Strategic Communications Plan (OPJV 2015). We will discuss the first 2 strategies in the context of the NBCI Coordinated Implementation Program as an example of the "tiered delivery approach" envisioned by the NBCI. We will also discuss lessons learned from building a landscape-level approach to deliver conservation practices through GRIP to achieve OPJV partners' shared grassland conservation goals.

ESTABLISHING A SIMPLE AND SCIENCE-BASED GRASSLAND RESTORATION INCENTIVE PROGRAM

The Grassland Restoration Incentive Program (GRIP) started with the desire of OPJV partners and staff to create a simple financial incentive conservation program focused solely on native grassland habitat management that could remove common obstacles to conservation implementation. The idea was also to facilitate ownership of the program by the full spectrum of wildlife professionals who routinely work with private landowners. First, 40 focal counties were established, representing about 1/3 of the total counties in the OPJV geography, in an effort to concentrate financial and technical resources, and increase the likelihood of having a measurable, positive impact on grassland bird populations. Second, the number of conservation practices available in GRIP was limited to 7 select native grassland management practices: brush management, cross fencing, firebreak construction, herbaceous weed treatment, prescribed fire, prescribed grazing, and range planting. And third, to further simplify the design of the program, OPJV partners adopted existing U.S. Department of Agriculture (USDA) conservation practice standards and specifications already in place, all to address one problem—declining grassland bird populations. GRIP also used the most recent USDA Natural Resources Conservation Service (NRCS) practice cost list to determine conservation practice costs. Diverse state, private, and corporate funding sources were used ($5,000–$450,000 single- and multi-year grants) to complete practices along with landowner match. Non-governmental organization partners served as fiduciary organizations, holding grants and handling payments to landowners, to reduce administrative burden and create opportunities for private landowners.

All projects submitted for consideration were evaluated by OPJV staff and partners to ensure limiting factors for grassland birds were addressed and that a plan was in place to continue to address those limiting factors for at least 5 years. The minimum project size was set at 10 ha (25 acres) of proposed management, equal to the estimated territory size of a northern bobwhite breeding pair (Lee 1994, Brennan et al. 2020). After enrollment was opened, a group of OPJV staff and local partner biologists reviewed projects on a rolling basis. The partner biologists were stationed within or near focus areas and had grassland management and grassland bird experience. Collectively, these reviewers were called Local Initiative Teams (LITs). Biologists or project managers (qualified individuals with grassland management or biology backgrounds) and private landowners subsequently implemented approved GRIP projects. Contracts were evaluated, signed, and implemented, usually within 2–4 weeks. This quick turnaround time was essential to address time-sensitive practices such as prescribed fire and native range plantings.

A grassland bird monitoring plan was initiated in 2013. We established roadside bird survey routes in 39 focal counties to tie conservation work to bird population objectives and to potentially detect changes in populations at the county level. Our surveys followed similar methodology to the Breeding Bird Survey (Sauer et al. 2008). Additionally, the OPJV conducted spring bird point counts and fall covey counts on one officially designated NBCI Coordinated Implementation Program (CIP) area to identify effects of practices at a local level. As a result, local-, regional-, and landscape-level data were collected, which were applied to a variety of analyses to assess success and effectiveness.

ADDING PROGRAM COMPLEXITY AND RESOURCES

With the advent of new programs in the 2014 Farm Bill, the OPJV pursued a Regional Conservation Partnership Program (RCPP) grant with NRCS. The RCPP was designed to foster diverse partnerships capable of spending federal conservation dollars in a new and innovative fashion. After two unsuccessful OPJV partner attempts, the National Wild Turkey Federation, on behalf of the OPJV, was awarded an RCPP grant in 2016. The grant resulted in a $6.1 million, 5-year investment. About half of the funds came from OPJV partners and half through NRCS programs. The grant included support for both technical assistance (salary for 3 conservation delivery biologists) and financial assistance through NRCS's Environmental Quality Incentive Program (EQIP). The newly hired biologists would have NRCS planning credentials and access to the NRCS computer system to guide contracts through the federal contracting process from start to finish. This RCPP grant, while not necessarily innovative from a conservation practice standpoint, continued the same approach of vastly narrowing conservation practice options to increase both the quality and quantity of enhanced native grassland habitat within OPJV focal counties. The result was a model that followed portions of the first iteration of GRIP enmeshed with NRCS guidelines to acclimate project managers and biologists not employed through NRCS to the process of using EQIP financial assistance.

Adding RCPP resources to GRIP dramatically increased funds available for technical and financial assistance through the OPJV. The RCPP-funded biologist positions received funding for 5 years and were strategically located in Oklahoma, North Texas, and South Texas (Figure 2). This allowed for more direct communication with project managers in each of the focus areas across the OPJV geography. The addition of these positions increased both the total number of projects and communication among partners (Figure 3); those increases were due in large part to the positions serving as liaisons between project managers and the complex NRCS systems. Another benefit was having a wildlife-centric presence in NRCS field offices, particularly in the offices where biologists were stationed. Financial assistance from RCPP provided not only a significant increase in project funds but also a more consistent conservation funding source. Over $2.1 million in

financial assistance was made available to private landowners, which ultimately led to a proportional increase in hectares impacted on an annual basis (Figure 3).

The expansion of GRIP with federal support added much-needed certainty for annual financial assistance availability with the 5-year agreement, but it also added layers of complexity. For example, the RCPP process was slower overall, with contracts being executed approximately once every 6 months. Additionally, all RCPP-funded projects were required to be run through the NRCS contracting process and were subject to NRCS sign-up, or "batching" deadlines that included a 30-day sign-up period. In contrast, prior to adding NRCS-RCPP, GRIP projects were planned, completed, and reimbursed within weeks or a few months based on the amount of conservation dollars available and the types of practices.

Most of the projects approved during the early years of GRIP were brush management, our most expensive practice per hectare, and grazing-oriented with little emphasis on the use of prescribed fire, our least expensive practice per hectare. In an effort to stretch funding, increase overall impact, and address partner concerns, a new scoring process (i.e., screening tool) was implemented in 2018. This process helped shift project design toward more extensive and cost-efficient practices such as prescribed fire and prescribed grazing (Figures 4, 5). The scoring process allowed for arithmetic evaluation of project benefit with project cost. Projects implemented since 2018 have shifted focus toward prescribed fire and away from more intensive and expensive brush management activities in project design. To date, over

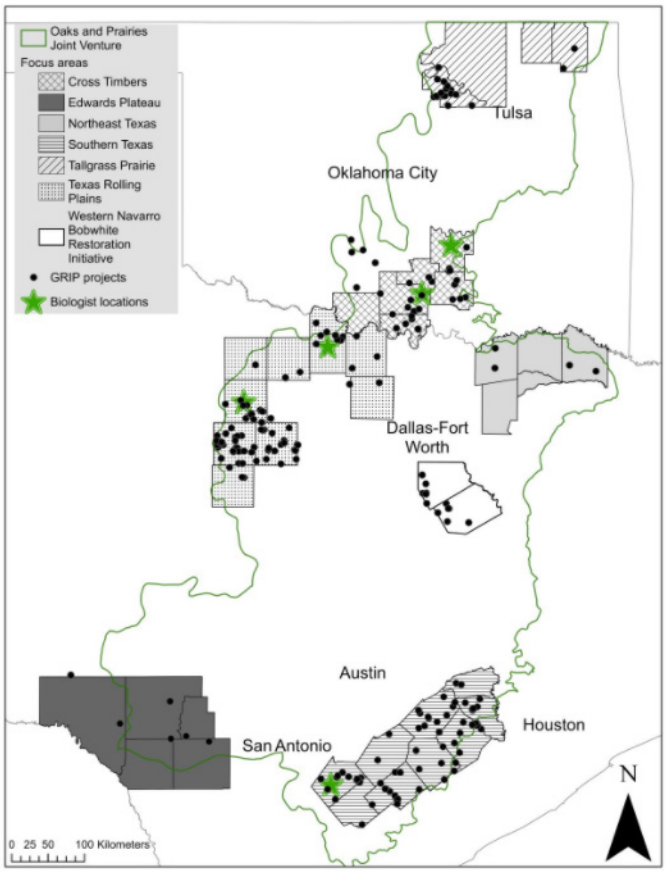

Fig. 2. The location of Grassland Restoration Incentive Program (GRIP) focal counties and GRIP projects from 2013–2021 in the Oaks and Prairies Joint Venture. Focal counties include 30 counties in Texas and 10 counties in Oklahoma. Staff members are located in key areas in focal counties, and projects typically are most concentrated around staff locations or locations of active partner biologists.

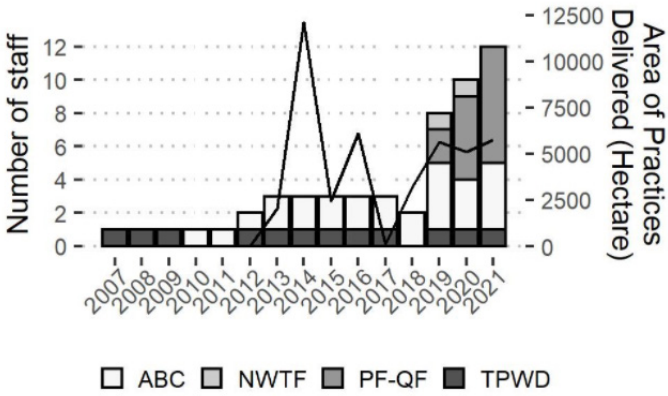

Fig. 3. Number of Oaks and Prairies Joint Venture (OPJV) and partner staff members and area of practices delivered (ha), 2007–2021. The number of staff of the OPJV has increased since its establishment in 2007–2008, and has grown most significantly since the incorporation of the Regional Conservation Partnership Program (RCPP) grant into the Grassland Restoration Incentive Program (GRIP) in late 2018. Additionally, the number of OPJV partners contributing staff has increased since 2018, including American Bird Conservancy (ABC), National Wild Turkey Federation (NWTF), Pheasants Forever-Quail Forever (PF-QF), and Texas Parks and Wildlife Department (TPWD). Over time, the number of hectares delivered has also increased due to increases in staff and new sources of financial assistance such as the RCPP.

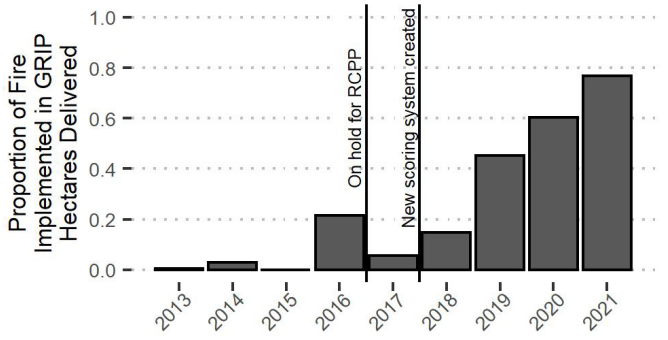

Fig. 4. The proportion of all delivered hectares that were prescribed fire hectares in the Grassland Restoration Incentive Program (GRIP), 2013–2021. This proportion has changed considerably over the years since program establishment. In the early years of GRIP (2013–2017), prescribed fire treatments were not as frequently implemented as other practices. During 2017, the number of projects in general decreased as the OPJV entered a holding pattern while it waited for implementation of the Regional Conservation Partnership Program (RCPP) grant. Once the grant was implemented, and with the establishment of a new scoring system that prioritized prescribed fire treatments, the proportion of fire-treated hectares out of all project hectares vastly increased.

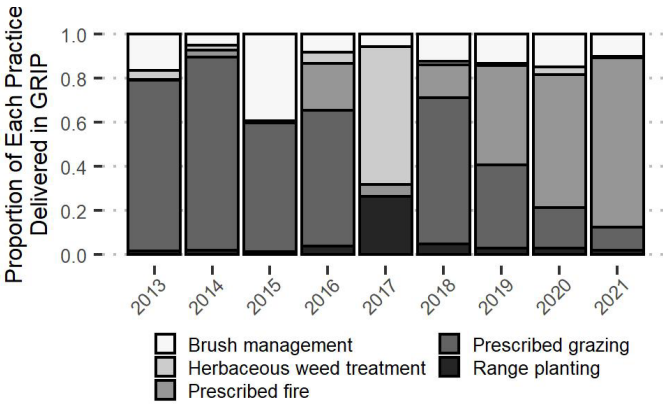

Fig. 5. The proportion of all delivered hectares by each treatment type in the Grassland Restoration Incentive Program (GRIP), 2013–2021. This proportion varied over time, with a dramatic shift in project priorities post-2017. In 2013–2016, many projects incorporated prescribed grazing and brush management. However, after the incorporation of the Regional Conservation Partnership Program (RCPP) grant into GRIP, and the development of a new scoring system in 2018, prescribed fire was prioritized, and prescribed grazing and brush management accounted for a smaller proportion of delivered hectares.

44,515 ha (110,000 acres) have been treated, with over 12,140 ha (30,000 acres) of those treatments as prescribed fire (Figures 4, 5). This shift in focus from intensive management practices to extensive management practices created more opportunities for grassland bird conservation in line with OPJV objectives. Brush management alone has not adequately addressed the grassland conservation crisis across the southern Great Plains despite years of expensive efforts from many conservation organizations (Scholtz et al. 2021).

LESSONS LEARNED

It took >10 years of combined partner efforts to build GRIP. Many lessons have been learned along the way, including lessons regarding how to manage partnership-based, large-scale habitat incentive programs to better target location and habitat practice types. We have compiled a list of lessons learned to facilitate and guide the development of future programs that may encounter similar complexities.

Clearly identify goals of the plan and the program.

Identifying where to work and how many hectares would be needed to achieve objectives can be difficult. To identify these, we incorporated a scientific plan based on national and regional bird population objectives to create habitat goals (in hectares) needed to achieve those objectives within our focal counties (OPJV, unpublished document). Additionally, our conservation business plan tied area objectives to a plan of action which included the amount of funding needed to accomplish the conservation for that total area (OPJV 2015, Giocomo et al. 2017). The inclusion of straightforward and focused goals in both the science and business plans greatly assisted in obtaining buy-in from partners, funders, and program beneficiaries while also keeping the larger, long-term project on track. We found that buy-in works at the "speed of trust." It is a slow process that requires multiple conversations, a significant time investment, and frequent communication of program efforts and effectiveness to all partners.

We found active partner participation to be critical when designing a conservation delivery program. As with the aforementioned plans, one of the first steps in our program design was the development of straightforward and focused goals intended to keep the program on track throughout the design process and through revisions made during the lifetime of the program. Developing these goals also would help assess the overall success of the program. These goals incorporated not only habitat objectives, but also the underlying bird population objectives, the people (i.e., staff and partners) required to achieve those habitat objectives, and the placement of projects within focus areas (based on biological and partner needs). Collaborating with partners who agree on shared, concise, and consistent objectives may be difficult in practice, but we found this approach to be essential. In an effort to minimize initial workload concerns, a roles and responsibilities document for GRIP was developed, outlining the responsibilities of each partner organization and all personnel. Over time, partners may disagree on various aspects of any program. As such, creating and fostering effective conflict management is vital to the partnership and to the success of the program; the roles and responsibilities document is the primary tool for this purpose. We have also found that relying on multiple partner organizations leads to a better chance for success. We have learned that including multiple partners at every level of the program fosters the communication necessary for a partnership-based program to address issues and opportunities effectively. We left ultimate responsibility and control of the program in the hands of the Joint Venture management board, giving our main partners the final say in program direction.

Simplify. Make the process as easy as possible.

We found that the delivery program should be as simple, seamless, and transparent as possible to ensure acceptance by project managers, biologists, partners, and end-user—private landowners. Unnecessary bureaucracy creates confusion, distrust, and eventually, complacency. A program that is easy to understand and implement in a timely manner stands a greater chance of success than one that gets bogged down in unnecessary processes. For example, project managers who facilitate conservation delivery on the ground appreciate the responsiveness and short feedback times created by open enrollment and swift project reviews. This approach leads to fewer surprise outcomes and disappointed project managers and private landowners, which in turn fosters partner enthusiasm and generates constituent interest and participation. Even in the best-case scenario, not all partners and not every landowner will be or stay motivated and adjustments may be required.

Create focus areas.

More often than not, resources (e.g., staff, budget, time) are limited. As such, finding strategies to prevent the dilution of conservation actions is key to a successful program. One method that we found useful was to concentrate partner efforts in specific geographies. The creation of focus areas allowed us to concentrate resources and increase the probability of effecting meaningful change. We found that focus area selection needed to be driven by science through species-specific habitat models derived from incorporating species population and habitat objectives, while considering the location of existing, motivated partner delivery staff. We wanted to avoid working in areas with little chance of success, such as those with poor existing habitat conditions, low delivery staff capacity, or few resources. Types of resources considered include prescribed burn trailers, native seed drills, native seed availability, contractors, and presence of active landowner-led prescribed burn associations and wildlife cooperatives. We discovered that accounting for available resources helped shape specific geographies more likely to achieve habitat objectives. We also created Local Initiative Teams (LITs) for each focus area to address regional differences among practitioners and landscapes. These teams were able to direct funding toward the practices believed to be most beneficial for a specific focus area. Creating LITs also helped organize partner staff and generate excitement for the program. We wanted to avoid making the entire OPJV geography a priority, because we felt that when everything is a priority, then nothing is a priority.

Track progress at the same scale as conservation delivery.

As with any good study design, we believed that measurable objectives should be identified before program implementation and included in goal development. We developed measurable objectives and a monitoring plan that occurred at the same temporal and spatial scale as the program to quantify success and estimate project effectiveness. We believed that this monitoring plan helped increase potential partner buy-in and funder interest. Our monitoring plan included a data storage plan to avoid issues with interagency cooperation. Our data storage included a plan for management of project information that could be used to supplement the monitoring plan and may become essential for development of future research projects and reporting.

Maintain flexibility.

Listening to project managers and local landowners was essential to maintain support and grow our programs. Provided that the habitat delivery objectives are being addressed, how the practice is applied is less important than whether it is applied. We found that by allowing for flexible preferred practice delivery methods and then tailoring the program to fit those methods, we were able to improve participation by project managers. In our diverse partnership, other organizations may have programs better suited for certain practices or properties. We believe that effective conservation delivery is knowing not only your program, but also other partners' programs. Then we were able to connect private landowners to the most appropriate funding partner or source. We were constantly looking for win-win scenarios in which a private landowner meets their management objectives and the project results in more hectares of restored or enhanced habitat for wildlife species like northern bobwhite and other grassland birds.

Spend grant funding in a timely manner.

Applying for a mixture of private, corporate, state, and federal funding sources ultimately put more dollars on the ground by leveraging non-federal funds to meet funder match requirements. GRIP was able to use private funds for projects requiring a short lead time and for practices that many traditional conservation funding sources were unlikely to support, such as prescribed fire. Despite this, we found that using multiple fund sources can allow for open enrollment periods as overlapping grants can help to ensure that incentive funds are constantly available, reducing frustration among project managers and private landowners. Benefits of a program with multiple funding streams include flexibility and durability; in other words, we could choose how to pay for a given project and we could keep funds flowing through time with no breaks in availability.

Grant organizations want to see quick results for their investment. A grant recipient's failure to meet stated objectives or spend funds in allotted time frames can reduce an organization's desire to fund, or more importantly, renew program support. Conservation projects often suffer from delays in implementation due to weather and unanticipated factors. To avoid grant extensions or having to return unspent funds, we set internal deadlines well before grant expiration dates to have money tied to projects. By employing this method, we have avoided use-it-or-lose-it project selection scenarios, which if followed, often result in hastily designed, poor quality projects. We found open- or rolling-enrollment creates flexibility in choosing good projects as they are submitted and increases the likelihood of spending grant funds in a timely manner.

Invest time and money into training, equipping, and supporting private lands staff.

Positive relationships with private landowners are vital for delivering high quality projects in private-lands wildlife management. Personal relationships take time and deliberate attention to develop. Often, new employees are not from the local area and may need to learn about local conservation challenges, strengths, and opportunities. They may have very different backgrounds than their potential clients (private landowners and partner biologists) and these differences may take time and effort to overcome. Partner staff members are likely to rely on more experienced practitioners to help develop their own style and knowledge base for working with private landowners, and we found that having available

partner staff to mentor new biologists has been helpful. New conservationists need to become competent and confident, and to feel that they belong before they are likely to become top performers. Further, each person is different and is likely to require customized on-boarding and training plans. We found that it is imperative to invest significant time and energy, sometimes for ≥2 years, to help new biologists feel a sense of belonging in the partnership. Constant outreach and communication are needed, such as making sure that they are invited to all local and regional partner meetings and are provided with introductions to landowners with existing projects in the area. Ensuring that multiple partner organizations, and especially new biologists, are included in landowner visits will also foster a sense of cooperation and build consistency in project development. In the absence of mentorship or a sense of belonging in the partnership, new biologists have had a hard time flourishing.

In our case, we had staff employed by multiple organizations who worked for the partnership as a single team. This arrangement meant that they had a supervisor in one organization who had certain human resources responsibilities, and another supervisor who served as the day-to-day leader and had mentorship responsibilities. However, when all partners shared and accepted the developmental roles that they may play (especially leadership and mentorship), we saw that new team members were very successful. Because we had staff employed by several organizations serving on one OPJV team, our delivery staff positions are in itself a partnership. Leaders from the participating organizations need to be in regular and meaningful communication in order to provide appropriate feedback.

Finally, we found that conservation staff members were likely to be more effective if stationed within or close to focus areas to address local conservation objectives. However, since they were often transplants to the area, this arrangement often put them in unfamiliar areas or rural areas that may have made them feel like being on an island. We believe these situations are where the strength of partnership becomes invaluable. Partners can help connect new employees to other conservation practitioners across organizations and agencies within their area. We found that when partners facilitated the establishment of connections for new employees, these networks would in turn connect new employees to private landowners and community leaders who have a history of being early adopters of programs and who are trusted for the conservation choices they make. This strategic and collaborative approach can greatly accelerate program effectiveness.

Don't try to micromanage for a hidden agenda.

As conservation professionals, we viewed it as our job to be an advocate for the resource(s) (e.g., grassland birds, northern bobwhite, grassland habitat) first, and for the private landowners second. We recognized that it was often too easy to start pushing programs because of deadlines, hectare goals, and expiring grant funds, or providing only what the landowner asked for without proper regard for the resource objectives. We can easily become narrowly focused about what programs our particular organization offers, as opposed to all opportunities, resources, and programs available in certain areas for the best management and conservation of a species or habitat type. The lesson here is to be diligent about achieving program objectives.

Working together across organizations, as well as within, opens many avenues for partnerships, collaboration, interagency trainings, and overall increased success with directed species and habitat conservation. In a partnership, we find it vital to be honest and transparent about partnership activities, to be open to sharing information and resources with partners, and to operate within the predetermined shared objectives of the overall mission. In the case of a sizable program such as GRIP, it is unlikely that our core OPJV team will ever be able to effectively work with all interested private landowners, or achieve the necessary landscape-level objectives by ourselves. We must rely on the power of the partnership and transparent communication to meet our broad objectives effectively and efficiently.

Don't ignore the social aspects of a successful program.

As mentioned earlier, our OPJV partners and landowners worked at the "speed of trust," which is slow to build and easily lost. We found that building trust within a local community took about 1–2 years for driven biologists. Using proven methods of spending time in the field with both experienced partner biologists and respected landowners is an important first step for new staff to gain confidence. We think that partners that have invested time and resources to develop and nurture both landowner leaders and confident field-level biologist mentors will observe greater dividends when new staff members are learning how to effectively deliver programs and conservation concepts.

Once a biologist knocks on enough doors, sits at enough kitchen tables, and becomes a regular at the local café, the demand for the biologist's technical assistance and program financial assistance can be expected to eventually reach a desired level. In addition, there is evidence to suggest that Texas landowners and land managers are more likely to participate in conservation programs that maximize cost-share (≥50%) and minimize labor inputs (≤30 days/year) and that certain types of landowners may be reached through strategic marketing and communication efforts (Valdez et al. 2019). Reaching out to and supporting local landowner cooperatives may be important since this may be where information is locally exchanged and new ideas potentially embraced. Once neighbors begin to see positive impacts in the fields and pastures of trusted early adopters, program acceptance and use often accelerate. The OPJV has worked diligently to encourage early adopters among private lands biologists and private landowners, and publicly recognize efforts when possible.

MANAGEMENT IMPLICATIONS

The partners of the Oaks and Prairies Joint Venture have worked at implementing the tiered-delivery vision of the National Bobwhite Conservation Initiative's Coordinated Implementation Program for the past decade. We feel our efforts are starting to pay off, but there is much work remaining to be done. We made some mistakes and tried to incorporate the lessons that we learned into successive iterations of our conservation delivery programs. The Grassland Restoration Incentive Program concept has been adopted in at least 3 other Migratory Bird Habitat Joint Ventures across the Great Plains, and most are within the existing northern bobwhite range. As efforts ramp up to address grassland bird population losses, we hope that some of the lessons we have learned will help others set up additional successful regional programs.

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RESULTS FROM KENTUCKY'S 10-YEAR BOBWHITE RECOVERY PLAN

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ABSTRACT

The northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) has experienced a precipitous population decline through almost all its historical range over the last 6 decades. We initiated a 10-year restoration plan in Kentucky, USA in 2008 and reported on it through 3 published "Road to Recovery" reports along with 30 peer-reviewed articles and abstracts, 2 technical documents, 7 theses or dissertations, and 11 popular literature pieces. Seven Quail Focus Areas were selected across the state based on site personnel, geographic position (east to west), and land ownership (e.g., private, public, state, federal) for monitoring and habitat management. The focus areas averaged 11,895 acres and area managed for quail on an annual basis ranged from 9% to 42%. Management took the form of herbicide applications, disking, fire, planting, grazing, control of woody vegetation, and mowing. Hierarchical distance sampling models using time-of-removal information to inform detection processes were used to assess bobwhite density on each focus area. Models were based on spring breeding bird point counts in which a suite of grassland songbirds were recorded and fall covey counts in which only bobwhite were recorded. Roadside surveys (direct observation) and hunter harvest information were also used for statewide comparisons of focus areas and statewide trends. Across all years and focus areas a 40% increase in the quail population was observed in 20 years (38%) of the possible 53 years of survey data. Stable to increasing trends were also observed in focal area populations of dickcissel (*Spiza americana*), eastern meadowlark (*Sturnella magna*), eastern kingbird (*Tyrannus tyrannus*), field sparrow (*Spizella pusilla*), prairie warbler (*Setophaga discolor*), and Bell's vireo (*Vireo bellii*). A focus on habitat management and associated monitoring on relatively small (<20,000 acres) areas was shown to be successful on an individual area, as determined by increases in bird numbers across years and challenges completed in the Quail Plan but did not result in an observed increase in statewide quail indices. Future quail restoration plans in Kentucky should be directed more toward open production land, which is made up of 6 million acres of pastureland, hay land, row crop agriculture, reverting fields, reclaimed mineland, and grasslands. This work will be completed by utilizing working lands, such as field borders in row crop systems and grazing native warm-season grasses in pasture or hay systems, for wildlife activities. Monitoring systems on these production lands will be in the breeding season only and autonomous recording devices will be used in lieu of human observers to cover the greater area of open landscape.

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Key words: *Colinus virginianus,* focus area, Kentucky, northern bobwhite, plan, point count, quail, Road to Recovery, southeast, survey

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A BIRD MONITORING PROGRAM TO EVALUATE THE EFFECTIVENESS OF THE COASTAL GRASSLAND RESTORATION INCENTIVE PROGRAM

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ABSTRACT

The Gulf Coast Joint Venture (GCJV) is a regionally based, biologically driven, landscape-oriented volunteer partnership of private, state, and federal conservation organizations dedicated to the delivery of habitat important to priority bird species. The GCJV partnership's Coastal Grassland Restoration Incentive Program (C-GRIP) provides financial incentives to private landowners for conducting habitat treatments that address the greatest limiting factor(s) to providing suitable grassland bird habitat on their property. The C-GRIP program is a way for the GCJV to deliver bird habitat to meet planning objectives for grassland birds, including northern bobwhite (*Colinus virginianus*). Our monitoring objective is to evaluate whether the C-GRIP program is effective in providing a relative increase in the density (number/acre) of priority grassland bird species in focal delivery areas versus control areas over a 10-year period. Twenty survey routes (2 within each of 5 focal areas and 2 outside of each area, serving as controls), located on secondary and tertiary roads, were designated in the Texas Mid-Coast Initiative Area of the GCJV. Each route is 15 miles long and the land cover is similar along all survey routes. Each route has ≥30 point-count stations separated by ≥0.5 mile. We recognize that some routes will experience increased development over time, especially in counties neighboring large population centers such as Houston and Victoria. The plan is to continue to monitor these routes, as long as safety concerns do not increase. Survey data will be analyzed using Program Distance 7.3, release 1. Our poster will include details about the monitoring objective, survey route selection, and survey methods.

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Key words: *Colinus virginianus*, density, distance sampling, Gulf Coast Joint Venture, habitat delivery, monitoring, northern bobwhite

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NEST HATCH CHRONOLOGY OF NORTHERN BOBWHITE IN MISSOURI AND IMPLICATIONS FOR MANAGEMENT

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ABSTRACT

Managers in Missouri, USA, and in other Midwestern states have long operated under the belief that the peak of nest hatching for northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) is 15 June. Though it is widely understood that bobwhite nests hatch throughout the summer, many management decisions are made based on the accepted peak. Fully understanding the dynamics behind bobwhite nest timing is critical, as management activities in nesting cover during summer are common. To better understand nest chronology, we used radio-telemetry to monitor nest incubation initiation, hatch date, and renesting rate on 6 conservation areas in southwestern Missouri from 2014 to 2018. Nest hatch date varied by area and year, but only 8.5% of nests hatched on or before 15 June. The 7-day interval during which the most nests hatched was 15–21 June, but we also saw high numbers of nests hatch in early July and mid- to late August. The median hatch date across all 5 years of the study was 17 July. Our results suggest that the entire summer is critical for bobwhite nesting activities, with late summer being just as important as the early summer months. We encourage bobwhite managers and conservation program policymakers across the Midwest to rethink previously held constructs of bobwhite nest timing. We also recommend that summer disturbances to nesting cover be kept to a minimum when the goal is to maximize bobwhite reproductive output.

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Key words: *Colinus virginianus*, incubation, Missouri, nest timing, northern bobwhite, renesting

Reproductive ecology of northern bobwhite (*Colinus virginianus*; hereafter, bobwhite), including dates of peak nest hatch, has historically been used to inform habitat management activities (Stanford 1972, Klimstra and Roseberry 1975, Burger et al. 1995). For instance, researchers often recommend delaying summertime management activities such as hay harvest and routine mowing until after some defined peak of hatch. Government programs such as the Conservation Reserve Program administered by the U.S. Department of Agriculture also have rules prohibiting certain field disturbance practices until after the primary nesting season (PNS). However, nesting chronology, including peak hatch date, varies across the country and even among years (Stanford 1972). Research shows hatching occurs throughout the summer, with some nesting effort into September and October in places. Simpson (1972) found 2 peaks of nest initiation in Georgia, USA, as did Dimmick (1971) in Tennessee, USA. In northern Missouri, USA, mean incubation dates varied from 14 June for female incubated first nests to 15 July for male incubated first nests and incubation initiation occurred throughout the summer (Burger et al. 1995). Mean nest initiation dates for bobwhite in western Oklahoma, USA were 30 April for first nests and 17 July for second nests (Cox et al. 2005). Klimstra and Roseberry (1975) reported a mean hatch date for 213 nests in southern Illinois, USA, of 21 July and found "an essentially unfirm distribution" of hatches from 17 June through 18 August. Stanford (1972) used roadside observation of broods from June through August to demonstrate a peak hatch of 15 June, by which 27% of the annual production occurred in favorable weather years. He also noted that 64% of annual production in those years occurred before 15 July. He described these figures as Missouri's average production pattern. In years with higher-than-normal rainfall during the early nesting season, the average peak occurred 2 weeks later than during normal

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years. Additionally, Murray (1948) reported that 70% of nests on 2 central Missouri study sites hatched in May and June based on estimates of age from brood observations, though he noted that the hatch was likely earlier than normal due to a warm spring.

The historical Missouri research, especially the 15 June hatch peak, became the standard in Missouri for making management recommendations to landowners about summertime field activities. This hatch peak date is commonly provided in publications including the Missouri Natural Events calendar and other landowner management publications. Public land managers have used this date when making plans for haying, mowing, and prescribed burning. Policymakers with the U.S. Department of Agriculture's Farm Services Agency (FSA) have defined a primary nesting season of 1 May–15 July, during which certain management activities on Conservation Reserve Program (CRP) lands are not allowed. The idea is to restrict field activities during the period when most nesting and brood rearing of grassland bird species occurs. Field management is allowed outside of these dates, including the balance of the summer months.

Data obtained from wings of harvested bobwhites from the Robert E. Talbot Conservation Area in southwestern Missouri during 2006–2011 showed that few birds were hatched before 15 June (Loncarich, unpublished data). In fact, in some years no wings were collected from birds hatched before 15 June. This finding held significant implications for bobwhite habitat management on the area as field activities in the summer were long based on the 15 June hatch peak. As a result, there was potential that nests and vulnerable broods were disturbed by management that was occurring in late June–July.

As a part of a larger study on reproductive ecology of bobwhite in southwestern Missouri, we sought to use radio-marked individuals to determine hatching chronology across 6 study sites in southwestern Missouri. Bobwhite management is often the top priority for many landowners and certain public land areas, and it is critical to determine how nesting effort is spread out through the summer and to use that information to define better prescriptions for summertime management activities.

STUDY AREA

We tracked bobwhites on 6 publicly owned Conservation Areas (CAs) in southwestern Missouri: Robert E. Talbot CA in Lawrence County (1,764 ha), Bois D'Arc CA in Greene County (1,284 ha), Shawnee Trail CA in Barton County (1,471 ha), Wade and June Shelton Memorial CA (130 ha) and Stony Point Prairie CA in Dade County (516 ha), and Wah'Kon-Tah Prairie (WKCA) in St. Clair County (1,226 ha). Shawnee Trail CA and Bois D'Arc CA are composed of a mixture of native warm-season grass and forb plantings, grain crop fields and food plots, and old fields that consist of a mixture of early successional vegetation with scattered woody cover in the form of mature fencerows, shrub plantings, and brush-covered fields. Robert E. Talbot CA is similarly composed but has a significant open woodland and closed-canopy hardwood component. Wah'Kon-Tah, Shawnee Trail, and Stony Point Prairie conservation areas are remnant tallgrass prairies that contain scattered low-growing woody vegetation and areas of larger trees found in deep drainages.

METHODS

We trapped bobwhites in February–March with walk-in type funnel traps baited with corn and milo (Stoddard 1931). We sexed, aged, banded, and fitted trapped bobwhites with an approximately 4 g necklace-style transmitter with a live or dead sensor (American Wildlife Enterprises, Monticello, FL, USA). All birds were released at the capture site. Tracking began within 2 days of release and birds were located via homing ≥3 days/week beginning in May. We made every attempt to not flush the birds during tracking.

When a bird was found with a live signal in the same location >2 detections in a row, we assumed the bird was incubating. When incubating birds were detected off the nest, we would visually locate the nest and determine clutch size and nest condition. We tracked all incubating birds a minimum of 5 days/week until nests successfully hatched, were depredated, or were abandoned. Nests were classified as successful when ≥1 eggshells showed evidence of pipping. Depredated nests were classified by the presence of strewn and crushed shell fragments and obvious disturbance of the nest bowl. Nests were classified as abandoned if the incubating individual did not return to the nest after 5 consecutive days.

We categorized all nests hatched into 7-day intervals from 1 June through 5 October and plotted these through time to determine distribution. We had no nests hatch prior to 1 June or after 5 October. For this study we included only hatched nests for our nest timing analysis. Because technicians did not track all non-incubating birds on a site on a daily basis early in the nesting season and because no birds were tracked on weekends, we could not identify the exact date of incubation onset, and by extension, estimated hatch dates for unsuccessful nests. Therefore, unsuccessful nests were excluded from analysis.

RESULTS

We recorded 176 successfully hatched nests over 5 years. Only 10 nests, or 5.6% of the total, were hatched before 15 June (Table 1). We recorded 5 hatches on 15 June and when they were added to the 10 nests hatched prior to 15 June, the total represents 8.5% of all nests hatched. The busiest 7-day interval for hatching was 15 June–21 June when 23, or 13% of all nests, were hatched. Hatching remained steady through 12 July, by which time 48.7% of nests had hatched, and hatching tailed off during mid- to late July (Figure 1). A second peak of hatching occurred 27 July–6 September, when 38.5% of nests hatched. Hatching activity dramatically declined later in the summer, with only 16 nests hatching after 1 September.

Table 1. Number of nests hatched and percentage of total hatch for each 7-day interval for northern bobwhite (*Colinus virginianus*) in Missouri, USA, 2014–2018.

7-day Interval	Number of nests	Percentage of total nests hatched
1–7 Jun	2	1.1
8–14 Jun	8	4.5
15–21 Jun	23	13.0
22–28 Jun	15	10.2
29 Jun–5 Jul	14	8.5
6–12 Jul	20	11.4
13–19 Jul	8	4.5
20–26 Jul	7	4.0
27 Jul–2 Aug	16	9.0
3–9 Aug	8	4.5
10–16 Aug	9	5.1
17–23 Aug	17	9.7
24–30 Aug	10	5.7
31 Aug–6 Sep	8	4.5
7–13 Sep	2	1.1
14–20 Sep	6	3.4
21–27 Sep	1	0.60
28 Sep–4 Oct	2	1.1

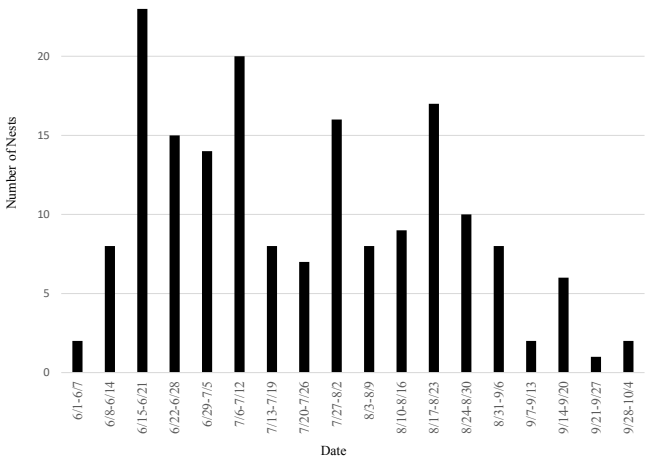

Fig. 1. Nest hatch chronology for northern bobwhite (*Colinus virginianus*) in Missouri, USA, across all study sites pooled from 2014 through 2018.

Hatching chronology was also plotted by Julian date to provide a better representation of distribution of hatching across years (Figure 2). Median hatch date for our study based on Julian date was 17 July.

DISCUSSION

Our results showed 2 peaks of hatching activity (Table 1). However, the entire summer period was important for hatching, as shown by the median Julian date of hatch. Like Stanford (1972), we found significant bobwhite nest hatching in June. However, the percentage hatched on or before 15 June

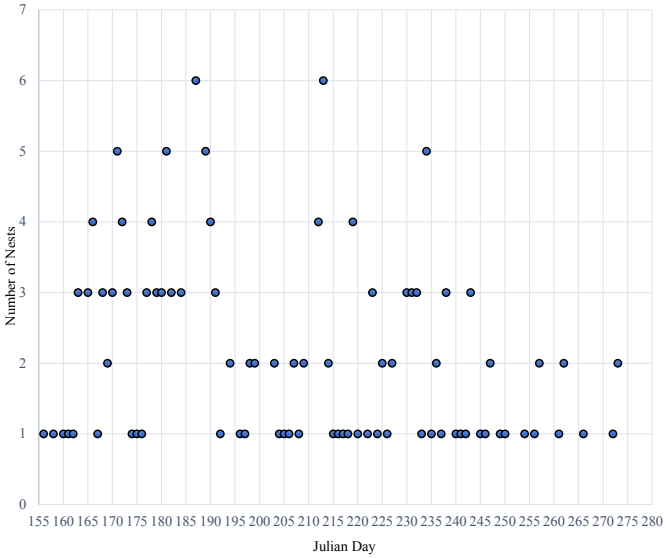

Fig. 2. Julian date nest hatch chronology for northern bobwhite (*Colinus virginianus*) in Missouri, USA, across all study sites pooled from 2014 through 2018.

in our study was only 8.5%, compared to Stanford's 27%. Additionally, Stanford's finding of 64% of nests hatching prior to mid-July is counter to our results. The hatching rate for May and June from our study is even more disparate from Murray (1948) as we had no nests hatch in May. Our results matched closely those of Klimstra and Roseberry (1975), who found similar peaks of hatching and a mean hatch date of 21 July. However, the distribution of hatching in their study was more uniform throughout the summer than ours.

Stanford's (1972) determination of the June peak of hatching relied on roadside observations of broods by field agents during their routine activities. These agents estimated the age of broods based on body size, and variation among observers relative to estimating brood age likely existed. Whether the bias resulted in an overestimation of age for observed broods is unknown. Stanford's determination of the full nest hatching chronology also included examination of primary feather replacement on hunter-harvested wings. From these data he defined a second peak of hatching of around 15 August. The estimated date of hatch based on hunter-harvested wings data may have been a better estimate of true hatch date than the roadside observations as they more closely align with other published estimates of hatch dates and our radio-collared bird findings. However, Klimstra and Roseberry (1975) found that backdating wings underestimated the percentage of birds harvested after 29 July by nearly 16%, thus possibly overestimating the amount of early hatched clutches. Whatever the case, estimation of peak hatch date based on backdating wings and estimates from roadside observations of broods are less reliable than radio-telemetry or other nest observation studies.

While our data differ from the widely cited and applied historical Missouri data, the emphasis should not be on

whether our data concur. Methods of determining nest hatch were vastly different among the studies and may not be directly comparable. The extent to which climate differences between the mid-1900s and our study resulted in the disparate findings is unknown, but it is doubtful that climate change could explain the wide disparity in results. Whatever the cause, the differences are less important than our finding that the entire summer period is critical for nesting bobwhites. While hatch date was our focus, it is important to remember that the date of hatch is merely the culmination of a nesting season that can take up to 55 days (Rosene 1969). A nest hatched on 1 July was initiated in mid-May and a nest that hatched on 15 Sept was initiated in early August. The entire late spring through late summer is of critical importance to nesting bobwhites.

MANAGEMENT IMPLICATIONS

The historical emphasis on the 15 June peak of hatch date in Missouri, whether to make local habitat management decisions or statewide policies, has been misplaced. The inference has been that after 15 June, or after 15 July in the case of Conservation Reserve Program policy, field management can occur without fear of harming most nests or vulnerable broods. Our data, however, show that bobwhite nest in significant numbers throughout the summer. Even if most nests were hatched on or before 15 July, vulnerable broods would still be threatened by large-scale disturbances such as prescribed fire, mowing, haying, and heavy disking for at least 2 weeks after hatch (Rosene 1969). We recommend that management activities which will cause disturbance to nesting habitat occur prior to 1 May, before most nests are initiated, or after 15 September, when most nests are hatched, if the primary goal is bobwhite management. This will not only protect nests, but also minimize management-related disturbance of vulnerable chicks due to direct mortality or displacement.

We also urge the U.S. Department of Agriculture's Farm Service Agency in Missouri and nearby states with a similar bobwhite nesting chronology to reevaluate the primary nesting season or allowable management therein. The number of active nests and vulnerable broods on the landscape after 15 July is significant and heavy disturbance of nesting cover in late July and August could cause unacceptable losses of nests and broods. This may be especially evident where native grass CRP fields represent most of the available nesting cover in a local area.

Delaying management until mid-September will require tradeoffs. Mowing native warm-season grass hay in late summer will result in lower protein content in the hay but is likely to produce more tons of hay per acre. Prescribed fire is essential for managing bobwhite habitat throughout much of the species' range. Fire can temporarily reduce plant density and increase bare ground, control woody plant succession, and increase forbs (Engle and Bidwell 2001), and we encourage expansion of prescribed fire. Many managers implement prescribed fire in the summer to reduce woody encroachment and increase forbs. However, Weir and Scasta (2017) found that prescribed fire in July and August increased woody plant cover in tallgrass prairie whereas September and October fires reduced woody plant cover. They also found that burning in September and October resulted in a greater forb response than July and August burns. Forbs are critical for insect attraction and seed production for bobwhite food. If disturbance must occur during the summer months, we encourage managers to disturb one-third or less of local nesting habitat and focus on the most successionally advanced cover to reduce the chance of encountering nests and vulnerable broods (Sinnot et al. 2021).

There is some argument that disturbance which causes nest loss early in the season can be mitigated by the bobwhite's propensity to renest. While renesting does occur, we found that only 13% of birds in our study renested after a first nest was destroyed (Loncarich and Hedges, unpublished data). Therefore, the success of first nests is vital, and it is important to reduce habitat management activities during May through September in areas where the potential for bobwhite nests is high.

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HOME RANGE AND SPACE USE OF NORTHERN BOBWHITE UNDER TWO DIFFERENT MANAGEMENT MODELS IN SOUTHWESTERN MISSOURI

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ABSTRACT

Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) management in Missouri, USA has traditionally been focused on providing an interspersion of grass, crop, old field, and woody cover juxtaposed to disked idle areas and food plots to maintain bobwhite populations. This traditional model is implemented with the goal of providing all essential habitat components within 40-acre blocks throughout a larger area used by a population. While this model can produce usable bobwhite space in agriculture-dominated landscapes, it may not be the most effective or efficient approach to producing and maintaining bobwhite in grassland-dominated landscapes. In southwestern Missouri native tallgrass prairie conservation areas are managed primarily with historical ecological processes, such as fire and grazing, to produce the desired patchy habitat mosaic. Additionally, it has been on these native tallgrass prairie conservation areas that managers have seen the most stable and productive bobwhite populations. Over a 5-year period (2014–2018) we quantified movements of northern bobwhite on 3 traditionally managed areas (n = 185) and on 3 managed native tallgrass prairie conservation areas (n = 211) to determine whether home range sizes and space use differed between these two management models. We used the 6-month (Apr–Sep) breeding period to determine core area, home range, mean movement rate, and maximum distance moved. Overall (pooled) home ranges of bobwhite did not differ significantly between traditional and grassland managed areas; however, there were significant yearly differences between management models and study areas. Males generally had larger home range sizes and had higher movement rates than females. For the 5 years of the study few birds made long-distance movements (>1.6 km; 3%), and all remained relatively close to capture locations in winter (Feb–Mar). For both traditional and grassland managed areas, bobwhite selected for areas that had disturbance (fire and grazing) in the last 2 years and for the native grassland vegetation type. These findings suggest that areas managed under the grassland management model provide preferred habitat for bobwhite and could result in significant improvement in habitat quality for tallgrass prairie wildlife.

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Key words: burning, *Colinus virginianus*, grazing, habitat management, home range, northern bobwhite, southwestern Missouri, space use

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BREEDING SEASON SURVIVAL AND REPRODUCTION IN A HIGH-DENSITY BOBWHITE POPULATION: A CASE STUDY

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ABSTRACT

The demographic behavior of northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) populations at high densities could provide important insights into why bobwhite populations fluctuate. Therefore, we documented breeding season demographics of bobwhites to understand how prebreeding density influenced reproductive effort and postbreeding density on an intensively managed property in Leon County, Florida, USA, 2002–2006. We estimated prebreeding bobwhite density each April using multi-observer strip-transects and postbreeding densities each November using covey call grid surveys. We radio-tagged 217 bobwhites in March and located bobwhites at least 5 days/week, 15 April–30 September to determine vital rates. Prebreeding density ranged from 1.5–8.6 birds/ha, peaking in 2002, declining through 2005, then increasing in 2006. Breeding season survival was 0.55, 0.17, 0.20, and 0.59, and nesting rate was 0.47, 0.67, 0.80 and 0.89, 2002–2005, respectively. Postbreeding density ranged from 5.2–13.6 birds/ha, also peaking in 2002 and declining through 2004 before increasing beginning in 2005 and 2006. High breeding season survival and nesting success (>0.55) resulted in greater chick production during periods of population growth. Nesting rate was inversely related to prebreeding density. Declines in bobwhite nesting rate at high prebreeding densities appeared to regulate population growth near population peaks. Lower adult survival and nesting success appeared to cause population declines. We suggest density-dependent intraspecific competition limited population growth at high bobwhite densities by reducing nesting rate while predation of adults and nests explained population fluctuations.

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Key words: *Colinus virginianus*, demographics, density, nesting, northern bobwhite, population, quail, reproduction, survival

Modern management of northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) on some private lands in the southeastern United States sustains bobwhite populations at relatively high densities (Palmer and Sisson 2017), but population fluctuations remain common. Intensive management (Palmer and Sisson 2017) to reduce the effect of limiting factors and infrequent episodes of severe weather provides for population stability and the opportunity to sustain high densities. On managed lands in the Red Hills and Albany regions of northern Florida, USA and Southwest Georgia, USA, bobwhite populations are commonly sustained at >3 quail/ha because managers apply techniques that reduce limiting factors (Palmer and Sisson 2017, Terhune et al. 2017). Management actions, such as habitat management, predation management, and supplemental feeding, collectively moderate density-dependent and -independent factors that limit population growth. Under these management scenarios bobwhite populations may reach postbreeding densities of 8–12 quail/ha (Kellogg et al. 1972; Dimmick et al. 1982; Palmer and Sisson, unpublished data). These high densities may last ≥2 years before moderating to more typical densities of 3–6 quail/ha. This raises the question of why we do not see even higher densities (i.e., population growth peaks) if management provides abundant usable space, low predation pressure, and abundant food resources. Further, can managers influence factors responsible for the observed negative density dependence to maintain populations at high densities for longer?

High densities are observed on managed quail ranches in the southwestern United States during periods of adequate rainfall and moderate temperatures (Lehman 1984). Declines in populations following peaks are attributed to recurring

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drought cycles and extreme heat (Lehman 1984, Guthery et al. 1988, Hernández et al. 2005). In the southwestern portion of the bobwhite's range, severe droughts impact quail recruitment, providing a clear explanation for bobwhite population declines. However, elsewhere in the bobwhite range, populations fluctuate because of a combination of density-independent and -dependent factors (Stoddard 1931, McConnell et al. 2018). Adult survival and recruitment are both important to explaining bobwhite population dynamics (Roseberry and Klimstra 1979, Sandercock et al. 2008, Demaso et al. 2013, McConnell et al. 2018). For declining populations, survival explained more variation in population growth than recruitment (Sandercock et al. 2008), and for stable populations recruitment was more important than survival, although both were important (McConnell et al. 2018). These studies examined long-term datasets, but no studies have monitored prebreeding and postbreeding densities along with breeding season demographics in an effort to determine which parameters were sensitive to bobwhite density and the mechanisms that limit postbreeding populations.

We investigated demographic rates associated with bobwhite populations at or near peak densities (i.e., carrying capacity) and what demographic rates explained declines from peak densities. We estimated prebreeding and postbreeding population density of bobwhites on an intensively managed quail property and breeding season survival, nesting rate, clutch size, and nesting success to determine how these variables related to prebreeding densities. Further, we provide a broader regional perspective from 19 sites in which we had postbreeding densities and nesting data to explore the relationships we found from our main study site. Though this study is observational, we believe it provides the first demographic-based evidence of intraspecific competition that could be further explored through research. Our results and subsequent findings could be expected to improve population modeling efforts.

STUDY AREA

We studied bobwhite population dynamics on a 380-ha portion of a 3,300-ha private quail hunting property in the Red Hills region of Leon County, Florida, USA, 2002–2006. The property was primarily composed (>95%) of pine (*Pinus* spp.) savanna, frequently burned with a stocking density <12 m^2 of basal area and with <5% fields and no hardwood drains or hammocks. Approximately 60% of the property was burned each year of the study with the 40% unburned portion distributed in small 5- to 10-ha patches of cover. We mapped the unburned habitat patches using hand-held geographic positioning units (Trimble Geospatial, Inc., Sunnyvale, CA, USA) each year of the study. The groundcover comprised a mixture of grasses, forbs, and shrubs typical of post-agriculture successional "old field" vegetation in the Red Hills region (Carr et al. 2010). Collectively, prescribed fire and mechanical treatments were used to maintain groundcover vegetation with suitable composition and structure for bobwhites while also facilitating hunting access. Supplemental feeding occurred year-round on the property by spreading >174 L/ha/yr (~2 bushels/acre) of sorghum or corn (or both) broadcast into bobwhite habitat along roads or dedicated feeding trails (or both) spread evenly throughout the property. Mesomammal nest predators were reduced using live-traps throughout the year and periodically using leg-hold trapping methods during the furbearer trapping season. The property was divided into half-day hunting courses. Our study area covered 2 hunting courses. Hunting pressure was relatively low with each course hunted no more than 5 times/season. Harvest rates were <10% of the estimated fall population. The management and hunting staff recorded the number of unique coveys flushed per day of hunting throughout the study.

METHODS

We determined spring densities of bobwhites on the study area each April by conducting multi-observer transect flush counts (Dimmick et al. 1982). We used 12–15 observers walking parallel to one another along 8 randomly selected transect lines bisecting the study area. Observers were spaced approximately every 3 meters and remained parallel while walking the transects. Observers at each end of the line geo-referenced the transect boundaries using global position units to estimate actual area flushed. We set the number of transects to achieve a minimum sampling intensity of 15% coverage of the study area. When quail were flushed, the total observed was recorded and their destination was noted to avoid double counting.

We determined the likelihood of flushing a bobwhite from radio-tagged quail on the study area during the survey. An independent observer monitored the location and movements of radio-tagged bobwhites within the transect area and recorded whether a radio-tagged bobwhite was observed or not. Detectability was calculated by dividing the total number of observed radio-tagged bobwhites by the total number of radio-tagged bobwhites within the transect during the surveys.

To estimate prebreeding density, we first calculated a naïve estimate of density of bobwhite in burned and unburned patches by dividing the number of bobwhite flushed in burned and unburned areas by the area of burned and unburned surveyed, respectively. This naïve estimate was adjusted by dividing it by our estimate of detectability to calculate burned and unburned habitat-specific densities. Habitat-specific densities were then multiplied by area of burned and unburned habitat on the study area to determine an overall estimate of bobwhite population size and density of bobwhite on the study area.

We estimated postbreeding autumn densities each October and November by counting coveys during early-morning covey call counts on 6 12.1-ha grids randomly placed on the study area (Wellendorf et al. 2004, Wellendorf and Palmer 2005) or an approximately 20% sampling intensity. We used smaller than normal 24.3-ha grids to aid in identifying individual coveys. At each grid, 4 observers stationed at the

mid-point of each side recorded the time and location of each calling covey inside the grid during peak calling times, which occurred approximately 15–25 minutes before sunrise. Once locations of coveys were identified, coveys within the grid were flushed with the assistance of bird dogs to determine an average covey size. We used estimated calling rates, covey counts, and average covey size to determine postbreeding densities following Wellendorf et al. (2004).

We radio-tagged quail on the study area during March using 5.5 g necklace-style transmitters with 12-month battery life (American Wildlife Enterprises, Monticello, FL, USA) to determine breeding season demographics. We located bobwhites 5 days/week during the breeding season to determine breeding season survival, nesting, clutch size, and nesting success. Bobwhites that survived until 15 April of each year were considered the "breeding population" and radio-tagged bobwhites alive at this point were used to determine the per capita nesting and brood rearing estimates for each year. To remove the effects of survival rate on per capita nesting, nesting rate was determined as the proportion of hens that survived the nesting season to incubate at least one nest. We estimated breeding season survival (15 Apr–30 Sep) using the Kaplan-Meier staggered entry method (Pollock et al. 1989).

Each October of the study, we conducted a mesomammal scent station survey to estimate the nest predator activity and abundance on the property (Jackson et al. 2018). We randomly placed 15 scent stations along the roads system throughout the property. Scent stations were monitored for 3 consecutive days and total number of mesomammal nest predators observed divided by 45 station-days was used to assess predator activity. A predator index <0.15 indicates that predators are not likely to significantly reduce nesting success on similarly managed properties (Jackson et al. 2018).

Regional Nesting and Density Study

We monitored bobwhite population density and reproductive effort on 19 properties where bobwhites were being radio-tracked from 1998 to 2020. Eighteen of these sites were private quail hunting properties located within the Albany, Georgia to Tallahassee, Florida region and as such were managed similarly to our primary study area. Each site was monitored between 1 and 5 years. Management intensity varied across sites. Primary differences were that some sites had greater pine basal area, others had more hardwood basal area, and some did not conduct predator management. However, all were specifically managed for bobwhite and as such had sustainable quail populations. These properties provided a range of bobwhite densities from which to assess the relationship of density and bobwhite nesting activity.

Depending on the size of the study site (100–2,000 ha) we conducted 1–12 covey call grids/site to provide an estimate of bobwhite postbreeding density. Covey call grids were conducted during October and November each year using similar methods as for our focal area. We grouped each site and year combination into 3 categories: those with fall densities <3.7 quail/ha, those with 3.7–6.2 quail/ha, and those with >6.2 quail/ha to represent low, medium, and high bobwhite densities. These densities correspond to below-average to average, above average, and well above average bobwhite densities for intensively managed properties in this region.

We considered each site and year combination as independent for our analyses. We justify independence of site and year combinations as annual changes to predator abundance, weather, and alternative prey-base that influence bobwhite populations independently from year to year on our study areas (Ellis-Felege et al. 2012, Palmer et al. 2019). We graphed the relationship between bobwhite density and nests per hen determined from a radio-tagged sample to examine the relationship between bobwhite abundance and per capita nesting. Significance of the differences was tested using a basic ANOVA.

RESULTS

Prebreeding and Postbreeding Density

We counted 737, 356, 198, 99, and 113 bobwhites during flush counts, April 2002–2006, respectively. Forty-four radio-tagged individuals were within transects during flush counts, of which 39 (89%) were observed, one held and was not flushed, and 2 moved out of the survey path before we encountered them. Prebreeding densities peaked in 2002 at 8.6 quail/ha and then declined to 7.1 quail/ha in 2003, 3.7 quail/ha in 2004, and 1.5 quail/ha in 2005 before increasing to 2.7 quail/ha in 2006.

Postbreeding densities were highest in 2002 at 13.6 quail/ha, then declined to 6.2 quail/ha in 2003 and 5.4 quail/ha in 2004. Postbreeding densities then increased to 6.9 quail/ha in 2005 and increased again to 10.3 quail/ha in 2006. Hunting success was highly correlated to bobwhite densities ($r = 0.92$, $P = 0.02$) with an average of 64 coveys seen per day in 2002, declining to 26 coveys/day in 2005, and increasing to 42 coveys/day in 2006.

Nest Predator Index

The predator index was highest in 2002 at 13.8%. The predator index ranged between 5% and 8.4% from 2003 to 2006. The relative abundance of predators was approximately equally distributed among raccoons (*Procyon lotor*), Virginia opossum (*Didelphis virginiana*), nine-banded armadillos (*Dasypus novemcinctus*), and bobcats (*Lynx rufus*).

Breeding Season Demographics

We radio-tagged 217 bobwhites between 2002 and 2005 to determine breeding season demographics (Table 1). A total of 181 bobwhites (144 females) were utilized to develop breeding season statistics. Survival was highest in 2002 and 2006 and was significantly lower in 2003 and 2004. This resulted in lower nests per hen in 2003 and 2004. Nevertheless, nesting rate for surviving hens was greatest in

Table 1. Breeding season demographics for radio-tagged northern bobwhites (*Colinus virginianus*; *n* = 144) on an intensively managed quail hunting property, Leon County, Florida, USA, 2002–2005.

Year	n	Number of hens	Number of nests	Nesting rate[a]	Nests per hen	Number of renesters[b]	Nesting success	Clutch size	Survival rate
2002	39	31	18	0.47	0.58	3	0.61	13.8	0.55
2003	45	32	11	0.67	0.34	0	0.36	13.7	0.20
2004	46	42	17	0.80	0.40	1	0.7	13.1	0.17
2005	51	39	34	0.89	0.87	10	0.51	13.1	0.59

[a] Number of hens that survived 14 April–15 September to incubate at least one nest.
[b] Number of hens to incubate more than one nest.

2004 and 2005 and corresponds to the lower observed spring densities. Conversely, nesting rate was lowest in 2002 and 2003 when prebreeding densities were >7 quail/ha (Figure 1). Clutch size was consistent across all years. Nesting success was lowest in 2003, but we had a low sample size during that year due to low survival; otherwise nest success was >0.50. We observed the highest level of double clutching in 2005 when prebreeding density was lowest (Table 1).

Regional Nesting and Density

We had 50 site and year combinations for which we had monitored an adequate radio-tagged sample of hens to assess nesting activity and also obtained an estimate of postbreeding densities. Of the 50 site and year combinations, 24, 17, and 9 were in the low, medium, and high quail density categories, respectively. Nests per hen was related to density and averaged 0.77 (standard error [SE] = 0.049), 0.85 (SE = 0.071) and 0.61 (SE = 0.066) for the low, medium, and high quail density categories ($F_{2,47} = 2.61$, P = 0.08; Figure 2).

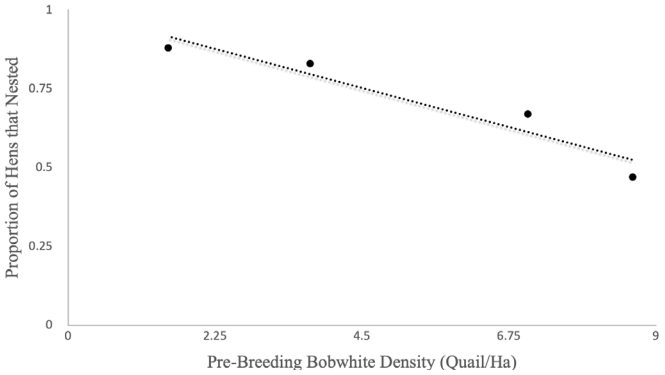

Fig. 1. Relationship between northern bobwhite (*Colinus virginianus*) prebreeding density (quail/ha) and nesting rate (proportion of hens to survive the nesting season to incubate at least one nest) on a privately managed quail hunting property, Leon County, Florida, USA, 2002–2005.

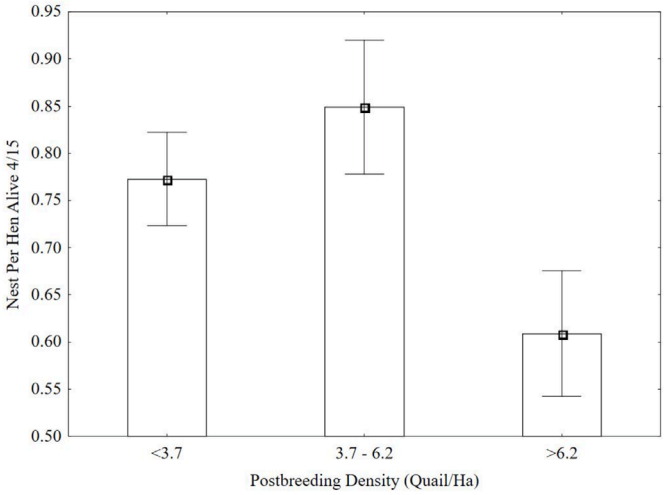

Fig. 2. Mean number of nests per hen alive on 15 April from radio-tagged sample of northern bobwhites (*Colinus virginianus*) on 19 properties (50 site and year combinations) grouped by bobwhite postbreeding densities as measured from covey call grids, October and November, 1999–2020. Properties were mainly located in the Albany, Georgia, USA and Tallahassee, Florida, USA region.

DISCUSSION

We believe that this is the first study to document bobwhite prebreeding and postbreeding densities along with breeding season behavior of bobwhites at the individual level to assess population dynamics and investigate density dependence. Previous studies have measured prebreeding or postbreeding densities (or both) but did not have individual-based estimates of reproductive behavior to dissect which parameters were most sensitive to density. Studies have relied on population-level parameters such as percent summer gain, age ratios, and total nests found relative to prebreeding season abundance on the study areas (Roseberry and Klimstra 1972, Dimmick et al. 1974, Guthery et al. 1988). Given our findings, it is interesting that these studies found that nest production largely explained postbreeding densities of bobwhites more than other reproductive variables. More recent and robust analyses of long-term band-recapture data derived estimates of productivity (McConnell et al. 2018) and found evidence for density-dependent recruitment and survival. What has been missing, and a value of our study, was individual-based

behavior from radio-tagged individuals, providing insight into bobwhite reproductive behavior that explained observed changes in population-level parameters and apparent density-dependent relationships.

We utilized strip-transect flush counts to estimate prebreeding density. We observed a greater proportion of radio-tagged bobwhites during our flush counts than previously reported. Dimmick et al. (1982) reported flushing 50% of radio-tagged coveys with observers spread 20 m apart. Janvrin et al. (1991) observed 56% of individuals and 61% of coveys with observers 10 m apart and reported an average flush distance of 5 m from observers. We maintained a closer distance between observers, which improved detection. The higher density of bobwhites on the study area, the timing of flush counts after covey break-up in spring, and the relatively open habitat conditions contributed to observed detection and provided reliable estimates of prebreeding density.

Of the parameters measured, we observed lower nesting rate of hens in years with higher prebreeding densities on our intensive study site, and across multiple sites we observed lower overall per capita nesting rate by hens when bobwhite densities were highest. We believe this is the first study to document a negative relationship between nesting rate of individual hens and bobwhite breeding densities. The low nesting rate observed at high density occurred despite other population parameters remaining above-average, such as nesting success and breeding season survival. This is counter to the logic that for r-selected species, such as the bobwhite, density dependence is more important at low densities than high densities (Fowler 1981). We suspect that strategic management of habitat, predation, and food resources moderates density-dependent factors typically found in the bobwhite (Guthery and Shaw 2012). This also suggests that bobwhites in our study exhibited lower nest production at high densities due to some form of intraspecific competition for space, as food and cover were likely maximized, and predator abundances were minimized through management.

Roseberry and Klimstra (1972) suggested that low nesting rates observed on their study areas were a result of habitat loss or unfavorable weather conditions, or a combination thereof. In our study, none of these conditions occurred, yet less than half of the hens that survived the nesting season were observed to have incubated a nest following the peak in prebreeding densities and only 67% of hens nested in the year with the second highest prebreeding density. The cause of low nesting rate could have been some factor other than intraspecific competition. For instance, it is possible that we failed to count hens that initiated nests but never reached incubation due to predators depredating their nests during egg-laying. However, we do not believe this is the case as we did not observe characteristics and behaviors we would expect to see when predators depredate nests during egg-laying. For instance, when nesting initiation is limited by predators, we would expect to see low nesting success as well (Staller et al. 2005). However, nesting success was high during the study and was 61% during the year with greatest prebreeding density and lowest nesting rate. Breeding season survival also peaked during the year with the highest prebreeding density, indicating low overall predation pressure. Further, if hens were losing nests during pre-incubation, but surviving the nesting season, we would have expected to see renesting later in the nesting season. Finally, nest predators were maintained at low levels by trapping, and scent station surveys confirmed low activity and abundance on the study area (Jackson et al. 2018). Snakes can also be a significant nest predator (Staller et al. 2005, Ellis-Felege et al. 2012). However, snakes often fail to depredate the entire nest and tend to depredate nests during the incubation phase (Staller et al. 2005). We did not witness low nesting success, high renesting, partial depredations by snakes, or low adult survival during years with the highest prebreeding and postbreeding densities, suggesting that nest predation was not limiting nesting on our study area.

We also do not believe that weather or nutrition was limiting during the period. Low nesting rate in some bobwhite populations has been attributed to severe drought conditions (Hernández et al. 2005). The peak in population in our study occurred during a period of near ideal weather conditions for bobwhites and their populations increased throughout the Red Hills region (McConnell et al. 2018, Palmer et al. 2019). Bobwhite were provided with supplemental food, suggesting that energy requirements were at least met at a minimum level, but likely exceeded (Whitelaw et al. 2009).

Analyses of 30 years of data from Tall Timbers determined that both recruitment and annual survival were responsible for population growth (McConnell et al. 2018). Our observational study provides insight into why per capita nesting declines as populations reach carrying capacity. At lower nesting rates, populations can maintain themselves only by sustaining high survival rates. Even though per capita nesting rate declines at high densities, there is still a high amount of per hectare production due to the number of quail on the landscape. As a result, populations can increase, or remain stable at high densities, despite the lower nesting rate. However, as nesting declines due to intraspecific competition, population maintenance becomes more dependent on survival. If some factor causes survival to decline, the population declines. In our study the population declined due to decreasing survival rates the year following the peak density in 2002. We continued to observe low nesting rate the year following the peak as prebreeding densities remained high. Following 2 years of declines due to lower survival, nesting rate increased, resulting in population increases during the last 2 years of the study. This suggests that if survival was not impacted by avian predation, the densities may have remained high for some period of time. But ultimately, with per capita production relatively low, it is only a matter of time until something impacts survival of adults, or young (Palmer and Sisson 2017, Terhune et al. 2019). A decline in populations ultimately results in an increase in productivity through increased nesting of hens and male incubation, and populations begin to recover. Therefore, when management lessens the effects of predation, weather, and habitat on quail populations, we

believe that population growth is limited by reduced nesting propensity of hens. We observed reduced nesting propensity when bobwhite density exceeded approximately 7 quail/ha.

This study documented a declining population due to reduced survival and low nest production. It is important to mention that quail densities were high on this property for 2 years before the beginning of this study. We estimated fall densities >7 quail/ha the year prior (2001) to beginning this project. We have observed other properties, including our main study area in Albany, Georgia, that have sustained high densities for 3–5 years prior to some factor impacting survival (such as avian predation) or reproduction (such as drought) and causing a decline. High density of bobwhites may reduce nesting, but management of food resources, habitat, and predation can maintain high survival and overall reproduction, thereby sustaining high abundances for multiple years. This is counter to the idea that management cannot influence carrying capacity above what is maximized by usable space (Guthery and Shaw 2012).

At lower densities bobwhite nesting rate is higher and nearly every surviving hen is thought to have produced at least one nest. We observed 80% and 89% of surviving hens incubating at least one nest at lower prebreeding densities and populations began to recover. This nesting rate was similar to rates reported by Miller et al. (2012) when prebreeding season quail densities were <3 quail/ha. When prebreeding densities are lower, and populations and conditions favorable, we observe higher male incubation of nests along with high incubation rates by females (Palmer, unpublished data; Palmer et al. 2019; Jackson et al. this volume). The propensity of males to incubate nests during increasing phases provides increased productivity. At high density we predict that male incubation opportunities are lower as fewer hens are producing more than one nest, and based on this study, some hens produce no nests. Additional research is needed to determine what behavioral or physiological differences occur in hens that appear to forgo reproduction versus hens that reproduce normally, and what triggers males to incubate nests.

MANAGEMENT IMPLICATIONS

This study suggests that reproduction of bobwhites is affected by their density and that at postbreeding densities above approximately 7 quail/ha, and prebreeding densities above approximately 4 quail/ha bobwhite, nesting rate declines significantly. While the exact mechanism remains unknown, our results do suggest managers focused on sustaining high postbreeding densities should manage habitat to maximize usable space during the prebreeding and breeding season to uniformly distribute bobwhites across a management area and reduce apparent bobwhite density. Further, for bobwhite translocation, this study suggests that managers avoid releasing too many bobwhites into a small area, but rather spread out the translocated bobwhites at a reasonable (~1 quail/ha) prebreeding density to maximize reproduction. Our study also shows the importance of maintaining high bobwhite survival to maintain high densities over time. Finally, our study suggests that the nesting rate of hens could be an important vital rate in bobwhites for invoking compensation in response to harvest or removal for translocation. Understanding the degree to which nesting rate may govern regulation near a population carrying capacity has important management implications for harvest and translocation policy. Increasing the harvest and translocation rate in high density populations may be acceptable for sustaining populations at high density when weather conditions are stable and favorable.

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DIURNAL OCCURRENCE OF GREAT-HORNED OWLS ON NORTHERN BOBWHITE HUNTING PROPERTIES IN SOUTHWEST GEORGIA

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ABSTRACT

Understanding interactions between prey species and their predators is essential to discerning the ecology and management fundamentals of a species. Great-horned owls (*Bubo virginianus*) have long been considered an opportunistic predator of northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) and recent studies have demonstrated that bobwhite survival is reduced at higher great-horned owl densities (Rectenwald et al. 2021). Managers on quail properties often mechanically remove live oak (*Quercus virginiana*) hammocks as part of larger predation management plans to reduce the amount of suitable predator habitat. While scattered live oaks are typically left for aesthetic purposes, these serve as preferred day roosts and hunting perches for great-horned owls. To improve bobwhite survival and fitness, managers on quail properties broadcast supplemental grain along designated trails at a density of 2.4 km/40.5 ha of upland habitat. From the peak of bobwhite brooding season to the end of the breeding season (i.e., Jun–Sep), it is common for managers to switch from broadcasting grain from feed trails to broadcasting grain from mowed roads to reduce tractor activity in obscured cover where broods or nests may be run over and destroyed. Bobwhite are potentially at higher risk for predation where live oak hammocks are intersected by feed trails due to increased exposure time in areas with higher predator occurrence. Additionally, bobwhite may be at higher predation risk when feeding on mowed roads in the summer, particularly when in close proximity to live oaks, due to the lack of screening cover from opportunistic owls perched above.

We evaluated the probability of use for great-horned owls in relation to live oak hammocks, feed trails, and roads that are fed in the summer. We compared use versus availability for landscape features using a resource selection function in a Bayesian framework. As part of a larger study detecting all raptors that were threat-specific to bobwhite, driving surveys using line-transect distance sampling on a 32.2-km route were conducted twice per month from September 2014–December 2020 between 0800–1000 at a speed of 16 km/hr. The surveys encompassed a 5,400-ha privately owned property in Baker County, Georgia, USA. Surveys were conducted only on days with fair weather (i.e., no fog or rain). When great-horned owls were visually detected, their location was recorded on a Global Positioning System (GPS). Great-horned owl density on the property averaged approximately 0.86 owls/km^2 during the bobwhite breeding season and 0.58 owls/km^2 in the non-breeding season (Rectenwald et al. 2021). The site was 60% upland pine (*Pinus elliottii, P. palustris, P. taeda*), 20% fallow field, 10% pine for timber production, 5% live oak, and 5% wooded wetland. Habitat features were delineated using satellite imagery and GPS units. Random locations were generated to determine resource availability and we used observed locations in a logistic model using vague priors to estimate probability of use with increasing distance from landscape features.

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We detected 111 great-horned owls during 135 surveys. Our study indicated that great-horned owls were 9.1 times (odds ratio, 95% credible interval [CrI]: 6.0–16.6) more likely to use an area for every 48.3 m closer to live oak hammocks. Great-horned owls were also 1.8 times (95% CrI: 1.4–2.6) more likely to use an area for every 38.8 m closer to feed trails that were being fed. Our results suggest that great-horned owls were 1.9 times (95% CrI: 1.0–4.6) more likely to use an area for every 29.3 m closer to roads being fed in the summer compared to unfed roads other times of the year. Our study indicates that great-horned owls are more likely to select areas within close proximity to live oaks even though hammocks are found at a low density of 1 hammock/8 ha of upland habitat. While great-horned owls are likely utilizing residual live oak hammocks largely because they are suitable day roosts, they are even more likely to use these areas where prey bases are likely to be higher. Feeding roads in the summer may increase the likelihood of bobwhite predation because of the lack of cover and changes in predator behavior (i.e., hunting roads). While great-horned owls are not the most common bobwhite predator, they influence bobwhite survival and research has indicated that bobwhite survival decreases when great-horned owl density increases. To mitigate predation potential, we suggest that managers should either remove existing live oaks that are within 50 m of feed trails and roads or disengage the feed wagon when approaching live oak hammocks. Alternatively, new feed trails could be established so that they avoid being near live oak hammocks altogether. Considering that roads fed in the summer may attract higher predator levels, we also recommend blowing feed into the cover from the roadway to reduce exposure on mowed, open grass. Further studies should investigate how survival rates vary when road feeding occurs on mowed roads versus only on designated feed trails.

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Key words: *Bubo virginianus, Colinus virginianus,* great-horned owl, habitat use, live oak, northern bobwhite, predation, raptor, supplemental feed, survival

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MEASURING MULTIPLE DEMOGRAPHIC RATES IN TWO POPULATIONS OF NORTHERN BOBWHITE

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ABSTRACT

Demographic rates of northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) may vary spatially and temporally, and understanding the significance of these individual rates to population performance is critically important to bobwhite management. We present descriptive evidence from 2 populations that were simultaneously monitored from 2015–2020 that suggests different demographic rates can be more important to population performance than other demographic rates within the same region. Our objective was to understand the relative importance of various demographic rates to population performance in separate and seemingly stable populations. We monitored bobwhite seasonal survival and reproductive demographics on 2,475 bobwhites via radio-telemetry and estimated fall density using fall covey counts. Both sites maintained high densities (i.e., ≥3.45 birds/hectare) and remained relatively stable throughout the study period. On one site in the Red Hills region near Monticello, Florida, USA, bobwhite experienced comparatively low seasonal survival, but higher reproduction, including more frequent multiple-brood production. One hundred and twenty-nine kilometers away on a study site near Albany, Georgia, USA, bobwhite demonstrated consistently higher survival and lower reproductive output, including less multiple-brooding compared to the Red Hills population. This suggests, at a minimum, that compensatory or density-dependent reproduction may be occurring in these populations and regional population dynamics can vary locally even among stable populations.

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Key words: *Colinus virginianus*, density dependence, Florida, Georgia, multiple-brooding, northern bobwhite, productivity, survival

A common objective in wildlife research is identifying the relative influence of multiple demographic parameters on population stability. Identifying and prioritizing these life stages for management may improve population performance. Much research has centered around demographic sensitivity of northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) populations including components of fecundity (DeVos and Mueller 1993, Burger et al. 1995) and survival (Curtis et al. 1988, Robinette and Doerr 1993, Madison et al. 2002). The first major comprehensive review and sensitivity analysis of both fecundity and survival utilizing telemetry information from field studies throughout the bobwhite range (Sandercock et al. 2008) concluded that adult over-winter survival had the greatest contribution to population growth. Conversely, recruitment was found to be the most important demographic variable for population persistence in a Florida, USA, bobwhite population (McConnell et al. 2018). Initially, demographic sensitivity was thought to vary regionally depending on climate, with adult survival more important in southern latitudes and reproduction driving northern populations (Folk et al. 2007). More recently, in New Jersey, USA, reproductive parameters were shown to be the driving force and management actions to increase over-winter survival and reproduction were recommended (Williams et al. 2012). Further research is needed to determine which demographic rates influence regional and local bobwhite populations to better inform parameter-based management and influence long-term population persistence.

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The ability of northern bobwhites to produce multiple broods (i.e., multiple-brooding) in a single nesting season contributes to high levels of productivity. In fact, second broods may be an important factor for population recovery following periods of extreme lows (Stanford 1972). However, the frequency of multiple-brooding in northern bobwhite populations is not well understood and its significance to population stability likely varies both spatially and temporally. While multiple-brooding was once considered a rare, perhaps nonexistent, trait among bobwhite (Stoddard 1931), radio-telemetry observations from across the range suggest multiple-brooding may be more common than previously thought (Sermons and Speake 1987, Taylor 1991, Curtis et al. 1993, DeVos and Mueller 1993, Suchy and Munkel 1993, Burger et al. 1995, Sisson 2017). Nonetheless, it has been postulated that the relative contribution of multiple-brooding under average nest success has little effect on fall populations (Guthery and Kuvlesky 1998), and that triple brooding is rare and does not contribute significantly to recruitment (Sandercock et al. 2008, Sisson 2017). We compared brood production as a component of reproductive effort between two stable populations, in addition to rates of nest incubation, breeding season survival, over-winter survival, and fall density. Our objective was to demonstrate that not all seemingly stable bobwhite populations persist under the same demographic assumptions by comparing reproductive effort and survival probabilities of 2 bobwhite populations. We predict that varying demographic parameters likely drive different populations and these parameters can vary by site, region, and year.

STUDY AREA

Bobwhite demographics were monitored on 2 large, intensively managed wild bobwhite plantations in the southeastern United States. One study site was Livingston Place, a 3,683-hectare property owned by Tall Timbers located in the Red Hills region near Monticello, Florida and one study site was a 6,000-hectare privately owned property located in the Upper Coastal Plain physiographic region near Albany, Georgia, USA (Figure 1). Both study sites have managed bobwhite habitat with frequent prescribed fire, intensive timber management, seasonal disking of fallow fields, roller-chopping and mowing, supplemental feeding and meso-predator control programs (Yates et al. 1995, Burger et al. 1998, Terhune et al. 2007, Sisson et al. 2009, Sisson and Terhune 2017, Rectenwald et al. 2021). Both sites consisted of low-density (3–9 m^2/ha) upland pine forests composed of loblolly (*Pinus taeda*), slash (*P. elliottii*), shortleaf (*P. echinada*), and longleaf (*P. palustris*) pine with an herbaceous understory maintained by frequent prescribed fire. Seasonally disked fallow fields dominated by ragweed (*Ambrosia* spp.) were scattered across the properties and covered 10–20% of the total upland area. Mid-rotation pines and pine snags were intentionally removed on the Albany site to reduce avian predator habitat. Isolated wetlands and associated drain habitat make up 770 hectares dispersed throughout Livingston Place. Agricultural fields and hardwood hammocks accounted for the remaining area.

METHODS

Bobwhite fall density, over-winter survival, and breeding season demographics were monitored from 2015–2020 on both study sites. Fall density (birds per hectare) was determined from early morning covey calls using a 24.3-hectare grid count technique (Wellendorf et al. 2004, Terhune 2017, Howell et al. 2021). Livingston Place had 5 grids and the Albany study site had 10 grids. Grids were distributed across the landscape to most accurately monitor areas dominated by habitat representative of the uplands. Grid counts were conducted by 4 observers per grid, each at the mid-point of a side connecting the corners of the grid. Observers counted coveys calling from within the grid and calculated grid density (i.e., birds per hectare) as the total number of coveys calling within the grid, multiplied by the average covey size of the site, divided by grid area. Overall density of the site was determined as the average density across all grids.

Bobwhites were trapped twice each year (Oct–Nov and Mar–Apr) using wire funnel traps baited with cracked corn or grain sorghum (Stoddard 1931). All captured birds were classified by sex and age, weighed, and leg banded and a

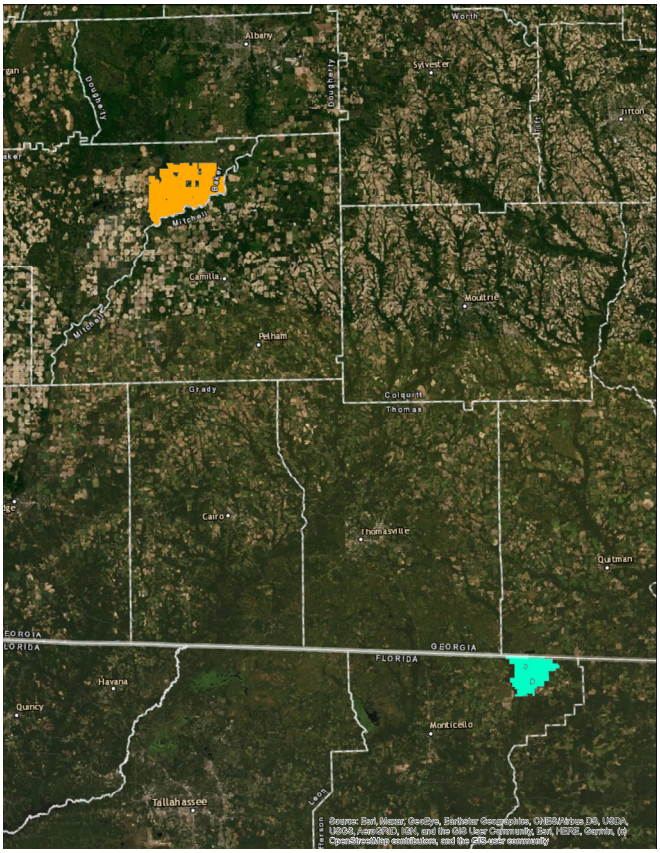

Fig 1. Locations of study sites at Livingston Place (blue), Florida, USA, and near Albany (orange), Georgia, USA.

subset of birds weighing ≥132 g (<5% of body weight) were fitted with 6.2 g necklace-style radio transmitters equipped with motion-sensitive switches (Holohil Systems, Ltd., Carp, Ontario, Canada) and released at the capture site. The radio-tagged sample of bobwhite was evenly distributed across season, site, and year (i.e., ≥50 radio-tagged birds per season, site, and year). Bobwhite over-winter survival was monitored via radio-telemetry from 1 October–31 March. Radio-tagged birds were tracked ≥2 times/week and survival was estimated weekly using the Kaplan-Meier staggered entry method for each site and each year (Kaplan and Meier 1958, Pollock et al. 1989). Bobwhite breeding season demographics were monitored 1 April–30 September using radio-telemetry to track individuals ≥3 times/week. Bobwhite nest success was monitored during incubation after adults were tracked to identical locations on consecutive days. Nests were checked daily until success (≥1 egg hatched) or failure (Taylor et al. 1999, Ellis-Felege et al. 2012). We were specifically interested in nests per hen, double nests per hen, triple nests per hen, and the corresponding brood production. We quantified the number of nests incubated per hen, as well as the frequency of double and triple nesting attempts. We also quantified the number of nests hatched per hen and the frequency of successful double and triple nests. We followed the strict definition provided by Sisson (2017) for double and triple broods as second and third broods hatched from the same hen.

RESULTS

Average fall population density on the Livingston Place study site from 2015–2020 was 3.85 birds/hectare (standard error [SE] = 0.25, range = 3.45–4.20). The population growth rate (i.e., λ) on Livingston Place averaged 0.99 (SE = 0.06, range = 0.88–1.21). Over-winter survival on Livingston Place was calculated from 749 radio-tagged bobwhite and was 0.45 (SE = 0.04, range = 0.33–0.56), resulting in a derived spring density averaging 1.81 birds/hectare (SE = 0.15, range = 1.38–2.33; Table 1). Average fall population density on the Albany study site was 6.18 birds/hectare (SE = 0.45, range = 4.69–7.17). The population growth rate (i.e., λ) on the Albany site averaged 1.14 (SE = 0.11, range = 0.88–1.37). Mean over-winter survival from 600 radio-tagged bobwhite was 0.63 (SE = 0.03, range = 0.53–0.68) and mean spring density was 3.60 birds/hectare (SE = 0.34, range = 2.22–4.45; Table 2).

We tracked 526 radio-tagged hens on Livingston Place and 600 hens on the Albany site to estimate breeding season survival, annual survival, nest production, and brood production. On Livingston Place, breeding season survival averaged 0.32 (SE = 0.03, range = 0.23–0.42) across all years, resulting in an average annual survival of 0.15 (SE = 0.02, range = 0.09–0.23; Table 1). We found 422 nests and documented 258 broods on Livingston Place. Annual nests per hen averaged 0.75 (SE = 0.06, range = 0.51–0.91) and annual broods hatched per hen averaged 0.46 (SE = 0.05, range = 0.30–0.67). Of the 422 nests, 104 were double incubations by hen (i.e., 0.20 double nests/hen) and 24 were triple incubations by hen (0.05 triple nests/hen). Similarly, 49 broods were double broods (0.09 double broods/hen), and 4 were triple broods (0.01 triple broods/hen; Table 3). On the Albany site, average breeding season survival was 0.42 (SE = 0.03, range = 0.36–0.51), resulting in average annual survival of 0.26 (SE = 0.02, range = 0.21–0.36; Table 2). We found 333 nests and documented 171 broods. Overall annual nests per hen averaged 0.50 (SE = 0.03, range = 0.40–0.58) and annual broods hatched per hen averaged 0.26 (SE = 0.01, range = 0.20–0.30). Of the 333 nests, 67 were double incubations by hen (0.11 double nests/hen) and 9 were triple incubations by hen (0.02 triple nests/hen). We found 11 double broods (0.02 double broods/hen) and there were no triple broods (Table 3).

Table 1. Northern bobwhite (*Colinus virginianus*) density and seasonal survival estimates for the Livingston Place study site in the Red Hills region, Florida, USA, 2015–2020.

Metric	Mean	Standard error	Minimum	Maximum
Fall density (birds/ha)	3.85	0.25	3.45	4.20
Over-winter survival	0.45	0.04	0.33	0.56
Spring density (birds/ha)	1.81	0.15	1.38	2.33
Breeding season survival	0.32	0.03	0.23	0.42
Annual survival	0.15	0.02	0.09	0.23
Growth rate (λ)	0.99	0.06	0.88	1.21

Table 2. Northern bobwhite (*Colinus virginianus*) density and seasonal survival estimates for the Albany, Georgia, USA, study site, 2015–2020.

Metric	Mean	Standard error	Minimum	Maximum
Fall density (birds/ha)	6.18	0.45	4.69	7.17
Over-winter survival	0.63	0.03	0.53	0.68
Spring density (birds/ha)	3.60	0.34	2.22	4.45
Breeding season survival	0.42	0.03	0.36	0.51
Annual survival	0.26	0.02	0.21	0.36
Growth rate (λ)	1.14	0.11	0.88	1.37

Table 3. Number of radio-tagged northern bobwhite (*Colinus virginianus*) hens and associated reproductive parameters from the Livingston Place (Red Hills region, Florida, USA) and Albany, Georgia, USA, study sites, 2015–2020.

Metric	Livingston Place	Albany
Radio-tagged hens	526	600
Total nests	422	333
Nests per hen	0.75	0.50
Double nests per hen	0.20	0.11
Triple nests per hen	0.05	0.02
Total broods	258	171
Broods per hen	0.46	0.26
Double broods per hen	0.09	0.02
Triple broods per hen	0.01	0.00

DISCUSSION

As an r-selected species, northern bobwhite have adopted a flexible mating system to maximize potential productivity and to offset high annual mortality (Burger et al. 1995). However, the relative contributions of reproduction and survival to population growth remain unclear. As intensive research over the past 3 decades has added insight to detailed demographic information, modern modeling efforts have been improved through more accurate demographic parameterization, allowing for a more thorough investigation (Curtis et al. 1988, DeVos and Mueller 1993, Guthery et al. 2000, Madison et al. 2002, Sandercock et al. 2008, McConnell et al. 2018). Although adult survival probabilities and reproductive effort are both important contributions to population growth (Guthery et al. 2000, Folk et al. 2007, Sandercock et al. 2008), site-specific differences in risk among varying age-classes may favor specific population demographics to achieve population stability.

Abundance in stable populations may negatively affect recruitment (McConnell et al. 2018). We present data from 2 populations in the same region that achieve moderate stability across simultaneous years in different ways. The Albany population experienced high over-winter survival and high spring densities; therefore, high levels of production were not as necessary to maintain similar densities across years. On Livingston Place, low over-winter survival probabilities resulted in lower spring densities, requiring higher recruitment to maintain similar densities across years. Our results provide additional evidence of density-dependent reproductive effort. Greater nest production, brood production, and frequency of multiple brooding on Livingston Place compared to the Albany site likely reflect density-dependent reproductive effort.

Individual bobwhite have a high propensity to produce multiple nests during the same breeding season (Sandercock et al. 2008). However, population density likely contributes to the frequency of occurrence of this physiological adaptation. We documented lower seasonal survival, annual survival, and densities on Livingston Place compared to the Albany study site. However, overall average number of nests incubated per hen was 40% more on Livingston Place. Multiple-broods occurred every year of the study on Livingston Place, accounting for 21% of total brood production, with triple-brood production in 4 out of the 6 years. While relatively insignificant to fall populations (Guthery and Kuvlesky 1998), the multiple occurrences of triple broods are noteworthy given that Sisson (2017) previously documented only one triple brood occurrence in 25 years (1992–2016) of monitoring the same Albany population discussed in this study. While multiple-brooding occurred in 5 years of the 6-year study in Albany, they accounted for only 6% of total brood production. Therefore, we contend that while survival is important, populations that experience comparatively low levels of seasonal and annual survival, must rely heavily on reproduction to maintain stability from year to year.

The higher level of multiple-brooding in the Livingston Place population is only part of the overall reproductive effort required to overcome lower over-winter survival in Red Hills populations. Per capita reproduction (including multiple nests and broods) on Livingston Place averaged 0.75 ± 0.06 nests/hen and 0.46 ± 0.05 broods/hen, but only 0.50 ± 0.03 nests/hen and 0.26 ± 0.01 broods/hen in Albany (i.e., 40% and 56% difference, respectively). However, further research should investigate the prevalence and importance of male incubation to population performance, as this metric is relatively unknown. Additionally, future investigations should incorporate a metric of brood success to investigate the uncertainty in this period that we did not account for in this descriptive study.

Differences in reproductive effort between the 2 sites may reflect differences in over-winter survival probabilities. Harvest rates are relatively light on both properties, averaging 12% on Livingston Place and 5% in Albany, with most of the additional mortality attributed to avian predation (Rectenwald et al. 2021). The landscape in the Red Hills region has more habitat conducive to avian and mammalian predators and larger surges of migrating raptors in winter (Rectenwald et al. 2021). In addition to landscape differences, the Albany site had intentionally removed avian predator habitat (i.e., mid-rotation pines and pine snags), which had reduced the number of raptors seen on survey routes over time (Rectenwald et al. in press). These practices have not been applied on Livingston Place and a higher percentage of hardwood drains remain intact. Given that the Albany site has both higher over-winter survival and a higher fall density, it is possible that elevating over-winter survival in the Red Hills could increase fall densities in this region. Management actions that increase over-winter survival in the Red Hills may increase fall densities if that is the desired objective.

MANAGEMENT IMPLICATIONS

We provide evidence of differing seasonal survival probabilities and resulting reproductive efforts for 2 distinct bobwhite populations within the same region. While one population experiences high survival and moderate reproduction, the other experiences moderate survival and high reproduction. Increases in reproductive effort may be a compensatory mechanism when over-winter survival is low. However, more data would be needed to determine whether variation within a single population is compensatory over time and how those actions influence population growth. This work demonstrates that demographic rates of seemingly stable populations within the same region may vary and targeting management for a specific demographic can vary spatially and over time. Comprehensive management plans promoting both high over-winter survival and reproductive output are recommended, as it is uncertain when or where one particular demographic might be most important.

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BEHAVIORAL STATE-SPECIFIC NORTHERN BOBWHITE CHICK RESOURCE SELECTION

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ABSTRACT

Determining resource selection rates for all life stages of a species is critical to enable a holistic management approach that focuses on bolstering populations across all life stages. Moreover, tying these selection rates to specific life history needs (e.g., foraging, roosting, and loafing) can provide valuable information to guide management practices. Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite), a gallinaceous species of North America, has experienced steady population declines throughout much of its range over the last 50 years. Although the species has been well studied, chick ecology is still relatively unknown. We studied bobwhite chick resource selection on a private property in Brunswick County, North Carolina, USA to better understand daily and within home range selection. The site was managed intensively for bobwhite using prescribed fire, seasonal mowing and disking, mesomammal control, and supplemental feeding. We radio-tagged 156 chicks 11–15 days of age from 29 unique broods and collected location data for nocturnal roost sites, daily movement tracks, and diurnal use sites during a 2-year span. We had selection models for 3 behaviors: roosting, foraging, and general movements within home range (third-order). All models were mixed-effects conditional logistic regression models under a Bayesian framework. We determined foraging behavior using a straightness index for daily track segments; more tortuous segments were designated as foraging locations. Upland pine stands (burned and unburned) were selected for foraging and roosting. Chicks were more likely to select areas closer to feedlines for roosting, foraging, and diurnal habitat; however, selection of these areas decreased as birds grew older. Chicks avoided fallow fields and hardwood drains or Carolina bays as roost site locations yet selected them as foraging habitat. Roosting birds avoided fallow fields as roost sites and instead selected areas adjacent to them. Probability of use for diurnal and roosting habitat decreased as distance to fallow fields increased. Our study results shed light on how circadian habitat use can vary and illustrate that one specific land cover may not provide ideal diurnal and nocturnal habitat for bobwhite chicks. The results also reinforce the need to provide resources that meet diurnal and nocturnal requirements within biologically reasonable distances from each other.

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Key words: *Colinus virginianus*, chick, fallow field, foraging, northern bobwhite, precocial, radio-telemetry, resource selection, roosting

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NORTHERN BOBWHITE SURVIVAL AND PRODUCTIVITY IN RELATION TO FOOD SUPPLEMENTATION

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ABSTRACT

Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) populations have experienced a 3.4% decline annually nationwide from 1966 to 2018. Limitations on resources, such as food, can regulate population growth. Supplemental food could alleviate resource limitation by raising carrying capacity, leading to increased survival and breeding productivity. Studies have shown higher survival rates and higher nest production when food is supplemented; however, repeating experiments in different contexts allows for strong inference. Our objectives were to assess how supplemental food influenced survival and breeding productivity of resident and translocated bobwhite during a 2-year study on public lands in Leon County, Florida, USA within the Apalachicola National Forest. In accordance with the food limitation hypothesis, we predicted that provisioning of supplemental food would have a positive influence on survival rates and nest productivity. We split the study site into 4 approximately 400-ha zones and randomly assigned 2 treatment (fed) and 2 control (unfed) replicates. Treatment and control zones were flipped during the second field season. Treatments received approximately 1.75 bushels of milo (*Sorghum bicolor*)/acre 2 times/month year-round via broadcast spreader. We radio-marked 205 bobwhites (102 treatment, 103 control) from February 2019 through October 2020. Individuals were tracked 3–4 times/week for location and survival via radio-telemetry to estimate the breeding season survival and reproduction rates. We estimated survival rates using the Kaplan-Meier product limit estimator. The survival rate during the breeding seasons was higher on average for treatment zones ($\bar{x}$ = 0.38, standard error [SE] = 0.040) than for control zones ($\bar{x}$ = 0.29, SE = 0.045). We also observed that 79% of nests found were located in treatment zones compared to 21% in control zones. Our results suggest that food supplementation can improve survival rates and nest production of bobwhite in a food-limited landscape.

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Key words: *Colinus virginianus,* food limitation, limiting factor, northern bobwhite, public land, translocation

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AVIAN ABUNDANCE AND DIVERSITY ON KNOXVILLE WILDLIFE AREA IN CALIFORNIA FOLLOWING THE COUNTY FIRE OF 2018

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ABSTRACT

Wildfires can have negative impacts on wildlife during and immediately after a burn event, yet these fires are also necessary for plant succession and biodiversity. Knoxville Wildlife Area (KWA) in Napa County, California, USA is a diverse environment that contains oak woodlands, chaparral, grasslands, and riparian corridors. In July 2018, the County Fire burned 36,353 ha in the Northern California Interior Coast Ranges, including 2,429 ha on KWA. California Department of Fish and Wildlife employees used this opportunity to monitor avian abundance and diversity as the burned area revegetates. From 10 June through 14 June 2019, we began a pilot season of distance-based point counts on KWA. We conducted 5-minute point counts at 80 points spaced 1 km apart. Twenty points were within the burned area. We used the half cosine model in Program Distance version 7.2 to determine density for the 5 most frequently detected species. We detected 47 avian species; the most frequently detected species were California quail (*Callipepla californica),* acorn woodpecker *(Melanerpes formicivorus),* mourning dove *(Zenaida macroura),* California scrub-jay *(Aphelocoma californica),* and oak titmouse *(Baeolophus inornatus)*. California quail populations were slightly denser in the burned area (0.22 birds/ha, 95% confidence interval [CI] = 0.11–0.44), compared to the nonburned area (0.19 birds/ha, 95% CI = 0.12–0.31). Acorn woodpecker density was similar in the burned (0.59 birds/ha, 95% CI = 0.34–1.02) and nonburned areas (0.58 birds/ha; 95% CI = 0.42–0.80). Mourning dove, California scrub-jay, and oak titmouse populations were slightly denser in the nonburned area; however, 95% CIs overlapped. We conducted approximately approximately 1 year post-burn, and revegetation had started, due in part to the wet winter and spring. Birds were using the burned area, though not at significantly higher densities compared to the rest of the wildlife area. The coronavirus pandemic and a second fire prevented us from surveying the site in 2020 and 2021, but we intend to conduct point counts for at least 2 more years to further monitor avian response to wildfire.

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Key words: abundance, California quail, *Callipepla californica*, distance sampling, diversity, wildfire

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CASCADING EFFECTS OF HUNTING DISTURBANCE ON NORTHERN BOBWHITE BEHAVIOR, PHYSIOLOGY, AND SURVIVAL

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ABSTRACT

The northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) is an important gamebird across the United States and has been in decline for several decades. As a commonly hunted prey species, the bobwhite provides an ideal study species to investigate the use of proactive and reactive antipredator behaviors in response to hunting pressure. We designed an experiment to understand how late-season hunting affects bobwhite demographics using fecal glucocorticoid (*f*GCM) concentrations, foraging and movement behaviors, survival, and breeding season metrics. Our results show that bobwhite responded to increased interactions with a shotgun through proactive responses. After one encounter with a discharged shotgun, bobwhite began foraging farther from supplemental feed where the risk of encountering a hunting party was the greatest ($\beta = 0.21$, 95% Bayesian credible interval [CrI]: 0.06–0.36). Bobwhite responded to increased hunting pressure, particularly late-season hunting pressure, via reactive responses through increased fecal glucocorticoid metabolite (fGCM) concentrations ($\beta = 2.18$, 95% CrI: 0.21–4.15), resulting in decreased survivorship in non-harvested individuals ($\beta = -0.42$, 95% CrI: -0.77 to -0.07) and decreased fecundity ($\beta = -0.17$, 95% CI: -0.31–0.09). These results can help inform hunting season regulations and management decisions aiding in bobwhite recovery.

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Key words: antipredator behavior, *Colinus virginianus*, ecology of fear, fecal corticosterone, fecundity, glucocorticoid, hunting pressure, nonconsumptive effects, northern bobwhite, stress

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IMPACTS TO QUAIL SPACE USE AND DEMOGRAPHICS FROM OIL AND GAS DEVELOPMENT

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ABSTRACT

Southern Texas contains some of the last relatively unfragmented habitat for northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) and scaled quail (*Callipepla squamata*) in the United States. Development of the Eagle Ford Shale hydrocarbon formation in this region could negatively impact quail and their habitat. Our objective was to examine the indirect effects of oil and gas activity (traffic and noise) on bobwhite and scaled quail on 2 private ranches in southern Texas. In 2015 and 2016, we radio-marked bobwhite and scaled quail in 2 areas where oil and gas activity was occurring (disturbed treatment) and 2 areas where little oil and gas activity occurred (undisturbed treatment). We measured vehicle passages and modeled noise propagation from oil and gas infrastructure at 2 biologically relevant frequencies (250 Hz and 1,000 Hz) in our study area to quantify oil and gas disturbance and examine its effects on quail space use (site selection and home range size) and demographics (survival, nest success, and density). Bobwhite and scaled quail selected areas 0–200 m and >425 m, respectively, from the primary, high-traffic roads in the disturbed treatment. In the undisturbed treatment, bobwhite and scaled quail selected areas 0–425 m and 0–300 m from primary roads, respectively. Bobwhite and scaled quail selected areas with sound levels 0–1.6 and 0–2.2 dB above ambient levels at the 250-Hz frequency level, respectively. At 1,000 Hz, bobwhite and scaled quail selected areas with sound levels 0–2 and 0–3.2 dB above ambient levels, respectively. We found no evidence that disturbance variables affected bobwhite and scaled quail home range size, survival, or density. We found bobwhite nest success decreased as sound levels (dB) at 250 Hz increased; we found no relationship between nest success and disturbance for scaled quail, possibly as they avoided major oil and gas disturbances. In calculations of the total footprint of quail habitat loss, indirect loss due to oil and gas activity needs to be considered in addition to direct loss due to conversion of rangeland to oil and gas infrastructure.

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Key words: *Callipepla squamata*, *Colinus virginianus,* northern bobwhite, noise, oil and gas, scaled quail, traffic

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Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) and scaled quail (*Callipepla squamata*) are the two most widespread species of quail in Texas, USA. Despite their relatively large geographic range in the state, both species have been in population decline for decades (Brennan 1991, Church et al. 1993, Brennan et al. 2005). Although many hypotheses regarding this decline have been proposed, habitat loss and fragmentation are reported to be the primary reasons for the decline (Brennan 1991, Brennan et al. 2005, Hernández et al. 2013). The decline has been smaller in the Tamaulipan Biotic Province of southern Texas and northern Mexico than other regions because large parcels (>5,000 ha) of unfragmented habitat remain (Fulbright and Bryant 2004). However, the recent increase in oil and gas exploration in this area, in particular above the Eagle Ford Shale hydrocarbon formation, has the potential to adversely affect quail and their habitat.

The Eagle Ford Shale is a hydrocarbon-producing geological formation spanning 4 million ha from the Texas-Mexico border into East Texas (EIA 2016, RRC 2021). Since the first well was drilled in 2008, the Eagle Ford Shale has been rapidly developed in nearly 30 counties in Texas. For example, the number of production sites increased from 98 wells in 2009 to over 24,000 wells in 2021 (a 24,000% increase; RRC 2021). Currently, little is known about how disturbance from hydrocarbon development may impact quail populations. Furthermore, other important regions for bobwhite and scaled quail in the United States, such as the Southwest, Southeast, and Midwest, potentially also could be impacted by oil and gas disturbance as the demand for these resources continues.

It is widely accepted that surface development and subsequent habitat loss and fragmentation from hydrocarbon development will have a negative impact on quail (Brennan 1991, Brennan et al. 2005, Hernández et al. 2013). However, the extent to which this development will hinder quail is unknown.

Construction of roads, drilling pads, flowlines, pipelines, pits, and other infrastructure often causes both acute and long-term direct loss of habitat. Quail are displaced when habitat is lost, and their survival may decrease. Habitat fragmentation due to road systems and other rights-of-way also can cause habitat loss. For example, quail can be killed by vehicles on roads and roads can be barriers to quail, as these birds prefer concealment during travel. Roads also can act as corridors for nonnative plant invasions (Tyser and Worley 1992, Gelbard and Belnap 2003). Nonnative grass invasions can create barriers to travel and render sites unusable to quail as nonnative grasses replace native vegetation (quail habitat; Kuvlesky et al. 2002, Sands et al. 2012).

Along with direct effects from oil and gas infrastructure, noise and traffic from oil and gas activity have the potential to cause indirect loss of habitat for quail by affecting behavior and physiology (Francis and Barber 2013). For example, noise can cause physical damage to ears; increased stress levels; and changes in temporal site use patterns, communication, predator and prey relationships, reproduction, and populations (Barber et al. 2009, Ortega 2012, Francis and Barber 2013). Oil and gas exploration is usually accompanied by a surge in vehicles and sound levels above levels typical of the ambient environment.

One way that indirect habitat loss may be manifested is through changes in space use by birds. For example, vehicle disturbance from natural gas development near greater sage-grouse (another member of the Galliformes; *Centrocercus urophasianus*) leks increased the distance from leks that hens moved when selecting nest sites (Lyon and Anderson 2003). The probability of lek abandonment by greater sage-grouse increased near oil and gas development in Montana and Wyoming, USA (Walker et al. 2007, Hess and Beck 2012). In a study during winter, greater sage-grouse in Wyoming avoided sagebrush habitat with coal-bed natural gas wells (Doherty et al. 2008).

Another way that oil and gas activity can indirectly impact quail and other birds is through changes in reproduction and survival. Noise caused by traffic resulted in lower reproductive success for great tits (*Parus major*; Halfwerk et al. 2011). The smaller clutches laid and fewer young fledged by great tits in areas with traffic noise were most likely due to the masking of the great tit's song by traffic noise, decreased parent-offspring communication, and stress (Halfwerk et al. 2011). Furthermore, habitat fragmentation from roads and rights-of-way may increase predator search efficiency for nests and individuals (Robinson et al. 1995, Hernández et al. 2013). Anthropogenic noise can interfere with birds' ability to hear predators (Ortega 2012). Yearling greater sage-grouse reared in areas with natural gas infrastructure had lower annual survival than those in areas without it, although the specific cause of this finding was unknown (Holloran et al. 2010). Both direct and indirect effects of oil and gas development on quail represent an area in need of study, especially in a landscape with great conservation value for wild quail.

Large areas over hydrocarbon formations support the last vestiges of wild quail across the United States, so it is imperative to understand how oil and gas exploration of these formations and the associated disturbance may affect quail populations. Our objective was to determine how bobwhite and scaled quail respond to localized oil and gas disturbance. Specifically, our goal was to document how this disturbance affected their 1) space use (site selection and fidelity) and 2) demographic performance (seasonal survival, nest success, and abundance). We predicted that both bobwhite and scaled quail would avoid sites with greater disturbance and that demographic performance would be lower in these areas.

STUDY AREA

Our study took place on 2 adjacent private ranches in southwestern Dimmit County, Texas. These ranches were within the subtropical steppe climate within the western portion of the Tamaulipan biotic province of southern Texas (Blair 1950). Rainfall was variable between years but averaged 51 cm annually (1981–2010; WRCC 2014). Rainfall amounts peaked in May and October. The average annual high temperature was 28.8° C, and the average annual

low temperature was 14.9° C (1981–2010; WRCC 2014). The ranches consisted of gently undulating (0–5% slopes) gravelly, loam, and sand hills. The dominant soil series were Dilley fine sandy loam, Antosa-Bobillo association, and Randado fine sandy loam (USDA NRCS 2014*b*). We grouped ecological sites (USDA NRCS 2014*a*) within the study area as "deep sands" and "shallow ridges." Vegetation on deep sands sites was composed of mottes of honey mesquite (*Prosopis glandulosa*), granjeno (*Celtis ehrenbergiana*), brasil (*Condalia hookeri* var. *hookeri*), and pricklypear (*Opuntia engelmannii* var. *lindheimeri*), interspersed within a matrix of little bluestem (*Schizachyrium scoparium*), Lehmann's lovegrass (*Eragrostis lehmanniana*), tanglehead (*Heteropogon contortus*), and purple threeawn (*Aristida purpurea*). Shallow ridges were dominated by blackbrush acacia (*Acacia rigidula*), guajillo (*Acacia berlandieri*), and cenizo (*Leucophyllum frutescens*). Common herbaceous species on shallow ridges included common curly mesquite (*Hilaria belangeri*), red grama (*Bouteloua trifida*), Hall's panicum (*Panicum hallii*), and purple threeawn (USDA NRCS 2015). Both ecological sites also contained a wide variety of other woody and herbaceous plant species (>500).

METHODS

We studied an 11.6-km-long oil and gas exploration corridor (primary roads, pipelines, flowlines, and pads) that straddled the border between the 2 ranches. Some disturbed surfaces in the corridor (such as pipeline and flowline rights-of-way) were restored to ecotypic, native herbaceous vegetation (South Texas Natives, Kingsville, TX, USA). We monitored birds for the effects of oil and gas disturbance in 2 spatially independent (separated by 2.3 km) 300-ha focal areas along 6.8 km of this corridor. These 2 areas were paired with 2 300-ha experimental controls ≥0.4 km away, which were undisturbed by oil and gas surface development. Focal area pairs were grouped by ecological type (deep sands and shallow ridges) to represent typical bobwhite and scaled quail habitat, respectively, in southern Texas.

There were a single disturbed experimental unit and a single undisturbed experimental unit for each quail species (i.e., the treatments were unreplicated in each study). However, the inferential statistics used herein were valid, as we intended to apply inferences to quail populations within the 2 units for each species.

Disturbance Measurement

We measured indirect habitat loss via disturbance along roads (vehicle passages and noise) and at point sources of noise in the exploration corridor and their respective paired control areas from March through September (2015 and 2016) to coincide with the quail breeding season. We estimated vehicle passage rate (vehicles/week) in each of the 4 focal areas using 4 Traffic Tally 2 single road tube accumulators (hereafter, traffic counters; Diamond Traffic Products, Oakridge, OR, USA). When a vehicle drove over the traffic counter, air was compressed within the road tube, which sent a pulse of air into the monitoring unit, resulting in a tally of axle passes. Two axle passes counted as 1 vehicle pass. We deployed traffic counters continuously for 1-week periods along each respective road segment and rotated among road segments in each focal area. We classified road segments as any road traversable by passenger vehicle which branched off another road. Road segments that changed direction (curve or bend), but did not cause a vehicle to leave the segment, were not considered an independent segment. We placed traffic counters on the ground 50 m from the beginning of each road segment. At the end of the week-long monitoring period, we moved traffic counters to a new road segment in each of the respective focal areas.

Similar to traffic monitoring, we characterized the noise environment along each road segment March through August (2015 and 2016) with a SoundTrackLxT® Class 1 sound level meter (hereafter, SLM; Larson Davis, Depew, NY, USA). We placed the SLM 100 m from the beginning of each road segment so that the sound of air pulses from the traffic counter would not be measured by the SLM. Since the noise environment is known to vary by time period (California Department of Transportation 2003), we stratified the deployment of the SLM among 4 3-hr time periods (sunrise–0900, 0901–1200, 1201–1500, and 1501–sunset) each day. The SLM was deployed and monitored for 1 hr during each sampling interval. We recorded the sound metrics, maximum sound level (L_{max}) and equivalent average sound level (L_{eq}), and the 1/3-octave band frequency profile, using an A-weighted filter in 1-sec intervals throughout the 1-hr period to produce the maximum and average sound level per second (dBA/sec; Pater et al. 2009, Blickley and Patricelli 2012). A-weighting excludes high and low frequencies to create a profile similar to what a human ear can hear (Blickley and Patricelli 2012), but has been shown to be best for bird studies (Dooling and Popper 2007). Generally, bobwhite can detect sounds that are about 15 dB at their most sensitive frequencies (1,000 and 3,500 Hz); sounds must be about 39 dB at their least sensitive frequencies (250 and 8,000 Hz) for a bobwhite to detect them (Barton et al. 1984). We took sound measurements during optimum weather conditions (27–41° C, wind speeds <18 km/hour, 60–90% humidity) so that measurements were comparable across time periods and focal areas (California Department of Transportation 2003). We excluded measurements during periods in which we could detect additional sources of anthropogenic noise not relevant to the study, such as aircraft noise (e.g., fighter jets passing over), or during nontypical weather events, such as thunderstorms.

In addition to taking disturbance measurements along road segments, we measured the noise environment around point sources, including compressor stations, generators, and pump jacks. We took these measurements with the SLM during May through September (2015 and 2016), using the sound metrics described previously. At each point source of noise, the SLM was placed 3 m away in a randomly chosen cardinal direction (N, S, E, or W). However, because sound

varies in relation to the distance from a unique point source, monitoring of sound from point sources was conducted at stratified distances of 200 and 400 m away in each of the 4 cardinal directions (9 sampling points/point source). The SLM was deployed for 20 min at each of the 9 points, once per field season during optimum weather conditions and similar time periods (sunrise–0900).

Trapping and Radio-telemetry

To determine effects of hydrocarbon exploration on bobwhite and scaled quail space use and demographics during the breeding season, we trapped quail February through July (2015 and 2016) and we tracked quail March through September (2015 and 2016). Handling procedures followed the protocols of the Texas A&M University-Kingsville Institutional Animal Care and Use Committee (permit 2015-03-23). We stratified trap-site placement by using the Create Fishnet tool in ArcMap 10 (Esri Inc., Redlands, CA, USA) to create a grid with 10-ha cells where 1 trap site was selected per grid cell for a total of 24 funnel traps/focal area (96 total; Stoddard 1931). We placed trap sites under dense-canopied shrubs with lateral screening cover to protect birds from heat and predators. Before trapping, we baited trap sites with 1.7 L of grain sorghum (*Sorghum bicolor*) every 4 days before trapping commenced at 12 days. As trapping began, we set and baited funnel traps at 4:00 a.m. We checked traps every 3 hr throughout the day and we closed traps before twilight (Abbott et al. 2005). If temperatures reached 35° C during midday, we set and checked traps only during morning and evening periods. Initially, we trapped quail February through March until a total sample size of 40 quail were fitted with transmitters (10 quail × 4 focal areas = 40 quail, evenly divided between bobwhite and scaled quail). Thereafter, we trapped throughout the field season as needed to maintain the sample size of 40. Trapping effort remained standardized among focal areas. Our goal was to trap bobwhite within the 2 focal areas exhibiting bobwhite habitat (deep sands) and scaled quail in the 2 focal areas exhibiting their habitat (shallow ridges). All captured quail were weighed (g), aged (hatch year or after hatch year), sexed, and leg-banded with a size 7 aluminum leg band (Rosene 1969, Fair et al. 2010). We fitted 40 quail with a 6 g, 150–151.999 MHz, necklace-style radio transmitter (American Wildlife Enterprises, Monticello, FL, USA) if they weighed >150 g (Hernández et al. 2004). Our sample was skewed toward females when possible; a 3:1 ratio of females to males was used to ensure the location of nests. We radio-marked ≤3 quail/trap site to ensure even sampling distribution over the focal areas.

From March through September (2015 and 2016), we located radio-marked quail 2–3 times/ week with a day between locations. We approached quail on foot using a handheld, 3-element Yagi antenna and a 150–151 MHz receiver (Advanced Telemetry Systems Inc., Isanti, MN, USA) until the bird was located via homing. Tracking times for all birds were stratified into 4 time periods throughout the day (sunrise–0900 hours, 0901–1200 hours, 1201–1500 hours, and 1501 hours–sunset) as quail site use is known to vary by time period (Lehmann 1984). Visitation time for each quail was stratified so that each bird eventually had an equal number of locations taken during each time period throughout the course of the field season. We recorded locations using a Garmin Dakota® 20 handheld Global Positioning System (GPS) unit (accuracy <10 m; Garmin International, Inc., Olathe, KS, USA). Data collected at each quail location included the date, time of day, the quail's association with other quail (single, paired, number in the covey, number of chicks present), plant species present within a volumetric 0.25-m^2 quadrat, and any other pertinent observations. When a mortality signal was detected, we retrieved the collar and attempted to determine the cause of mortality.

Nest locations found as a result of monitoring radio-marked birds were recorded using the handheld GPS unit. We did not flush birds off the nest, but rather, we documented clutch size and nesting substrate when the bird was absent from the nest, usually during late evening. Nests were checked 3 times/week without disturbing the hen during typical radio-telemetry sessions. If the radio-telemetry signal was strong at the nest location, it was assumed that the hen was on the nest. Once nesting concluded, we documented nest fate (depredation, destruction, abandonment, successful hatch, or other) and attempted to determine the cause of depredation, destruction, or abandonment.

Data Analysis

Vegetation.—We digitally classified woody cover within our focal areas to link this potentially important variable to site fidelity (home range and core area sizes) and demographic parameters (survival and nest success) for quail. Woody cover is important to quail for loafing, roosting, thermal protection, and protection from predators (Hernández and Peterson 2007, Silvy et al. 2007). To conduct this classification, we obtained 1-m Digital Orthophoto Quarter Quad (DOQQ) imagery from 2014 (TNRIS 2016) and used unsupervised classification in ERDAS IMAGINE (Hexagon Geospatial, Madison, AL, USA). Spatial data from 2014 were the nearest known temporal imagery to our study years and woody cover was similar between years. We performed an accuracy assessment to achieve an accuracy of ≥85% (Congalton 1991). We then related this classified woody cover to quail by creating a 10-m buffer around each quail or nest location with the Buffer tool in ArcMap 10. We then used the Split Raster tool in ArcMap 10 to divide the land cover classification raster into individual raster datasets, using the 10-m buffers as the templates. We used the percentage of landscape (PLAND) calculation in FRAGSTATS (University of Massachusetts, Amherst, MA, USA) to obtain percent woody cover in each individual raster. We then found the mean percent woody cover per quail (for home range size and survival models) by averaging the percent woody cover from all the rasters surrounding an individual quail's locations. Percent woody cover for a nest location was the percentage obtained from the single raster surrounding each nest.

Disturbance.—We conducted analyses in the area available for quail to use, not the original 300-ha focal areas. We determined the area available for use by creating a 402.3-m buffer around all trap sites in each of the 4 focal areas with the Buffer Tool in ArcMap 10. We chose this distance because it represents the average daily movement of a bobwhite (50% of bobwhite spend their life within 0.25 mile of where they hatched; Stoddard 1931). The new area (ha) for the disturbed deep sands, undisturbed deep sands, disturbed shallow ridge, and undisturbed shallow ridge sites were 554 ha, 531 ha, 535 ha, and 506 ha, respectively.

Indirect disturbance was compared between focal areas and modeled to determine effects on quail space use and demographics. For simple comparisons between focal areas, we reported means ± standard error (SE) for vehicle passage rates (vehicles/week) and sound levels (dB) at 250 and 1,000 Hz along primary roads between disturbed and undisturbed treatments in each study year for each ecological type.

To determine the impact of indirect disturbance on quail space use and demographics, we examined effects of distance to nearest road, mean vehicle passage rates of the nearest road, and mean sound level from point sources of oil and gas noise on 3 dependent variables (home range and core area size, seasonal adult survival, and nest success) using multiple regression analyses. We also examined the effect of distance to nearest road and mean sound level from point sources of oil and gas noise on another dependent variable, quail site selection, using continuous selection functions.

We assigned vehicle passage rates to roads in the study area to use distance to nearest road and vehicle passage rates of the nearest road as covariates in the models for home range size, core area size, seasonal adult survival, and nest success. We digitized roads in our study area into polygons with the Create Features tool in ArcMap 10 at a 1:3,000-m scale. Mean weekly vehicle passage rates/year (2015 and 2016) from traffic counter data were assigned to each road segment. We used the Generate Near Table tool in ArcMap 10 to find distance to the nearest road and vehicle passage rate of the nearest road from quail or nest point locations. We modeled noise propagation (dB; monthly average) from oil and gas point sources across our study area for each month of our study using the SPreAD-GIS tool (Reed et al. 2012). Each month during each study year (March though September 2015 and 2016) was modeled independently because noise propagation varies by weather conditions and the point sources present. The tool was implemented in ArcMap 10 and required the following inputs: 1) the point source location, 2) desired model extent (study area), 3) desired frequency level (250 or 1,000 Hz), 4) sound level (dB) of point sources at a specified frequency level (250 or 1,000 Hz), 5) measurement distance (3 m) from point sources, 6) a 30-m resolution digital elevation model (USGS 2016*b*), 7) a 30-m resolution land cover classification (unsupervised classification of LANDSAT 8 imagery from July 2016; USGS 2016*a*), 8) air temperature (°C), 9) relative humidity (%), 10) wind direction (°), 11) wind speed (km/hr), and 12) a 30-m resolution raster layer of ambient sound levels (dB) at a specified frequency level (250 or 1,000 Hz).

We chose to model noise propagation at 2 different frequency levels: 250 and 1,000 Hz. Two hundred fifty Hz is at the lower limit of bobwhite hearing and 1,000 Hz is a maximum level of hearing sensitivity for bobwhite (Barton et al. 1984). The lower limit of bobwhite hearing was chosen because most oil and gas or other human-generated noise has the highest intensity at frequencies below 1,000–2,000 Hz (Dooling 2002, Pohl et al. 2009). We assumed scaled quail had the same sensitivity as bobwhite at these frequencies as no known published information is available for their range of hearing. For the input of sound level of point sources at each of the 2 frequency levels, we used average values for each point source from the 1/3-octave band frequency profile. For land cover classification input, we performed unsupervised classification of 30-m LANDSAT 8 imagery from July 2016 (USGS 2016*a*) in ERDAS IMAGINE. The image was classified into woody, bare ground, herbaceous, impervious anthropogenic surface (e.g., paved roads, barns, houses), and water cover classes. We performed an accuracy assessment to achieve an accuracy of ≥85% (Congalton 1991). For weather data, we used monthly averages of daytime temperature, relative humidity, wind direction, and wind speed from the KFTN weather station (Iowa State University 2017) located ≤10.6 km away on the study site.

To create the final noise propagation models, we assigned ambient sound levels (dB) to each land cover class. Ambient sound levels were environmental sound levels recorded with no interference from vehicle, aircraft, or oil and gas activity for woody, bare ground, and herbaceous cover classes. Default ambient values for impervious anthropogenic surface and water classes were suggested from Harrison et al. (1980). After ambient sound levels were determined, a raster layer of modeled noise propagation was created for each individual point source per month. We then "summed" all raster layers for individual point sources in each month with the SPreAD-GIS tool to create a final raster layer of cumulative noise propagation across the study area per month (March through September 2015 and 2016).

The modeled sound environment in SPreAD-GIS must be validated with field measurements (Reed et al. 2012). Therefore, we tested the accuracy of the 250 and 1,000 Hz models using sound levels (dB) corresponding to each frequency level that we measured in the field (observed values) at each point source and at 200 and 400 m away from each point source in each of the 4 cardinal directions (n = 109). We tested for significant differences ($P < 0.05$) between means of observed values and modeled values. If the means were different, we regressed the observed values against the corresponding modeled values to correct the modeled raster layers in ArcMap 10.

Quail space use.—We conducted all analyses independently by quail species (bobwhite and scaled quail). We hypothesized that quail captured within the disturbed areas would use sites farther from the primary corridor road and there would be no trends in site in relation to the primary roads in undisturbed

areas. We also hypothesized that quail would exhibit greater use of sites closer to ambient sound levels than those sites with sound above ambient levels. We used simple saddlepoint approximation (SSA) to calculate continuous selection functions (DeMaso et al. 2011) to examine quail site use in response to exploration disturbance metrics. We used SSA to algebraically approximate the probability density function (pdf), f(x), of 3 selected variables (proximity of quail locations to the primary corridor road in disturbed areas, proximity of quail locations to the primary road in undisturbed areas, and modeled sound levels at quail locations). We also approximated the pdf, g(x), for the same 3 variables with randomly generated points (we created an equal number of randomly generated points in the area available for quail to use; DeMaso et al. 2011). The continuous selection functions were calculated with $u(x) = f(x)/g(x)$. A selection function value (hereafter, selection ratio) $u(x) > 1$ represented site selection (use greater than availability), $u(x) < 1$ represented site avoidance (use less than availability), and $u(x) = 1$ represented random use of the site (Guthery 1997, Kopp et al. 1998, DeMaso et al. 2011).

We calculated home range and core area sizes to examine second-order (Johnson 1980) site fidelity for quail in which ≥20 locations were collected because site fidelity is likely to be correlated to home range and core area sizes. Home range sizes were calculated using a 95% fixed kernel density estimator with least squares cross validation to choose the smoothing parameter (Seaman and Powell 1996) in BIOTAS (Ecological Software Solutions LLC, Hegymagas, Hungary). Core area sizes were calculated using a 50% fixed kernel density estimator with least squares cross validation to choose the smoothing parameter. Locations where a quail was found on a nest, except the initial location when the nest was discovered, were not included in the analysis of home range and core area sizes.

We used multiple linear regression to test for a relationship between home range and core area size (dependent variables) and independent variables with PROC GLM (generalized linear model procedure) in SAS 9.4 (SAS Institute Inc., Cary, NC, USA). One scaled quail was removed from the regression analysis because its home range size (78 ha) was 204% larger than the mean of the other individuals', and was therefore considered an outlier. Independent variables included in the models were 1) quail age (hatch year or after hatch year), 2) the year in which the quail was monitored (2015 or 2016), 3) mean percent woody cover in a 10-m buffer zone around all locations for each quail, 4) mean sound level at 250 Hz of all locations per quail, 5) mean sound level at 1,000 Hz of all locations per quail, 6) mean distance to the nearest road of all locations per quail, and 7) mean weekly vehicle passage rate of the nearest road of all locations per quail.

Quail demographics.—We estimated indirect oil and gas disturbance effects on the following bobwhite and scaled quail demographics: seasonal adult survival, nest success, and abundance. We calculated seasonal 7-month (Mar–Sep) survival of radio-marked quail with the known-fate model in Program MARK (White and Burnham 1999). Quail that survived ≤14 days were censored from the analysis to account for capture-related mortalities (Cox et al. 2004). Independent variables included in models potentially influencing survival (individual covariates; Table 1) were 1) a linear time trend, 2) encounter occasion, 3) quail age, 4) sex of quail, 5) year the quail was monitored, 6) mean percent woody cover in a 10-m buffer zone around all locations for each quail, 7) mean sound level at 250 Hz of all locations for each quail, 8) mean sound level at 1,000 Hz of all locations for each quail, 9) mean distance to the nearest road of all locations for each quail, and 10) mean weekly vehicle passage rate of the nearest road of all locations for each quail. We used these covariates to select 19 *a priori* candidate models (Table 1); the same models were used for both species. These were ranked using Akaike's Information Criterion corrected for small sample size (AIC_c; Hurvich and Tsai 1989). We chose the model with the highest AIC_c as the top model, if the parameter estimates in the model had confidence intervals that did not include 0. Models within 2 ΔAIC_c of the top model, which differed from the top model

Table 1. *A priori* candidate models used to assess seasonal (7-month; Mar–Sep) survival probability (S) of northern bobwhite (*Colinus virginianus*) and scaled quail (*Callipepla squamata*) using known fate models in Program MARK, Dimmit County, Texas, USA, 2015–2016.

Model number	Model	Number of parameters
1	S (T[a])	2
2	S (t[b])	31
3	S (Age[c])	2
4	S (Sex[d])	2
5	S (Year[e])	2
6	S (Woody[f])	2
7	S (dB250[g])	2
8	S (dB1000[h])	2
9	S (Road Dist[i])	2
10	S (Traffic[j])	2
11	S (.[k])	1
12	S (T + Age)	3
13	S (T + Sex)	3
14	S (Age + Sex + Age × Sex)	4
15	S (dB250 + Age + dB250 × Age)	4
16	S (dB1000 + Age + dB1000 × Age)	4
17	S (Road Dist + Traffic)	3
18	S (Road Dist + Age + Road Dist × Age)	4
19	S (Traffic + Age + Traffic × Age)	4

[a] Linear trend across time
[b] Encounter occasion
[c] Quail age
[d] Quail sex
[e] Year quail was monitored
[f] Percent woody cover
[g] Sound level (dB) at 250 Hz
[h] Sound level (dB) at 1,000 Hz
[i] Distance to nearest road
[j] Vehicle passage rate
[k] Constant probability

by one parameter and had essentially the same values of the maximized log-likelihood, were not considered competitive with the top model (Burnham and Anderson 2002, Arnold 2010). We used the derived estimate from the top model for each species to obtain the seasonal survival estimate.

We calculated probability of nest success with the Nest Survival model in Program MARK. Independent variables (individual covariates; Table 2) were 1) a linear time trend, 2) encounter occasion, 3) quail age, 4) year the quail was monitored, 5) mean percent woody cover in a 10-m buffer zone around each nest location, 6) mean sound level at 250 Hz of each nest location, 7) mean sound level at 1,000 Hz of each nest location, 8) mean distance to the nearest road of each nest location, and 9) mean weekly vehicle passage rate of the nearest road to each nest location. We used these covariates to select 12 *a priori* candidate models (Table 2); the same models were used for each species. These were ranked using AIC_c (Hurvich and Tsai 1989). We chose the model with the highest AIC_c as the top model, if the parameter estimates in the model had confidence intervals that did not include 0. Models within 2 ΔAIC_c of the top model, which differed from the top model by one parameter and had essentially the same values of the maximized log-likelihood, were not considered competitive with the top model (Burnham and Anderson 2002, Arnold 2010). We raised daily nest survival rate for each species (either from the top model or model averaging) to the 23rd power (23 days is the average incubation period for both species) to obtain an estimate of nest success.

Table 2. *A priori* candidate models used to assess northern bobwhite (*Colinus virginianus*) and scaled quail (*Callipepla squamata*) probability of nest success (S) with nest survival models in Program MARK, Dimmit County, Texas, USA, 2015–2016.

Model number	Model	Number of parameters
1	S (T[a])	2
2	S (t[b])	13
3	S (Age[c])	2
4	S (Year[d])	2
5	S (Woody[e])	2
6	S (dB250[f])	2
7	S (dB1000[g])	2
8	S (Road Dist[h])	2
9	S (Traffic[i])	2
10	S (.[j])	1
11	S (T + Age)	3
12	S (Road Dist + Traffic)	3

[a] Linear trend across time
[b] Encounter occasion
[c] Quail age
[d] Year quail was monitored
[e] Percent woody cover
[f] Sound level (dB) at 250 Hz
[g] Sound level (dB) at 1,000 Hz
[h] Distance to nearest road
[i] Vehicle passage rate
[j] Constant probability

We estimated density (ha/quail) with the Density Using Telemetry model in Program MARK for all quail, comparing disturbed and undisturbed areas within the 2 ecological sites. All quail, regardless of species, were considered in density estimates because both species were found in all focal areas (though there was definite resource partitioning). We also estimated density of each species in its respective focal areas (bobwhite in deep sands sites and scaled quail within shallow ridge sites). Density Using Telemetry models require encounter history of banded individuals from trapping, and the proportion of telemetry locations within the study site (of banded and radio-marked individuals) after trapping has ended. Encounter histories from all banded quail in the first trapping interval of the season were used because they took place before the peak nesting season began. This interval was chosen to help meet the model assumption of a closed demographic population (no births or deaths). We used the subsequent 4 telemetry locations after the trapping of each banded and radio-marked quail to estimate density because 4 locations would have been obtained within 2 weeks. Because trap sites were not perfectly spaced within focal areas, traps were buffered to 316.2 m (the length of one side of a 10-ha, square, trapping grid cell) with the Buffer tool in ArcMap 10 to create 4 polygons in which to determine if a telemetry location was in or out of the study site. Mean density estimates (±SE) for each species were reported for disturbed and undisturbed sites across both study years.

RESULTS

Habitat Loss

Although direct habitat loss is known to occur with oil and gas development, temporary habitat loss due to indirect effects has been less clear. We measured indirect habitat loss by measuring vehicle passage rates and the sound environment. Mean vehicle passage rates (vehicles/week) along primary roads during 2015–2016 were 444.2 ± 136.8 ($\bar{x} \pm SE$) in the disturbed deep sands site, 762.6 ± 229.3 in the disturbed shallow ridge site, 51.5 ± 15.1 in the undisturbed deep sands site, and 11.7 ± 4.0 in the undisturbed shallow ridge site. Mean sound levels (dB) at 250 Hz along primary roads during 2015–2016 were 39.9 ± 2.3 ($\bar{x} \pm SE$) in the disturbed deep sands site, 42.4 ± 2.7 in the disturbed shallow ridge site, 27.5 ± 1.8 in the undisturbed deep sands site, and 23.3 ± 0.7 in the undisturbed shallow ridge site. Mean sound levels (dB) at 1,000 Hz along primary roads during 2015–2016 were 34.3 ± 1.8 in the disturbed deep sands site, 36.5 ± 3.6 in the disturbed shallow ridge site, 21.0 ± 1.6 in the undisturbed deep sands site, and 17.5 ± 1.6 in the undisturbed shallow ridge site.

There were 11 point sources of oil and gas noise within the study area in 2015. Two of these ceased operations in 2016, so there were 9 point sources of noise within the study area in 2016. The mean ambient sound levels (dB) for the woody, bare ground, and herbaceous classes were 27.8 (n = 3 recordings)

and 22.4 (n = 3 recordings) for the 250 Hz and 1,000 Hz frequency levels, respectively. Although ambient sound level estimates were based on 3 field measurements from the study site, they were similar to ambient levels for shrubland reported by Harrison et al. (1980). Sound levels (dB) at the actual location of point sources for the 250 Hz frequency level averaged 71.1 for compressor stations (n = 4 recordings), 69.3 for diesel-powered generators (n = 1 recording), 64.4 for gas-powered generators (n = 4 recordings), and 55.0 for pump jack motors (n = 4 recordings). Furthermore, sound levels (dB) at the actual location of point sources for the 1,000 Hz frequency level averaged 57.8 for compressor stations (n = 4 recordings), 70.1 for diesel generators (n = 1 recording), 62.8 for gas generators (n = 4 recordings), and 55.7 for pump jack motors (n = 4 recordings). When modeling sound away from point sources, we found that the SPreAD-GIS software underestimated sound levels at both frequency levels when compared to observed values in the study area. We corrected the modeled values for each month of the study with a regression equation ($y = 13.50 + 1.16x$, $r^2 = 55.7$, $P \leq 0.001$ for 250 Hz; $y = 4.47 + 2.05x$, $r^2 = 53.7$, $P \leq 0.001$ for 1,000 Hz) specific to each frequency level.

Quail Space Use

We assessed bobwhite and scaled quail site use by analyzing selection in relation to 1) the primary roads in disturbed focal areas and the primary roads in undisturbed focal areas and 2) sound levels. We also estimated site fidelity of bobwhite and scaled quail through home range and core area sizes, as the size of these areas is likely to be correlated to fidelity of a given area. We banded 192 bobwhite and 197 scaled quail and radio-marked 68 bobwhite and 50 scaled quail during the study. In the disturbed area, bobwhite selected for areas 0–200 m from the primary road (Figure 1A) and selected for areas 0–425 m from primary roads in the undisturbed area (Figure 1B). Scaled quail selected for areas >425 m from the primary road in the disturbed area (Figure 1A) and selected for areas 0–300 m from primary roads in the undisturbed area (Figure 1B).

In addition to measuring site use in relation to primary roads, we measured selection in relation to the sound environment. Bobwhite selected for areas with sound levels 0–1.6 dB above ambient levels and avoided areas >1.6 dB above ambient levels at the 250 Hz frequency level (Figure 2A). At the 1,000 Hz frequency level, bobwhite selected for areas with sound levels 0–2 dB above ambient levels and avoided areas >2 dB above ambient levels (Figure 2B). Scaled quail selected for areas with sound levels 0–2.2 dB above ambient levels and avoided areas >2.2 dB above ambient levels at the 250 Hz frequency level (Figure 2A). At the 1,000 Hz frequency level, scaled quail selected for areas with sound levels 0–3.2 dB above ambient levels and avoided areas >3.2 dB above ambient levels (Figure 2B).

Although there was no oil and gas surface development in the undisturbed sites, modeled sound levels were greater than ambient levels in some parts of the undisturbed sites due to noise propagation from the disturbed sites. Therefore,

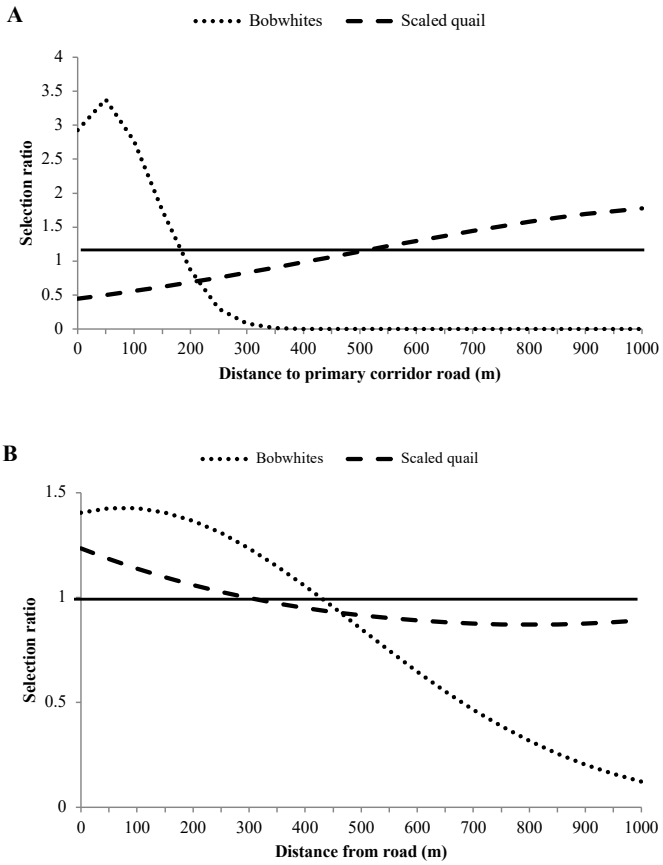

Fig. 1. Continuous selection functions for northern bobwhite (*Colinus virginianus*; dotted line) and scaled quail (*Callipepla squamata*; dashed line) distance A) to the primary road in the disturbed focal areas and B) to primary roads in the undisturbed focal areas, Dimmit County, Texas, USA, 2015–2016. Selection ratios >1 indicate selection and ratios <1 indicate avoidance.

habitat loss from oil and gas noise was estimated in both the disturbed and undisturbed sites. Based on sound modeling from SPreAD-GIS and sound level avoidance by bobwhite at the 250 Hz frequency (Figure 2A), we estimated that 43.0% (238.4 ha) and 13.2% (70.1 ha) of habitat may have been temporarily lost in 2015 in the disturbed deep sands site and undisturbed deep sands site, respectively. Furthermore, in 2016, we estimated that 47.4% (262.4 ha) and 21.5% (114.2 ha) of the total area within these focal areas may have been temporarily lost in the disturbed deep sands site and undisturbed deep sands site, respectively, based on bobwhite sound level avoidance at the 250 Hz frequency. Based on sound level avoidance by bobwhite at the 1,000 Hz frequency (Figure 2B), we estimated that 23.9% (132.4 ha) and 14.7% (77.9 ha) of habitat may have been temporarily lost in 2015 in the disturbed deep sands site and undisturbed deep sands site, respectively. In 2016, we estimated that 11.5% (63.9 ha) and 14.2% (75.4 ha) of the total area within these focal areas may have been temporarily lost in the disturbed deep sands site and undisturbed deep sands site, respectively, based on bobwhite sound level avoidance at the 1,000 Hz frequency.

For scaled quail, we estimated that 26.9% (144.1 ha) and

13.5% (68.5 ha) of habitat may have been temporarily lost in 2015 in the disturbed shallow ridge site and the undisturbed shallow ridge site, respectively, based on scaled quail sound level avoidance at the 250 Hz frequency (Figure 2A). In 2016, 26.8% (143.1 ha) and 3.4% (17.4 ha) of habitat may have been temporarily lost in the disturbed shallow ridge site and undisturbed shallow ridge site, respectively, based on scaled quail sound level avoidance at the 250 Hz frequency. Based on scaled quail avoidance at the 1,000 Hz frequency (Figure 2B), we estimated that 12.6% (67.4 ha) and 10.9% (55.4 ha) of habitat may have been temporarily lost in 2015 in the disturbed shallow ridge site and the undisturbed shallow ridge site, respectively. In 2016, 16.6% (88.8 ha) and 9.9% (50 ha) of habitat may have been temporarily lost in the disturbed shallow ridge site and undisturbed shallow ridge site, respectively, based on scaled quail sound level avoidance at the 1,000 Hz frequency.

We used home range and core area size as estimators of site fidelity. Home range and core area size estimates ($\bar{x}$ ± SE) were pooled by quail species, between disturbed and undisturbed focal areas, and between years because of sample size. Bobwhite home range size averaged 19.7 ± 3.1 ha (2015–2016) and bobwhite core area size averaged 3.6 ± 0.8 ha (2015–2016). Scaled quail home range size averaged 27.7 ± 2.9 ha (2015–2016) and scaled quail core area size averaged 4.9 ± 0.6 ha (2015–2016). For bobwhite, mean home range size was not statistically different ($F_{1, 19} = 0.32$, $P = 0.580$) between disturbed (21.9 ± 5.0 ha, $n = 8$) and undisturbed areas (18.2 ± 4.1 ha, $n = 12$; Figure 3A). Mean core area size for bobwhite also was not different ($F_{1, 19} = 0.27$, $P = 0.610$) between disturbed (4.1 ± 1.3 ha, $n = 8$) and undisturbed areas (3.2 ± 1.1 ha, $n = 12$; Figure 3B). For scaled quail, mean home range size was not different ($F_{1, 25} = 0.62$, $P = 0.438$) between disturbed (29.9 ± 4.04 ha, $n = 14$) and undisturbed areas (25.2 ± 4.4 ha, $n = 12$; Figure 3A). Mean core area size for scaled quail also was not different ($F_{1, 25} = 0.73$, $P = 0.402$) between disturbed (5.4 ± 0.9 ha, $n = 14$) and undisturbed areas (4.3 ± 0.9 ha, $n = 12$; Figure 3B). Home range and core area sizes for both species, however, were smaller in undisturbed areas compared to disturbed focal areas.

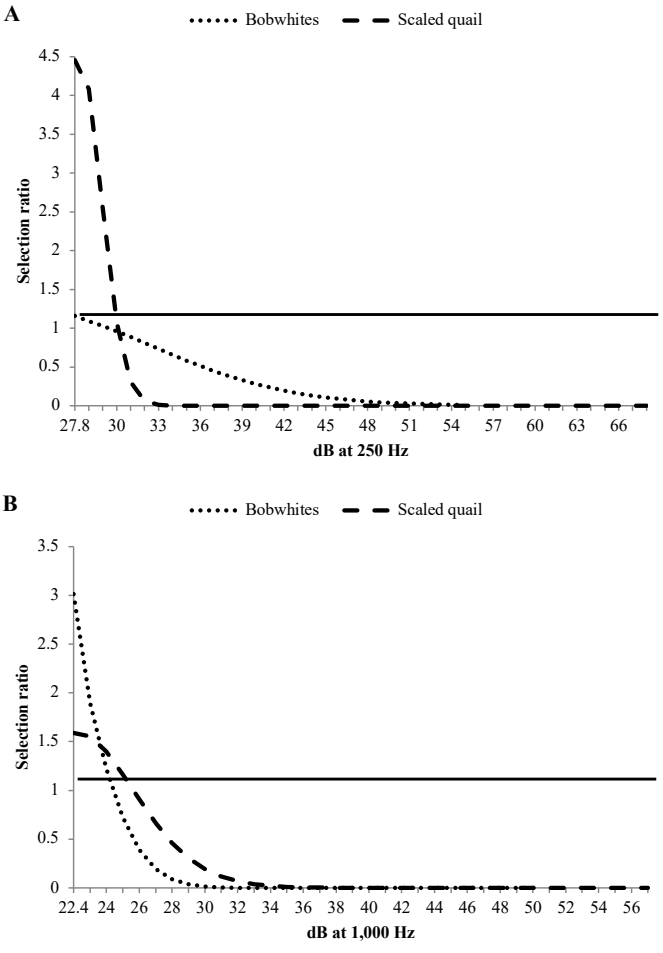

Fig. 2. Continuous selection functions for northern bobwhite (*Colinus virginianus*; dotted line) and scaled quail (*Callipepla squamata*; dashed line) at sound levels at the A) 250 Hz and B) 1,000 Hz frequency levels, Dimmit County, Texas, USA, 2015–2016. Selection ratios >1 indicate selection and ratios <1 indicate avoidance. The x-axes begin at ambient sound levels.

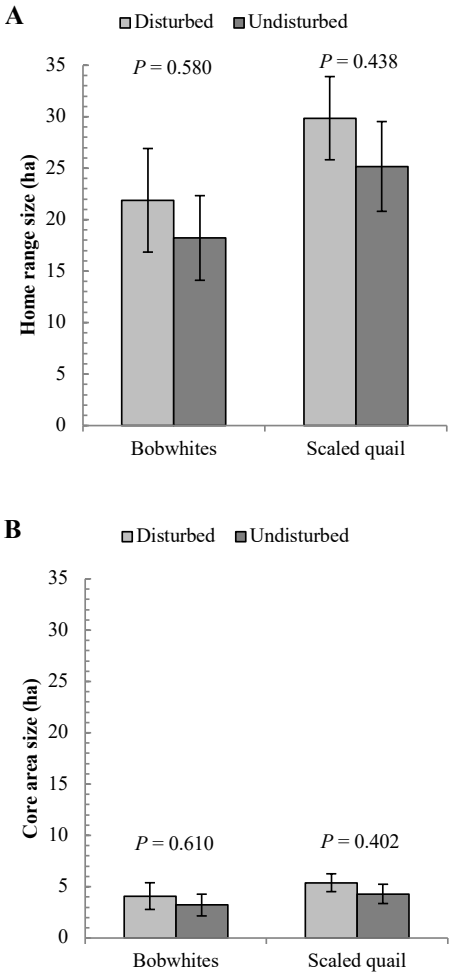

Fig. 3. Mean size (ha; $\bar{x}$ ± standard error) of A) home ranges and B) core areas of northern bobwhite (*Colinus virginianus*) and scaled quail (*Callipepla squamata*) in disturbed and undisturbed focal areas, Dimmit County, Texas, USA, 2015–2016.

We found no significant ($P > 0.359$ for bobwhite, $P > 0.127$ for scaled quail) effects (year, age, mean % woody cover, mean dB level at 1,000 Hz, mean dB level at 250 Hz, mean distance to the nearest road, and mean weekly vehicle passage rate) on home range and core area size for either species of quail ($n = 20$ for bobwhite, n = 25 for scaled quail).

Quail Demographics

Survival.—Bobwhite and scaled quail seasonal (7-month; Mar–Sep) survival averaged 11.9 ± 5.1% ($\bar{x}$ ± SE, $n = 44$) and 43.8 ± 9.0% ($\bar{x}$ ± SE, $n = 44$), respectively. According to AIC_c model rank, time since capture had the greatest influence on bobwhite survival probability. The model S(T) was competitive with the top model because it was within 2 ΔAIC_c of the top model and 95% confidence intervals around the parameter estimates did not include 0. The two models with the highest AIC_c had parameter estimates with 95% confidence intervals that included 0 (Table 3, Figure 4), so they were not considered the top model. According to AIC_c model rank, the null model best explained scaled quail survival (the model S[.] was the top model and models within 2 ΔAIC_c had parameter estimates with 95% confidence intervals that included 0; Table 4). We did not find any effects of oil and gas disturbance (sound levels at 250 Hz or 1,000 Hz, distance to the nearest road, and vehicle passage rates of the nearest road) on survival for either species of quail.

Nest success.—During the study, we located 26 bobwhite and 17 scaled quail nests. We monitored 1 quail nest (that was eventually unsuccessful) in 2016 that had 10 bobwhite eggs and 5 scaled quail eggs, and was incubated by a radio-marked bobwhite hen. We designated this nest as a bobwhite nest. Bobwhite and scaled quail nest success averaged 49.8 ± 12.4% ($\bar{x}$ ± SE, $n = 26$) and 38.1 ± 18.9% ($\bar{x}$ ± SE, $n = 17$), respectively. According to AIC_c model rank, bobwhite nest success was influenced the most by sound levels at 250 Hz (the model S[dB250] was the top model, 95% confidence intervals around the parameter estimates did not include 0, and there were no models within 2 ΔAIC_c of the top model; Table 5, Figure 5). According to AIC_c model rank, scaled quail nest success was influenced the most by study year (the model S[Year] was the top model, 95% confidence intervals around the parameter estimates did not include 0, and there were no models within 2 ΔAIC_c of the top model; Table 6).

Abundance.—Density of all quail (ha/quail; $\bar{x}$ ± SE) in both the deep sands site and shallow ridge site pooled across study years was not statistically different between disturbed and undisturbed areas as standard errors overlapped (Figure 6A). Density of just bobwhite in the deep sands site was not statistically different in disturbed (1.5 ± 0.5; $n = 40$) and undisturbed (1.5 ± 0.4; $n = 39$) areas as standard errors overlapped (Figure 6B). Density of just scaled quail in the shallow ridge site was 150% lower in the disturbed area (8.5 ± 3; $n = 7$) than in the undisturbed area (3.4 ± 1.1; $n = 16$; Figure 6B).

Table 3. Candidate models and their associated Akaike's Information Criterion (AIC_c) model rank, ΔAIC_c, number of parameters, and model weight used in seasonal (7-month; Mar–Sep) survival probability (S) analysis of northern bobwhite (*Colinus virginianus*), Dimmit County, Texas, USA, 2015–2016.

Model	AIC_c	ΔAIC_c	Number of parameters	AIC_c weight
S (T[a] + Sex[b])	217.5076	0.0000	3	0.2161
S (T + Age[c])	217.9236	0.4160	3	0.1755
S (T)	218.1207	0.6131	2	0.1591
S (.[d])	226.2356	8.7280	1	0.0028
S (Sex + Age + Sex × Age)	226.6847	9.1771	3	0.0022
S (Sex)	227.1913	9.6837	2	0.0017
S (Year[e])	227.3012	9.7936	2	0.0016
S (Age)	227.3819	9.8743	2	0.0016
S (dB250[f])	227.5340	10.0264	2	0.0014
S (Woody[g])	228.0885	10.5809	2	0.0011
S (Road Dist[h])	228.1296	10.6220	2	0.0011
S (Traffic[i])	228.2508	10.7432	2	0.0010
S (dB1000[j])	228.2509	10.7433	2	0.0010
S (dB250 + Age + dB250 × Age)	229.7362	12.2286	4	0.0005
S (Traffic + Road Dist)	230.1210	12.6134	3	0.0004
S (Road Dist + Age + Road Dist × Age)	230.4299	12.9223	4	0.0003
S (Traffic + Age + Traffic × Age)	230.9610	13.4534	4	0.0003
S (dB1000 + Age + dB1000 × Age)	231.3884	13.8808	4	0.0002
S (t[k])	245.7296	28.2220	31	0.0000

[a] Linear trend across time
[b] Encounter occasion
[c] Quail age
[d] Constant probability
[e] Year quail was monitored
[f] Sound level (dB) at 250 Hz
[g] Percent woody cover
[h] Distance to nearest road
[i] Vehicle passage rate
[j] Sound level (dB) at 1,000 Hz
[k] Encounter occasion

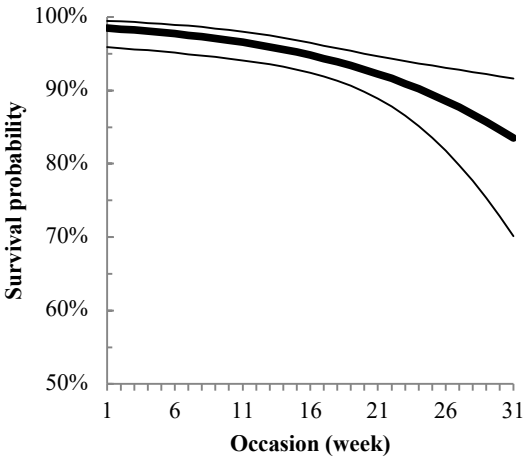

Fig. 4. Northern bobwhite (*Colinus virginianus*) seasonal (7-month; Mar–Sep) survival probability estimates (%; $\bar{x}$ ± standard error) across time since capture, Dimmit County, Texas, USA, 2015–2016.

Table 4. Candidate models and their associated Akaike's Information Criterion (AIC_c) model rank, ΔAIC_c, and number of parameters used in seasonal (7-month; Mar–Sep) survival probability (S) analysis of scaled quail (*Callipepla squamata*), Dimmit County, Texas, USA, 2015–2016.

Model	AIC_c	ΔAIC_c	Number of parameters	AIC_c weight
S (.[a])	150.0378	0.0000	1	0.1564
S (Road Dist[b])	150.8863	0.8485	2	0.1023
S (dB1000[c])	151.1821	1.1443	2	0.0883
S (Year[d])	151.5791	1.5413	2	0.0724
S (T[e])	151.6140	1.5762	2	0.0711
S (Age[f])	151.6673	1.6295	2	0.0692
S (Traffic[g])	151.7826	1.7448	2	0.0654
S (dB250[h])	151.9162	1.8784	2	0.0611
S (Woody[i])	151.9496	1.9118	2	0.0601
S (Sex[j])	152.0445	2.0067	2	0.0573
S (dB1000 + Age + dB1000 × Age)	152.7672	2.7294	4	0.0400
S (Road Dist + Traffic)	152.8058	2.7680	3	0.0392
S (T + Age)	153.1707	3.1329	3	0.0327
S (T + Sex)	153.6329	3.5951	3	0.0259
S (Road Dist + Age + Road Dist × Age)	153.6329	3.8500	4	0.0228
S (Traffic + Age + Traffic × Age)	153.8878	4.7584	4	0.0145
S (dB250 + Age + dB250 × Age)	154.7962	5.1599	4	0.0119
S (Age + Sex + Age × Sex)	155.6502	5.6124	4	0.0095
S (t[k])	189.7412	39.7034	31	0.0000

[a] Constant probability
[b] Distance to nearest road
[c] Sound level (dB) at 1,000 Hz
[d] Year quail was monitored
[e] Linear trend across time
[f] Quail age
[g] Vehicle passage rates
[h] Sound level (dB) at 250 Hz
[i] Percent woody cover
[j] Quail sex
[k] Encounter occasion

Table 5. Candidate models and their associated Akaike's Information Criterion (AIC_c) model rank, ΔAIC_c, and number of parameters used in probability of nest success (S) analysis of northern bobwhite (*Colinus virginianus*), Dimmit County, Texas, USA, 2015–2016.

Model	AIC_c	ΔAIC_c	Number of parameters	AIC_c weight
S (dB250[a])	66.9639	0.0000	2	0.3970
S (.[b])	69.5655	2.6016	1	0.1081
S (Road Dist[c])	70.0746	3.1107	2	0.0838
S (Year[d])	70.0790	3.1151	2	0.0836
S (dB1000[e])	70.0881	3.1242	2	0.0833
S (T[f])	70.8887	3.9248	2	0.0558
S (Woody[g])	70.9455	3.9816	2	0.0542
S (Age[h])	71.4454	4.4815	2	0.0422
S (Traffic[i])	71.5056	4.5417	2	0.0410
S (Road Dist + Traffic)	72.1076	5.1437	3	0.0303
S (T + Age)	72.8937	5.9298	3	0.0205
S (t[j])	82.4627	15.4988	13	0.0002

[a] Sound level (dB) at 250 Hz
[b] Constant probability
[c] Distance to nearest road
[d] Year quail was monitored
[e] Sound level (dB) at 1,000 Hz
[f] Linear trend across time
[g] Percent woody cover
[h] Quail age
[i] Vehicle passage rate
[a] Encounter occasion

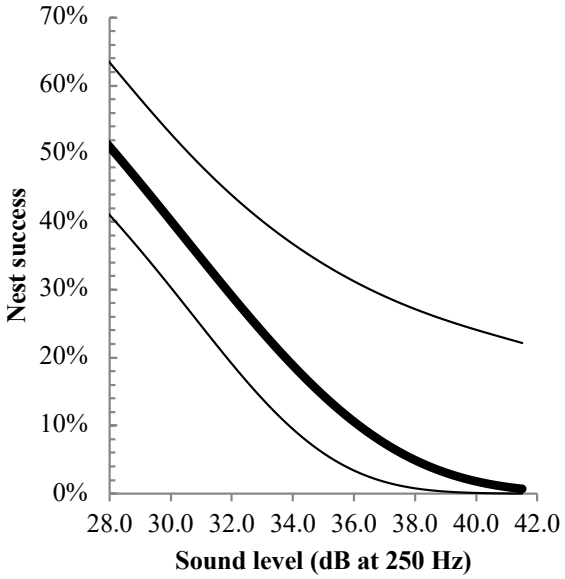

Fig. 5. Northern bobwhite (*Colinus virginianus*) nest success estimates ($\bar{x}$ ± standard error) across sound levels (dB) at the 250 Hz frequency level, Dimmit County, Texas, USA, 2015–2016.

Table 6. Candidate models and their associated Akaike's Information Criterion (AIC_c) model rank, ΔAIC_c, and number of parameters used in probability of nest success (S) analysis of scaled quail (*Callipepla squamata*), Dimmit County, Texas, USA, 2015–2016.

Model	AIC_c	ΔAIC_c	Number of parameters	AIC_c weight
S (Year[a])	43.1704	0.0000	2	0.2321
S (dB1000[b])	46.3150	3.1446	2	0.0482
S (.[c])	46.4215	3.2511	1	0.0457
S (Age[d])	46.4828	3.3124	2	0.0443
S (Road Dist[e])	46.9223	3.7519	2	0.0356
S (T[f])	46.9699	3.7995	2	0.0347
S (T + Age)	47.6830	4.5126	3	0.0243
S (dB250[g])	47.8073	4.6369	2	0.0228
S (Woody[h])	48.1627	4.9923	2	0.0191
S (Traffic[i])	48.4711	5.3007	2	0.0164
S (Road Dist + Traffic)	48.9945	5.8241	3	0.0126
S (t[j])	160.2032	117.0328	10	0.0000

[a] Year quail was monitored
[b] Sound level (dB) at 1,000 Hz
[c] Constant probability
[d] Quail age
[e] Distance to nearest road
[f] Linear trend across time
[g] Sound level (dB) at 250 Hz
[h] Percent woody cover
[i] Vehicle passage rate
[j] Encounter occasion

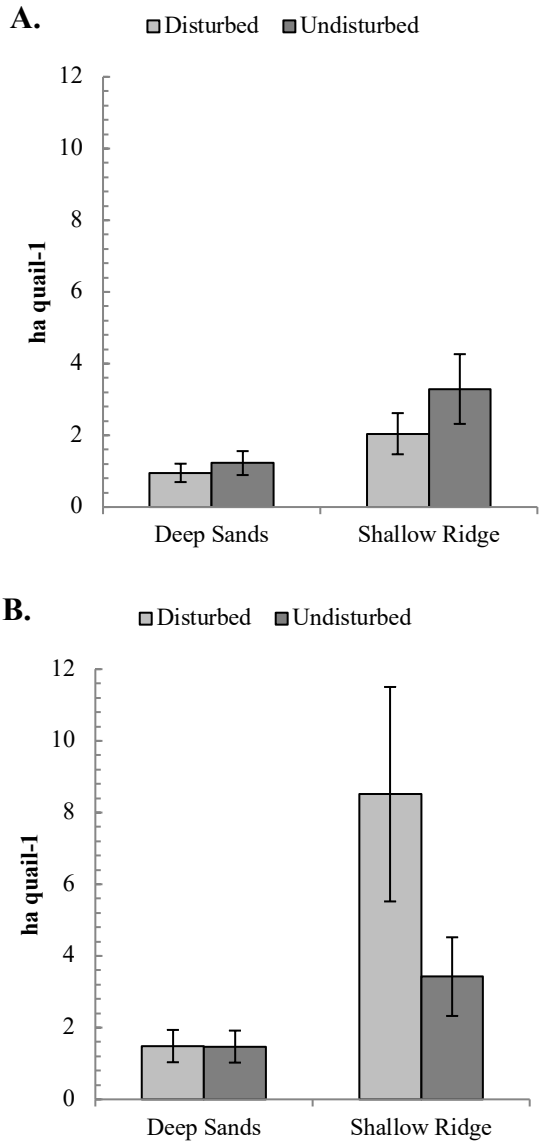

Fig. 6. Density (ha/quail; $\bar{x}$ ± standard error) pooled across study years of A) all quail (northern bobwhite [*Colinus virginianus*] and scaled quail [*Callipepla squamata*]) and B) just northern bobwhite in deep sands sites and just scaled quail in shallow ridge sites, Dimmit County, Texas, USA, 2015–2016.

DISCUSSION

We examined the effects of oil and gas activity on bobwhite and scaled quail space use and demographics. Site selection of quail was affected by disturbance along roads and among various sound levels. We found no evidence that sound levels or vehicle passages affected site fidelity (represented by home range and core area sizes) or quail survival. Bobwhite nest success decreased as sounds levels increased; we found no effects of disturbance on scaled quail nest success. Density of bobwhite was not different between treatments. Density of scaled quail was lower in the disturbed area than in the undisturbed area. We suggest that noise and traffic activity may cause indirect loss of habitat for quail (in addition to direct, physical loss of habitat caused by habitat destruction or habitat fragmentation due to development) by influencing their space use and nest success. This indirect loss potentially could be temporary if activity ceased.

Quail Space Use

Both bobwhite and scaled quail selected for sites close to primary roads in the undisturbed areas. However, site use varied by species in disturbed areas as bobwhite selected for areas near the primary road while scaled quail avoided areas near the primary road. There have been other studies that report differences in avian species responses to anthropogenic

disturbance. For example, Sutter et al. (2016) found greater abundance of vesper sparrow (*Pooecetes gramineus*) nests near a pipeline right-of-way during construction and clean-up activity in Canada, while Sprague's pipit (*Anthus spragueii*) nests were evenly distributed. Additionally, Bogard and Davis (2014) observed that some species of grassland songbirds were less abundant near natural gas wells in Canada, whereas abundance of other avian species was higher near gas wells or not affected. One possible reason quail species responded differently in our study is that bobwhite may be more tolerant of human-generated disturbance. Furthermore, bobwhite may have preferred disturbed areas along the road because soils disturbed by pads, pipelines, and flowlines were reseeded with native herbaceous plants. This practice may have improved potentially limiting habitat attributes for bobwhite such as nesting sites (bunchgrasses) in an otherwise xeric plant community. Third, traffic rates were highly variable on primary roads in disturbed areas; we were not able to associate site selection of roads with traffic levels as traffic levels were long-term averages. Bobwhite could have avoided these roads during high-traffic periods but selected for them during low-traffic periods. Last, it is possible that different responses between disturbed and undisturbed treatments for bobwhite or between quail species in the disturbed treatments were due to differences in overall habitat structure and select vegetation metrics.

Both bobwhite and scaled quail appeared to avoid use of sites with sound levels from point sources greater than about 2–3 dB above estimated ambient sound levels. Chronic noise from generators, compressor stations, and pumpjack motors may have caused quail to avoid loud noise due to increased stress or an inability to communicate (Blickley et al. 2012, Francis and Barber 2013). Our findings of quail site avoidance of high-noise areas were similar to those of Francis et al. (2009) and Blickley et al. (2012). The earlier study found that 4 species of passerines avoided using nest sites near well pads with noisy compressors (Francis et al. 2009). The other study found that greater sage-grouse had reduced attendance at leks subjected to playback of recorded natural gas drilling and traffic noise (Blickley et al. 2012).

We expected quail to have greater home range and core area size in disturbed areas. Although mean home range and core area size were not statistically different between disturbed and undisturbed areas for either species, mean sizes were greater in disturbed areas for both species. Sample sizes could have been too low to detect a significant difference in home range and core area sizes. Additionally, we did not detect an effect of sound levels or vehicle passage rates on home range and core area sizes. Our findings were generally similar to those of Drolet et al. (2016), as they found no effect of drilling noise on the home range sizes of white-tailed deer (*Odocoileus virginianus*). They suggested that philopatry of their home range or tolerance of the noise kept deer from changing their home range size. Our findings were dissimilar to those of Webb et al. (2011), as they found home range and core area size for female elk (*Cervus canadensis*) were negatively influenced by the proportion of human development in their respective ranges. Although elk had high levels of site fidelity (represented by home range and core area overlap) in the presence of human development, site fidelity level decreased as development increased. In our study, because quail avoided using areas with high sound levels from point sources, home range and core area sizes were not likely to be affected. This is similar to an explanation by Hershey and Leege (1982), who suggested that animals may not abandon home ranges if they have undeveloped areas to use in other portions of their home range. Alternatively, disturbance from sound or vehicles (or both) may have caused localized movements (such as flushing from a threat), but these movements may not have impacted home range or core area size.

Quail Demographics

We expected survival of both quail species to decrease as sound levels and vehicle passage rates increased because vehicle passage rate could result in increased collisions and noise could obscure sounds of approaching predators (Francis et al. 2012) or result in movements that could increase predation risk. For example, mortality of adult Florida scrub-jays (*Aphelocoma coerulescens*) living along a 2-lane highway was higher than birds not living along roads, due to vehicle collisions (Mumme et al. 2000). Similarly, yearling greater sage-grouse reared in areas with natural gas infrastructure had lower annual survival than those in areas without it (Holloran et al. 2010). It is not necessarily surprising that there was no impact of vehicle passages on scaled quail as they avoided the area along the primary road in the disturbed area. We did find an unmarked bobwhite on the primary exploration road during our study that apparently had been killed in a vehicle collision. Both quail species appeared to avoid noisy areas and therefore were less likely to be impacted by noise.

We may not have found an effect of disturbance on survival because we used average vehicle passage rates of the nearest road at quail locations as covariates in our models for quail survival. These measurements may not have been fine-scale enough to detect a one-time event that would cause quail death, such as being struck by a vehicle or intermittent traffic noise obscuring the sound of a predator. It should be noted that bobwhite had lower survival probability than scaled quail, which avoided the primary road in the disturbed area. Furthermore, survival probability of bobwhite was lower than other estimates reported in the literature (Burger et al. 1995, Sisson et al. 2009, Downey et al. 2017).

We found that nest success of bobwhite decreased as sound levels from point sources increased (at the 250 Hz frequency level). Other researchers have found similar impacts of noise-related disturbance on birds. For instance, Strasser and Heath (2013) found that American kestrels (*Falco sparverius*) had higher stress hormones in areas with traffic disturbance and human development, which led to increased nest abandonment. We did not detect impacts of oil and gas disturbance on scaled quail nest success. Again, this result is not surprising, as similar to adult site use, scaled quail generally placed nests

out of the range of sound above ambient levels at 250 Hz. As a comparison, bobwhite placed nests in areas ranging from ambient levels to 13.7 dB above ambient levels. The narrow range used by scaled quail when selecting nest sites suggests that scaled quail may be more sensitive to noise disturbance than bobwhite. Alternatively, bobwhite and scaled quail may have different ranges of hearing sensitivity.

We expected sound levels at 1,000 Hz also to impact nest success. However, both quail species selected nest sites with relatively low average sound levels at 1,000 Hz (ambient to 4.2 dB and 7.5 dB above ambient for bobwhite and scaled quail, respectively); therefore, nests were not subject to potential impacts of high sound levels. Similar to our findings, Pitman et al. (2005) reported that lesser prairie-chickens (*Tympanuchus pallidicinctus*) in Kansas, USA avoided areas near well heads and compressor stations when selecting nest sites, but they were unable to link apparent nest success to distance from these structures. In contrast to our findings for both quail species, gray flycatcher (*Empidonax wrightii*) nest success increased in areas with gas well compressor noise in New Mexico due to decreased nest predation by California scrub-jays (*Aphelocoma californica*; Francis et al. 2011). Similarly, sharp-tailed grouse (*Tympanuchus phasianellus*) nests had a higher chance of succeeding in an area of high-intensity energy development than in a low-intensity area in North Dakota, USA (Burr et al. 2017). Abundance of nest predators may be lower in noisier areas, which could actually increase nest success (Francis et al. 2012).

We expected quail density to be lower in disturbed areas than in undisturbed areas due to quail avoidance of disturbance. We found that density of all quail species was statistically similar between treatments. When examining density by individual quail species, we found that density of bobwhite was similar between disturbed and undisturbed areas. However, we found that density of scaled quail was lower in disturbed areas than in undisturbed areas. Although we did not observe a significant difference in densities for bobwhite between treatments, it can take time for demographics to impact population size when noise disturbance is new to an area (Francis and Barber 2013). Additionally, greater density is not necessarily an indicator of habitat quality (Van Horne 1983). Survival and reproduction of a population, along with density, better describe habitat quality, as high population size is not always an indicator of increased survival and reproduction (Francis and Barber 2013). Greater population sizes in the presence of disturbance could be a result of 1) chance or 2) immigration into an area representing an ecological trap. Oil and gas wells can remain in production as long as 20–30 years, which could be enough time for potential changes in behavior and physiology caused by anthropogenic disturbance to impact quail population size.

Currently, most hydrocarbon exploration takes place by giving exploration companies the greatest leeway in extracting oil and gas. This practice includes decisions made almost purely on a geological and economical basis, with little consideration of surface impacts, especially those unseen in regard to wildlife. Oil and gas could just as successfully be extracted after environmental impacts are considered. For landowners and managers, one key factor must be negotiated for landscapes where wildlife (including quail) and energy development are expected to coexist. Landowners and managers must negotiate a surface use agreement that takes into account both the needs of the exploration company(s) and surface use (wildlife). Informed by our study and partly by recommendations from prominent oil and gas attorneys, some key factors to include in order to mitigate impacts to quail are: 1) keeping all infrastructure in areas of lowest quality (areas not including habitat) and as concentrated as possible on a given parcel of land, 2) avoiding placement of oil and gas infrastructure in the proximity (<400 m) of scaled quail or their habitat, 3) mitigating, to the best extent possible, sources of indirect habitat loss from traffic and sound, and 4) negotiating the restoration of previously disturbed areas using the best management practices available (this step almost always includes care in handling topsoil and the reseeding of native ecotypic plant materials). To use contextual examples from our study site, oil and gas infrastructure could be placed in areas exhibiting monotypic stands of nonnative grass (e.g., buffelgrass [*Pennisetum ciliare*], or old-world bluestems [*Bothriochloa* spp.]), monotypic closed-canopy woodlands dominated by honey mesquite as a result of previous misguided brush management practices, or in areas with preexisting anthropogenic infrastructure (e.g., existing roadways or old exploration pads or flowlines). Exploration infrastructure must be kept out of large parcels of diverse natural rangeland if at all possible. In the case of the easement that we studied, nearly all oil and gas infrastructure was located in one area along the periphery of the ranches, and this disturbance was kept as concentrated as possible. If infrastructure were less concentrated, noise and traffic disturbance potentially could affect more habitat area and could have a greater impact on quail space use and demographics. Furthermore, all disturbed sites were restored to the best extent possible using practices such as the soil conservation strategies of double-ditching (preventing mixing of topsoil and subsoil when burying pipelines) and stockpiling (storing original topsoil on-site for future reclamation of well pads) in addition to reclamation efforts via pad reductions, soil restoration, and the subsequent seeding of ecotypic native plants. We attribute our results regarding bobwhite site selection to these practices, which very likely helped to minimize both direct and indirect habitat loss for quail.

MANAGEMENT IMPLICATIONS

Oil and gas production in the Eagle Ford Shale play has been increasing since 2008. New development directly decreases the amount of habitat available to quail. Furthermore, noise and vehicle disturbance from exploration and production activities have the potential to cause indirect habitat loss by influencing quail space use and nest success. Managers should avoid locating new development in areas of prime quail habitat if possible and should concentrate development along existing roads and corridors to combat direct and indirect habitat loss. Future research should focus on long-term direct

and indirect impacts of oil and gas disturbance on quail at a landscape scale.

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EFFECT OF FOOD DISTRIBUTION ON RESOURCE SELECTION OF NORTHERN BOBWHITE

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ABSTRACT

Supplemental feeding is a common management tactic used to increase survival and reproduction of northern bobwhite (*Colinus virginianus*; hereafter, bobwhite). Different supplemental feeding methods alter the distribution of resources across a landscape in unique ways and may influence the space use and resource selection of target species differently. Predators may concentrate their movements near fed sites, and different distributions of supplemental feed may encourage bobwhite to concentrate their movements closer to feed than other areas, thereby altering the potential for predator-prey interactions near feed. We used radio-tracked locations and movements in areas with stationary feeders ("feeder fed") and nonsupplementally fed ("unfed"; study 1, year 1) or nonstationary "broadcast fed" (study 2, year 2) areas to compare resource selection within a Bayesian framework. Second- and third-order resource selection functions indicated bobwhite were more likely to occur in proximity to feeders and feedlines when available, but bobwhite resource selection was more strongly affected by feeders. These results demonstrate that different distributions of food resources can affect prey resource selection, potentially altering the probability of overlap between nontarget predator and target prey species. Managers of bobwhite populations should broadcast feed instead of using feeders to avoid concentrations of bobwhites, which may lead to reduced survival.

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Key words: *Colinus virginianus,* home range, northern bobwhite, resource selection, supplemental feed

The distribution of resources across a landscape has a fundamental influence on many ecological processes. The movement patterns and distribution of both predator and prey are driven in large part by the distribution of resources (Sih 1982, Boyd 1996), thus contributing to the distribution of predation risk. The heterogeneous dispersion of risk and resource patches then affects risk-dependent decision making. According to optimal foraging theory, prey must weigh the cost of predation against the reward of potential resources gained when selecting resource patches (Kamil and Sargent 1981). Individuals may leave patches earlier and accept lower gains when foraging in areas perceived to have high predation risk (Brown 1992, Kotler 1997, Lima 1998), or as the quality of foraging patch increases, prey may be more willing to endure higher levels of predation risk, especially if they have high resource demands such as during juvenile growth or the production of eggs (Abrahams and Dill 1989, Lima 1998). Consequently, it is important to consider how management practices that alter the distribution of resources may alter managed prey species' resource selection.

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Supplemental feeding artificially alters the distribution of food within a landscape and is often used in an effort to increase the survival or reproductive rates of target species (Hawkins 1937, Townsend et al. 1999, Godbois et al. 2004, Guthery et al. 2004, Turner et al. 2008). However, some predators are more likely to appear near supplementally fed sites than expected (Godbois et al. 2004, Turner et al. 2008), and there is concern about potential unintended effects on target populations (Doonan and Slade 1995, Godbois et al. 2004, Guthery et al. 2004, Turner et al. 2008, Henson et al. 2012). Additionally, different distribution techniques may affect predator and prey selection of fed areas in unique ways. Using feeders can attract prey to small, fixed spaces and may result in concentrated movements of both predator and prey near feeders. In contrast, broadcasting feed across a large area gives prey the opportunity to forage more naturally (Kassinis and Guthery 1996, Buckley et al. 2015, Miller et al. 2017). Consequently, predators may also be less likely to forage in small, concentrated areas. Thus, different feeding techniques may uniquely alter the distribution of risk, resulting in differences in resource selection patterns that could influence the potential for predator-prey interactions.

Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) are fast-paced, ground-dwelling birds endemic to the United States, and a widely popular game species (Guthery et al. 2004). Their populations have been declining across the majority of their historical range for the past several decades (Stoddard 1931, Brennan 1991, Hernández et al. 2013), and they are now a species of conservation concern. Land managers use supplemental feeding in an attempt to increase population survival and reproduction rates, though it produces mixed results (Townsend et al. 1999, Sisson et al. 2000, Guthery et al. 2004, Haines et al. 2004, Rollins et al. 2006). While evidence suggests supplemental feeding may improve bobwhite survival (Sisson et al. 2000, Townsend et al. 1999), increased perceived risk may affect target species' resource selection, resulting in sublethal effects that may impact survival later on (Lima and Dill 1990, Sheriff et al. 2009, Mohlman et al. 2019). Most research on the impacts of supplemental feed on bobwhite occurs in the fall and winter (Townsend et al. 1999, Sisson et al. 2000, Doerr and Silvy 2002, Guthery et al. 2004, Haines et al. 2004, Buckley et al. 2015). However, bobwhite use supplemental feed during the summer despite an abundance of natural food sources (Miller et al. 2017, Wellendorf et al. 2017), and the distribution of supplemental feed and the subsequent distribution of risk are likely to impact breeding individuals.

Our objective was to determine how two different methods of distributing supplemental feed affected the resource selection of bobwhite. We compared bobwhite resource selection within 2 separate experiments. In the first, parameters of interest were compared between unfed treatment containing empty feeders and a feeder-fed treatment containing filled feeders (hereafter, study 1). In the second, parameters of interest were compared between a broadcast-fed treatment and a feeder-fed treatment (hereafter, study 2).

We hypothesized that bobwhite need to expend less energy to access feed near feeders than to find and exploit natural food sources in the unfed treatment, making supplemental feed a higher quality resource (Frye 1954, Landers and Mueller 1986, Sisson et al. 2000, Doerr and Silvy 2002, Guthery et al. 2004, Haines et al. 2004, Buckley et al. 2015, Wellendorf et al. 2017). Consequently, we predicted bobwhite in the feeder-fed treatment would select areas closer to feeders within the feeder-fed treatment than in the unfed treatment.

To our knowledge, there are no studies directly comparing resource selection of broadcast-fed and feeder-fed wild bobwhite. Previous studies show both feeding methods sometimes reduce home range size and concentrate and localize coveys (Frye 1954, Landers and Mueller 1986, Sisson et al. 2000, Doerr and Silvy 2002, Guthery et al. 2004, Haines et al. 2004, Wellendorf et al. 2017). Thus, we hypothesized that because feeders distribute feed within a small, fixed space while feedlines require bobwhites to move across larger areas to access grain, bobwhite would need to expend less energy to access feed near feeders than near feedlines and would view areas near feeders as a higher quality resource. Given that there are enough feeders <200 m apart to ensure multiple feeders are accessible to each individual within a resident bobwhite population, we predicted resource selection would differ between treatments. More specifically, we predicted bobwhites would select for areas closer to feeders than they would to feedlines.

STUDY AREA

Di-Lane Wildlife Management Area is managed for the growth of early successional vegetation with a management emphasis on bobwhite. This area is located in the Upper Coastal Plain of Burke County, Georgia, USA and is made up of roughly 3,300 ha of federally owned land. Prominent species of vegetation and land cover types included a mixture of fallow fields (mostly camphorweed [*Heterotheca subaxillaris*], common ragweed [*Ambrosia artimisiifolia*], partridge pea [*Chamaecrista fasciculata*], annual low panicgrasses [*Dichanthelium* spp.], and perennial broomsedge [*Andropogon virginicus*] and split-beard bluestem [*Andropogon ternarius*]), loblolly pine uplands (*Pinus taeda*), hardwoods (mostly oak [*Quercus* spp.], hickories [*Carya* spp.], sweetgum [*Liquidambar styraciflua*], and black gum [*Nyssa sylvatica*]), and dove field plantings (Clearfield® sunflowers [*Helianthus* spp.], wheat [*Triticum aestivum*], and browntop millet [*Urochloa ramosa*]). The Georgia Department of Natural Resources (DNR) burned the pine uplands and disked fallow fields on rotation every 2–4 years and implemented biannual meso-mammal predator control and year-round supplemental feeding of sorghum (*Sorghum bicolor*). Average temperatures for Burke County ranged from 31.6–15° C in May and 33.3–19.4° C in June–August. Average rainfall was approximately 6.4 cm in May and ranged from 12.6–13.4 cm in June–August (NOAA National Climatic Data Center 2019).

METHODS

Experimental Design

A total of 223 feeders, initially installed in 2008, were an average of 175 m apart within our treatments throughout both study years to minimize the distance among all available feeders. Most feeders were within patches of scrub shrub and covered with medium to high density vegetation on all sides. The Georgia DNR distributed all supplemental feed within feeders and along feedlines.

Study 1: unfed vs. feeder-fed treatments.—We randomly assigned the feeder-fed treatment to a treatment area on the eastern half of the property (1,501 ha) and filled all feeders within the treatment (n = 131) with sorghum on 12 June 2018. The unfed treatment was assigned to a treatment area on the western half (1,501 ha) and all feeders within the treatment (n = 92) were emptied of any remaining feed and left in place on the same day (Figure 1). The fill level of 10 random feeders within the fed treatment was checked every week.

Study 2: feeder-fed vs. broadcast-fed treatments.—Supplemental feed was distributed via feeders within the eastern treatment area to create a feeder-fed treatment and via feedlines within the western treatment area to create a broadcast-fed treatment using the same study area boundaries as the previous year (Figure 1). We checked the fill level of 10 random feeders within the feeder-fed treatment every week, and feeders were refilled when necessary. Beginning 20 May 2019, sorghum was broadcast along predetermined routes spaced an average of 100–300 m apart along preexisting roads and firebreaks. The spreader used in this study spread feed directly behind the machine (i.e., on the road or firebreak) and into the adjacent cover. Feed was spread once every 2 weeks as described by Buckley et al. (2015) along approximately 63 km of feed lines at a rate of 5.38 bushels/ha and at an average width of 13 m.

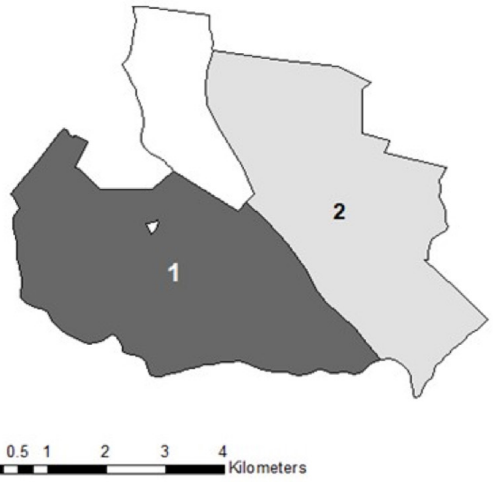

Fig. 1. Feeding treatments of northern bobwhite (*Colinus virginianus*) on Di-Lane Wildlife Management Area, Burke County, Georgia, USA. Treatment 1 indicates the unfed treatment in 2018 and the broadcast-fed treatment in 2019. Treatment 2 indicates the feeder-fed treatment in both years.

Feeders were full within the broadcast-fed treatment during turkey hunting season, between 21 March and 15 May 2019, to continue supplemental feeding of bobwhite while complying with Georgia law that prohibits turkey hunting over bait. Nearly all feeders within the broadcast treatment were empty following turkey season; only 11 of 92 feeders were still filled with seed in early July. Feed was removed from the 11 feeders and all others within the treatment were checked and verified to be empty.

Trapping and Processing

Stoddard funnel traps baited with sorghum were uniformly placed underneath dense vegetative cover 250–300 m apart throughout feeding treatments (Stoddard 1931). Trapping occurred over the course of 2 weeks in late February–early March (2018–2019). All individuals were weighed, sexed, aged, and given unique number leg bands (National Band and Tag Co. Newport, KY, USA) upon capture. Individuals with a body mass ≥130 g were fitted with very high frequency (VHF) radio-transmitters (Holohil Systems, Carp, Ontario, Canada and American Wildlife Enterprises, Monticello, FL, USA). Caution was taken to deploy transmitters equally across the study site and within feeding treatments. Between 60–100 radio-tags were deployed within a given trapping session. Transmitters had an estimated battery life of 10–12 months and emitted a mortality signal when transmitters remained stationary for greater than 12 hours. Radio-collared bobwhites left over from another study within the same study area were also included in our sample (Mohlman et al. 2019). All bobwhite trapping and tagging was carried out under Georgia DNR collecting permits and institutional approvals (Animal use protocol #A2019 06-018-Y3-A0).

Radio-telemetry

Bobwhite were relocated 5–7 days/week using Biotracker receivers and 3-element directional antennae from Lotek Wireless Inc. (Newmarket, Ontario, Canada) via homing telemetry (White and Garrott 1990, Amelon et al. 2009). Locations were taken approximately 20–30 m from individual bobwhites at varying times of the day to minimize disturbance and account for possible variation in diurnal resource selection. Bobwhite found in the same location 3 days in a row were relocated from within 3–5 m of the bird to visually confirm whether the individual was incubating a nest. Upon finding a nesting bird, technicians relocated nesting birds each morning until the nest either hatched or failed. Nest fate was visually confirmed by technicians. Individuals with broods were tracked daily and flushed at 14 and 21 days after hatch to confirm the presence of chicks. Global Positioning Systems (GPS) were used to obtain observer locations, and compasses were used to determine the azimuth to the bobwhite.

Statistical Analysis

To ensure that analyses only included data collected when supplemental feed was being reliably distributed within each

designated treatment, only data gathered between 12 June 2018–1 September 2018 and 20 May 2019–7 September 2019 were used in analyses. Bobwhites did not travel to other designated feeding treatments outside of their assigned treatment for the duration of each experiment. Data collected for bobwhites within each year were analyzed separately for ease of computation and interpretation.

All analyses were conducted within a Bayesian framework using R (R Core Team 2019) and R package 'jagsUI' (version 1.5.2, https://github.com/kenkellner/jagsUI, accessed 10 Dec 2019). All posterior distributions of model parameters were estimated using Markov chain Monte Carlo (MCMC). Three MCMC chains were generated for each analysis using varying numbers of adaptation, iteration, and burn-in values, and a thinning rate of 10 to obtain successful chain convergence and an adequate effective sample size to characterize the posterior distributions. We determined that a model successfully converged when R-hat values, which compare between- and within-chain variation values, were <1.1 (Gelman et al. 2004). Values of all estimated parameters had an R-hat value of ≤1.1, and further visual inspection of trace plots confirmed chain convergence. We reported posterior means, 95% and 50% credible intervals [CrIs], and Bayesian *P*-values for parameters of interest. The Bayesian *P*-values denote the probability of effect existence by calculating the Maximum Probability of Effect, which is equivalent to the proportion of the posterior distribution with the same sign as the mean (Makowski et al. 2019). We determined an effect to be of negligible size when the entirety of 89% of the highest density interval of the posterior distribution was within a region of practical equivalence (ROPE) ranging from -0.025–0.025 (Kruschke 2014). Partial overlap between the ROPE and posterior distribution indicated that effect significance was undecided (Kruschke 2014). As a general rule, only effects relating directly to our hypotheses and those in which >97.5% of the posterior distribution did not overlap the ROPE were mentioned in our results.

Resource Selection Function

To estimate the study species' selection of supplementally fed areas and scrub shrub and forest edge, which function as escape cover and may influence selection of fed sites (Stoddard 1931, Wiseman and Lewis 1981, Johnson and Guthery 1988, Taylor and Burger 2000), we used a resource selection function (RSF) to analyze the distance of used (telemetry relocations) and available (randomly generated) locations to the closest feature of each resource (Manly et al. 2002). Scrub shrub and forest edge were classified using the land cover classification methods described in Gardner (2020). We modeled RSFs at second- (i.e., selection of home ranges) and third-order (i.e., selection of resources within each home range) scales as described by Johnson (1980). Adequate area coverage is important when available locations are being generated (Buskirk and Millspaugh 2006). Because using equal numbers of available points to sample each home range may not equally sample all home ranges, we chose to incorporate the 5:1 ratio of available:used points used in discrete choice modeling as outlined by Cooper and Millspaugh (1999, 2001) to sample relevant areas.

Home ranges were estimated to determine availability at the third-order selection scale (Appendix A). We generated random points within each individuals' home range equal to 5 times the number of telemetry relocations recorded for each individual. For second-order selection, we created a minimum bounding polygon surrounding all used locations of bobwhites within each treatment using the 'Minimum Bounding Geometry' tool in ArcGIS (release 10.7, Esri, Inc., Redlands, CA, USA, 2019) and buffered the polygons to enlarge them by the bobwhites' average daily movement distance. The area was enlarged to avoid missing possible areas that bobwhites could have explored but not detected. Euclidean distance to each land cover type of interest (forest edge, scrub shrub, and feeder or feedline, depending on treatment) for all used and available locations was then calculated using the 'Generate Near Table' tool in ArcGIS.

We analyzed resource selection using separate logit models and included covariates for sex, nesting status, and brood rearing status along with distances to resources of interest (Taylor et al. 1999, Taylor and Burger 2000). Random intercepts were included to account for successive telemetry locations and individual variation in responses to feeding treatments (Gillies et al. 2006, Coppes et al. 2018). Random slopes further account for individual variation in treatment effects (Gillies et al. 2006); however, presumably due to small sample size, we were unable to obtain model convergence when we incorporated both.

We assigned normal distributions to random effects with a mean of 0 and with vague gamma-distributed precision terms (1/variance). We used vague normal priors for fixed effects (mean = 0, standard deviation [SD] = 0.001). Distance-related numerical predictors were divided by 10 to make a more meaningful output. Nondistance-related numerical predictors were scaled using the 'scale' package of base R to standardize measurements for comparison and decrease time until convergence. The model was parameterized using the "effects" parameterization, where the fixed effects represented the difference in resource selection from either the unfed control treatment (year 2018) or the broadcast fed treatment (year 2019) and the feeder-fed treatment as follows:

$$logit(p_i) = \beta_{0,j} + \beta_{1,j} \times X_1 + \beta_{2,j} \times X_2 + \cdots + \beta_{k,j} \times X_k$$

where, $use_i \sim Bern(p_i)$ is the model likelihood and

$$\beta_k \sim Norm(p_k, \tau_k);$$

$$p_k \sim Norm(0, 0.001);$$

$$\tau_k \sim Gamma(0.1, 0.1)$$

The model was fitted for $i = 1, 2, \ldots, N$ where N represents the total number of observations, $j = 1, 2, \ldots, n$ denotes the number of individuals, and $k = 1, 2, \ldots$ denotes the number of fixed effects. Here *use* represents the probability of use for each individual *j*. β_0 represents the random intercept of each individual. β_i represents the coefficient estimated from fixed effect predictors *Xi* described in Table 1.

Table 1. Description of covariates used in resource selection function analyses in 2018 and 2019.

Covariate	Description
SS	Distance to scrub shrub (m)
Edge	Distance to forest edge (m)
Treatment	Feeding treatment
Nest	Whether individual was classified as nesting
Brood	Whether individual had a brood
Sex	Male or female
Feed	Distance to nearest feeder or feedline depending on treatment (m)
Feed * Sex	Interaction between distance to nearest fed area and sex
Feed * Treatment	Interaction between distance to nearest fed area and treatment
Feed*SS	Interaction between distance to nearest fed area and distance to scrub shrub
Feed*Edge	Interaction between distance to nearest fed area and distance to forest edge
Feed * Nest	Interaction between distance to nearest fed area and nesting status
Feed * Brood	Interaction between distance to nearest fed area and brood status
Feed * Edge * Treatment	Interaction between distance to nearest fed area, distance to forest edge, and treatment
Feed * SS * Treatment	Interaction between distance to nearest fed area, distance to scrub shrub, and treatment

Table 2. Mean and percentiles of the posterior distributions for parameters in a logistic regression for northern bobwhite (*Colinus virginianus*) second-order resource selection in relation to unfed and feeder-fed treatments in 2018. Intercept denotes the effect of the unfed treatment on females. The region of practical equivalence (ROPE) % is the proportion of the posterior distribution that lies within a region of practical equivalence ranging from -0.025–0.025.

Parameter	2.50%	25%	Mean	75%	97.50%	Bayesian *P*-value	ROPE %
Intercept	-0.44	-0.26	-0.16	-0.07	0.12	0.87	-
Sex	-1.19	-1.01	-0.91	-0.82	-0.63	1.00	-
SS	-0.43	-0.34	-0.29	-0.24	-0.15	1.00	0.00
Edge	-0.02	0.01	0.03	0.04	0.07	0.89	44.98
Treatment	-0.57	-0.38	-0.28	-0.18	0.01	0.97	-
Nest	-1.07	-0.89	-0.78	-0.69	-0.49	1.00	-
Brood	-0.36	-0.07	0.08	0.23	0.52	0.63	-
Feed	-0.09	-0.08	-0.07	-0.07	-0.06	1.00	0.00
Feed * Sex	0.05	0.06	0.07	0.07	0.08	1.00	0.00
Feed * Treatment	-0.01	0.00	0.01	0.01	0.02	0.75	100.00
Feed * Nest	0.04	0.05	0.05	0.06	0.07	1.00	0.00
Feed * Brood	-0.03	-0.01	0.00	0.01	0.03	0.57	98.77
Feed * SS	-0.01	-0.01	-0.01	0.00	0.00	0.92	100.00
Feed * Edge	-0.01	-0.01	-0.01	0.00	0.00	1.00	100.00
Feed * Edge * Treatment	0.00	0.00	0.00	0.00	0.01	0.85	100.00
Feed * SS * Treatment	-0.01	0.00	0.00	0.00	0.01	0.52	100.00

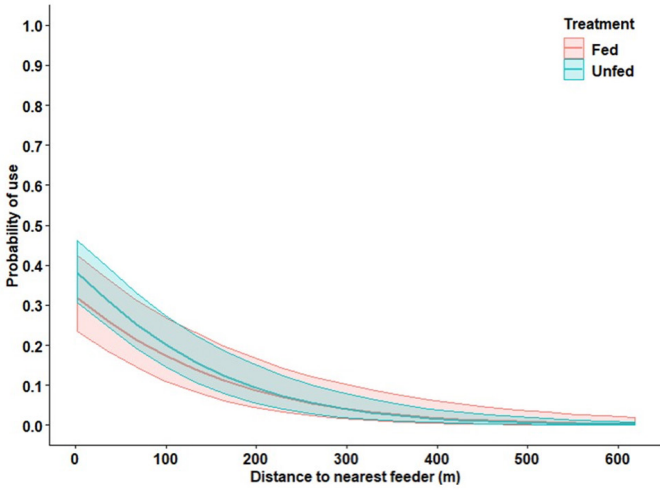

Fig. 2. Second-order resource selection model-predicted mean probability of use by northern bobwhite (*Colinus virginianus*) as a function of distance to feeder in fed and unfed treatments during study 1 in 2018.

RESULTS

Study 1: Unfed vs. Feeder-fed Resource Selection

Twenty-six individuals were used in our analyses of year 2018 data, 14 (8 female [F], 6 male [M]) of which were within the unfed treatment while the remaining 12 (7 F, 5 M) were within the feeder-fed treatment. It was unlikely that treatment affected probability of use of feeders on the landscape scale (Table 2, Figure 2); however, for every 10-m increase in distance to feeder, probability of use decreased by 7% (Bayesian *P*-value = 1.00; Table 2). In addition, for every 10-m increase in distance to scrub shrub, probability of use decreased by 33% (Bayesian *P*-value = 1.00; Table 2). Within their 90% kernel home ranges, the interaction between treatment and distance to feed had a somewhat small effect on probability of resource use, where for every 10-m increase in distance to feeder, probability of use decreased by 4% regardless of treatment (Bayesian *P*-value = 1.00; Table 3, Figure 3). Additionally, for every 10-m increase in distance to scrub shrub, probability of use decreased by 31% (Bayesian *P*-value = 1.00; Table 3). Within their 50% kernel utilization distributions (KUD) core use areas, bobwhites selected for areas closer to feeders within the feeder-fed treatment (Bayesian *P*-value = 1.00; Table 3), whereas bobwhites within the unfed treatment were much more likely to select for areas farther from feeders than feeder-fed bobwhite (Figure 4).

Study 2: Broadcast vs. Feeder-fed Resource Selection

Thirty-five bobwhite were included in our RSF analyses, 19 (9 F, 10 M) of which were within the broadcast-fed treatment while the remaining 16 (9 F, 7 M) were within the feeder-fed treatment. On all selection scales, bobwhites selected for areas closer to feed, but were more likely to select for areas closer to feeders than feedlines (Bayesian *P*-value = 1.00 for all; Tables 4, 5), though the effect size of the interaction between distance to feeder and treatment was somewhat small within their 50% core use areas (Figures 5–7). In addition, bobwhites selected for areas closer to scrub shrub on all scales, where for every 10-m increase in distance to scrub shrub, probability of use decreased by 26% on the landscape scale (Bayesian *P*-value = 1.00, Table 4), by 21% within their 90% home ranges (Bayesian *P*-value = 1.00; Table 5), and by 23% within their core use areas (Bayesian *P*-value = 1.00; Table 5).

DISCUSSION

We found support for our hypothesis stating the resource selection of feeder-fed and broadcast-fed bobwhites would differ. Bobwhites on all measured selection scales selected for areas closer to fed sites; however, bobwhites were more likely to select for areas closer to feeders than feedlines. In agreement with previous studies, this result suggests bobwhite viewed areas near supplemental feed as higher quality foraging patches regardless of the abundance of natural food resources or distribution method (Frye 1954, Landers and Mueller 1986, Sisson et al. 2000, Doerr and Silvy 2002, Guthery et al. 2004, Haines et al. 2004, Miller et al. 2017, Wellendorf et al. 2017). This is likely because consuming supplemental feed allows bobwhites to meet their energy demands more quickly than when utilizing natural food patches (Whitelaw et al. 2009, Miller et al. 2017). However, given that feed is more concentrated underneath feeders and does not diminish as time passes as it does along feedlines so long as the feeder is filled (McLaughlin et al. 2017), feeders may have been viewed as higher quality patches compared to natural food sources than feedlines. Our results suggest bobwhites have a higher probability of being closer to feeders than feedlines, potentially increasing their risk of interacting with predators focusing their foraging efforts near feed. As a result, future research should explore the survival implications of feeder use versus feedline use.

Evidence supported our hypotheses that resource selection of feeder-fed and unfed bobwhites would differ between treatments, though our predictions did not match all results. While bobwhites established their home ranges closer to feeders regardless of treatment, bobwhites within the feeder-fed treatment were more likely to select for areas closer to feeders within their home ranges and core use areas than those in the unfed treatment. This result suggests bobwhites are likely to forage near feeders (Johnson 1980) and may view fed sites as higher quality foraging patches than available natural resource patches. It is uncertain why unfed bobwhites selected for areas closer to feeders, but individuals may have established their home ranges prior to our study when all feeders had been full. Assuming individuals viewed areas near feeders as higher quality resource patches, resource selection may reflect past selection preferences. Additionally, the distance among feeders (<200 m apart) was such that bobwhites likely were making second-order decisions that go

Table 3. Mean and percentiles of the posterior distributions for parameters in a logistic regression for northern bobwhite (*Colinus virginianus*) third-order resource selection in relation to unfed and feeder-fed treatments in 2018. Intercept denotes the effect of the unfed treatment on females. The region of practical equivalence (ROPE) % is the proportion of the posterior distribution that lies within a region of practical equivalence ranging from -0.025–0.025.

Kernel %	Parameter	2.50%	25%	Mean	75%	97.50%	Bayesian *P*-value	ROPE %
90%	Intercept	-1.04	-0.86	-0.75	-0.66	-0.47	1.00	-
	Sex	-0.94	-0.74	-0.64	-0.53	-0.34	1.00	-
	SS	-0.37	-0.27	-0.22	-0.17	-0.07	1.00	0.00
	Edge	-0.03	0.00	0.02	0.03	0.06	0.78	63.39
	Treatment	-0.31	-0.10	0.01	0.12	0.33	0.53	-
	Nest	-1.33	-1.13	-1.02	-0.91	-0.72	1.00	-
	Brood	-0.52	-0.21	-0.05	0.11	0.41	0.59	-
	Feed	-0.05	-0.04	-0.04	-0.03	-0.02	1.00	8.76
	Feed * Sex	0.03	0.05	0.05	0.06	0.07	1.00	0.00
	Feed * Treatment	-0.03	-0.02	-0.01	0.00	0.01	0.85	96.32
	Feed * Nest	0.05	0.07	0.07	0.08	0.09	1.00	0.00
	Feed * Brood	-0.02	0.00	0.01	0.02	0.04	0.70	87.22
	Feed * SS	-0.02	-0.01	-0.01	0.00	0.00	0.96	100.00
	Feed * Edge	-0.01	-0.01	-0.01	-0.01	0.00	1.00	100.00
	Feed * Edge * Treatment	0.00	0.00	0.00	0.00	0.01	0.74	100.00
	Feed * SS * Treatment	-0.01	0.00	0.00	0.00	0.01	0.52	100.00
50%	Intercept	-3.17	-2.90	-2.76	-2.63	-2.36	1.00	-
	Sex	0.41	0.68	0.82	0.96	1.24	1.00	-
	SS	-0.25	-0.13	-0.07	-0.01	0.11	0.78	17.56
	Edge	-0.10	-0.04	-0.02	0.01	0.06	0.65	49.37
	Treatment	0.95	1.21	1.35	1.49	1.76	1.00	-
	Nest	0.05	0.27	0.39	0.51	0.73	0.99	-
	Brood	-0.29	0.10	0.31	0.52	0.90	0.85	-
	Feed	0.09	0.11	0.12	0.13	0.14	1.00	0.00
	Feed * Sex	-0.09	-0.07	-0.06	-0.05	-0.04	1.00	0.00
	Feed * Treatment	-0.13	-0.11	-0.10	-0.09	-0.08	1.00	0.00
	Feed * Nest	-0.05	-0.04	-0.03	-0.02	-0.01	1.00	30.14
	Feed * Brood	-0.06	-0.03	-0.02	-0.01	0.02	0.85	58.72
	Feed * SS	-0.04	-0.03	-0.03	-0.03	-0.02	1.00	18.27
	Feed * Edge	0.00	0.01	0.01	0.01	0.02	1.00	100.00
	Feed * Edge * Treatment	-0.04	-0.03	-0.03	-0.03	-0.02	1.00	5.56
	Feed * SS * Treatment	0.01	0.02	0.03	0.03	0.04	1.00	49.03

Table 4. Mean and percentiles of the posterior distributions for parameters in a logistic regression for northern bobwhite (*Colinus virginianus*) second-order resource selection in relation to feeder-fed and broadcast-fed treatments in 2019. Intercept denotes the effect of the broadcast-fed treatment on females. The region of practical equivalence (ROPE) % is the proportion of the posterior distribution that lies within a region of practical equivalence ranging from -0.025–0.025.

Parameter	2.50%	25%	Mean	75%	97.50%	Bayesian *P*-value	ROPE %
Intercept	-1.34	-1.23	-1.17	-1.11	-1.00	1.00	-
Sex	-0.17	-0.05	0.01	0.07	0.18	0.55	-
SS	-0.30	-0.26	-0.23	-0.21	-0.17	1.00	0.00
Edge	0.02	0.03	0.04	0.05	0.07	1.00	5.72
Treatment	0.26	0.40	0.47	0.55	0.69	1.00	-
Nest	-0.30	-0.09	0.02	0.12	0.34	0.54	-
Brood	-0.05	0.10	0.17	0.24	0.38	0.94	-
Feed	-0.02	-0.02	-0.01	-0.01	0.00	0.97	100.00
Feed * Sex	-0.01	0.00	0.00	0.01	0.01	0.55	100.00
Feed * Treatment	-0.11	-0.09	-0.09	-0.08	-0.07	1.00	0.00
Feed * Nest	-0.03	-0.01	-0.01	0.00	0.02	0.66	98.80
Feed * Brood	-0.04	-0.03	-0.02	-0.02	0.00	0.99	90.87
Feed * SS	0.00	0.00	0.00	0.01	0.01	0.99	100.00
Feed * Edge	-0.02	-0.02	-0.01	-0.01	-0.01	1.00	100.00
Feed * Edge * Treatment	0.02	0.02	0.02	0.03	0.03	1.00	64.54
Feed * SS * Treatment	-0.02	-0.01	-0.01	-0.01	0.00	1.00	100.00

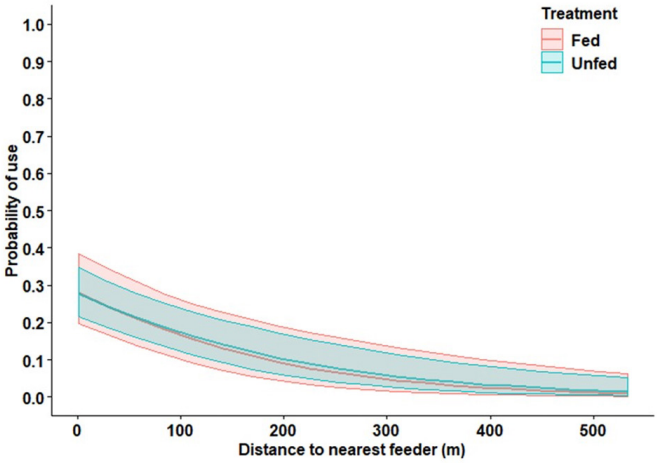

Fig. 3. Third-order resource selection model-predicted mean probability of use by northern bobwhite (*Colinus virginianus*) as a function of distance to feeder in fed and unfed treatments during study 1 in 2018 within their 90% home ranges.

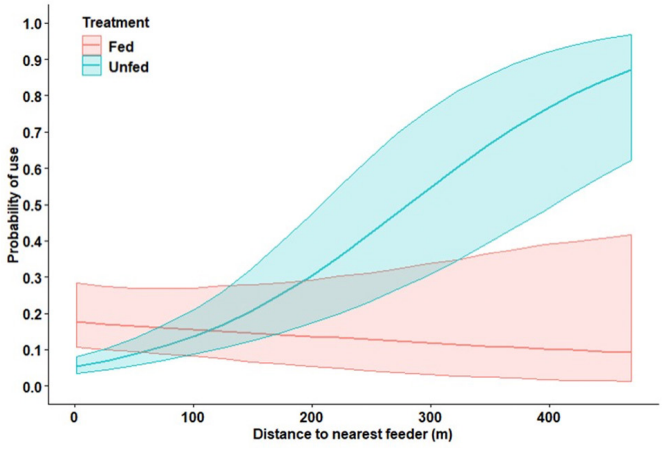

Fig. 4. Third-order resource selection model-predicted mean probability of use by northern bobwhite (*Colinus virginianus*) as a function of distance to feeder in fed and unfed treatments during study 1 in 2018 within their 50% core use areas.

Table 5. Mean and percentiles of the posterior distributions for parameters in a logistic regression for northern bobwhite (*Colinus virginianus*) third-order resource selection in relation to feeder-fed and broadcast-fed treatments in 2019. Intercept denotes the effect of the broadcast-fed treatment on females. The region of practical equivalence (ROPE) % is the proportion of the posterior distribution that lies within a region of practical equivalence ranging from -0.025–0.025.

Kernel %	Parameters	2.50%	25%	Mean	75%	97.50%	Bayesian *P*-value	ROPE %
90%	Intercept	-1.48	-1.36	-1.30	-1.24	-1.12	1.00	-
	Sex	-0.14	-0.01	0.06	0.12	0.25	0.71	-
	SS	-0.27	-0.22	-0.19	-0.16	-0.12	1.00	0.00
	Edge	-0.06	-0.04	-0.03	-0.02	0.00	0.98	37.49
	Treatment	0.21	0.38	0.47	0.55	0.70	1.00	-
	Nest	-0.84	-0.60	-0.49	-0.37	-0.14	1.00	-
	Brood	-0.64	-0.49	-0.41	-0.33	-0.18	1.00	-
	Feed	-0.03	-0.02	-0.01	-0.01	0.00	0.97	96.64
	Feed * Sex	-0.02	-0.01	0.00	0.00	0.01	0.64	100.00
	Feed * Treatment	-0.08	-0.07	-0.06	-0.06	-0.04	1.00	0.00
	Feed * Nest	0.02	0.05	0.06	0.07	0.09	1.00	0.00
	Feed * Brood	0.03	0.04	0.05	0.06	0.07	1.00	0.00
	Feed * SS	0.00	0.01	0.01	0.01	0.01	1.00	100.00
	Feed * Edge	-0.01	-0.01	-0.01	0.00	0.00	1.00	100.00
	Feed * Edge * Treatment	0.01	0.01	0.01	0.01	0.02	1.00	100.00
	Feed * SS * Treatment	-0.01	0.00	0.00	0.01	0.01	0.74	100.00
50%	Intercept	-1.61	-1.46	-1.39	-1.31	-1.17	1.00	-
	Sex	-0.13	0.02	0.10	0.18	0.33	0.80	-
	SS	-0.30	-0.24	-0.21	-0.17	-0.11	1.00	0.00
	Edge	-0.06	-0.03	-0.02	-0.01	0.01	0.89	61.70
	Treatment	-0.05	0.15	0.25	0.36	0.56	0.95	-
	Nest	-0.70	-0.46	-0.33	-0.21	0.03	0.96	-
	Brood	-0.54	-0.37	-0.26	-0.16	0.02	0.96	-
	Feed	-0.03	-0.01	-0.01	0.00	0.01	0.80	100.00
	Feed * Sex	-0.03	-0.01	-0.01	0.00	0.01	0.78	100.00
	Feed * Treatment	-0.06	-0.04	-0.03	-0.03	-0.01	1.00	21.81
	Feed * Nest	0.00	0.03	0.04	0.05	0.07	0.98	20.73
	Feed * Brood	0.00	0.02	0.03	0.04	0.06	0.99	25.04
	Feed * SS	0.00	0.01	0.01	0.01	0.02	1.00	100.00
	Feed * Edge	-0.01	-0.01	-0.01	-0.01	0.00	1.00	100.00
	Feed * Edge * Treatment	0.01	0.01	0.01	0.01	0.02	1.00	100.00
	Feed * SS * Treatment	-0.01	0.00	0.00	0.00	0.01	0.59	100.00

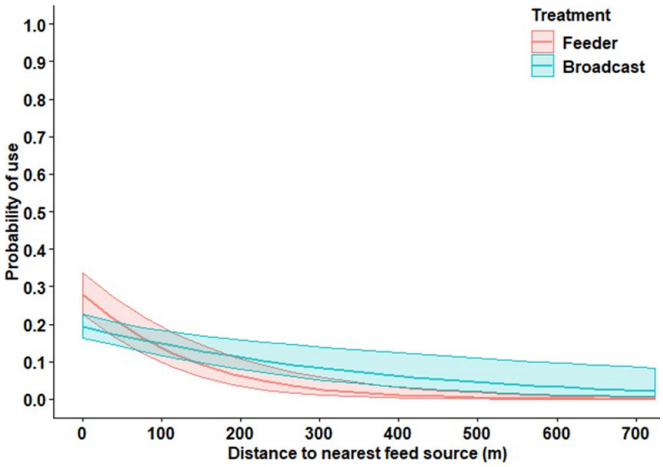

Fig. 5. Second-order resource selection model-predicted mean probability of use by northern bobwhite (*Colinus virginianus*) as a function of distance to feeder in feeder-fed and broadcast-fed treatments during study 2 in 2019.

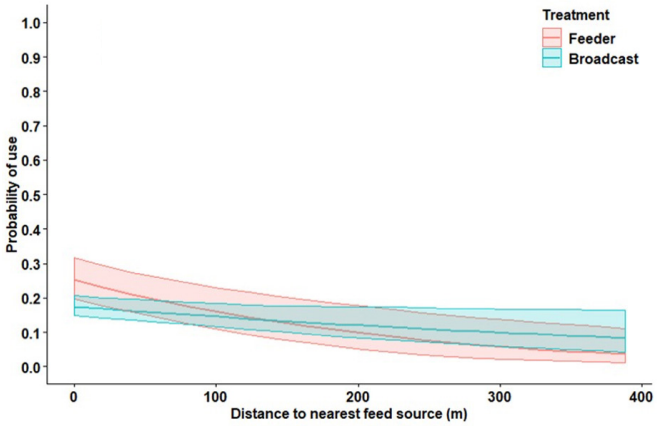

Fig. 6. Third-order resource selection model-predicted mean probability of use by northern bobwhite (*Colinus virginianus*) as a function of distance to feeder in feeder-fed and broadcast-fed treatments during study 2 in 2019 within their 90% home ranges.

beyond the distance between feeders (i.e., they could not avoid them). Moreover, the effects of the feeders that were filled with feed were more apparent at the third order. Regardless, an increase in concentration near feeders may increase the overall probability of predators focusing their foraging efforts near feeders.

The spatial context of the feed source location with respect to scrub shrub and forest edge did not play a role in selection of fed areas. However, distance to scrub shrub had a relatively strong impact on bobwhite resource selection in both study years at most selection scales. Bobwhites are likely to incorporate scrub shrub into their home ranges for its value as escape cover and for protection against weather extremes (Stoddard 1931, Wiseman and Lewis 1981, Johnson and Guthery 1988, Taylor and Burger 2000). Bobwhites can also increase their use of woody cover as level of perceived risk rises (Mohlman et al.

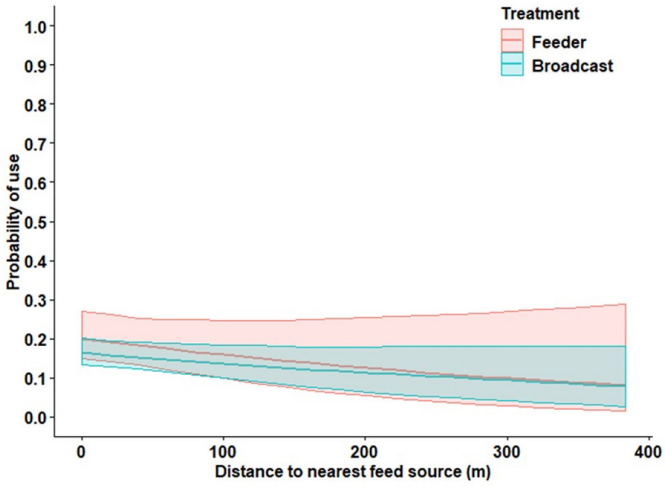

Fig. 7. Third-order resource selection model-predicted mean probability of use by northern bobwhite (*Colinus virginianus*) as a function of distance to feeder in feeder-fed and broadcast-fed treatments during study 2 in 2019 within their 50% core use areas.

2019). While we did not compare bobwhite selection of scrub shrub between treatments, it is possible that an increase in predator concentration near fed areas may influence bobwhite use of woody cover. Researchers interested in investigating the effect of different feed distributions on predator-prey relationships and risk-dependent behavior may benefit from investigating use of scrub shrub by bobwhites when exposed to different feeding treatments.

Due to the pseudoreplicated nature of the study, treatment effects may be confounded with site effects, and differences in selection may be attributable to differences in landscape configuration and resource availability between treatments instead of differences in supplemental feed distribution. However, taken collectively, our results imply different distributions of food resources can impact breeding season resource selection of bobwhites. Bobwhite were more likely to be closer to feeders than feedlines, potentially increasing their comparative risk of encountering predators foraging near feed. Even so, the full extent of the effect of different supplemental feed distribution methods on bobwhite needs further investigation. We were unable to determine whether bobwhites faced greater levels of perceived risk in either treatment, which could impact subsequent behavior and resource selection associated with nesting and brood-rearing behaviors (Lima and Dill 1990). In addition, we were unable to determine differences in bobwhite survival rates between treatments. Increased movement has been associated with increased predation rates (Sisson et al. 2000), and the increased movement of bobwhites foraging along feedlines may have a greater negative impact on survival than feeders. However, as there are many nontarget species that utilize supplemental feed besides bobwhites that may act as buffer prey (Guthery et al. 2004, Henson et al. 2012), overall risk of bobwhite predation may decrease near feed (Davis 1957). Additionally, nest depredation of ground-nesting species can increase in

supplementally fed areas (Cooper and Ginnett 2000, Hamilton et al. 2002, Selva et al. 2014), and the distribution of predators near feed may alter the potential for nest predation. Finally, the distribution of supplemental feed may impact the resource selection of individuals during times of resource scarcity such as in the fall and winter. Future research should attempt to quantify the effect of food distribution on the behavior, survival, and subsequent population dynamics of species of interest through the evaluation of fine-scale movement and resource selection of nesting birds, brood-rearing individuals, and winter coveys.

MANAGEMENT IMPLICATIONS

Managers for bobwhite populations with objectives that include bobwhite harvest and stakeholder satisfaction typically have to intensify their management to be successful. Supplemental feeding is one tool in the manager's toolbox to raise carrying capacity in food-limited systems. Managers should broadcast feed instead of using feeders to avoid overly concentrated use by bobwhites that may lead to reduced survival. Given that we observed weak biological effects of feed on space use, concerns over baiting should be minimal. Legal, financial, and ethical considerations should be a part of the decision process regarding supplemental feeding.

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APPENDIX A. BOBWHITE HOME RANGE ANALYSIS

We estimated fixed kernel density home ranges (50% and 90% contours) of bobwhites using r package "adehabitatHR" (Worton 1989, Börger et al. 2006, Calenge 2006). Although the least-squares cross-validation (LSCV) method is recommended for bandwidth selection in ecological studies (Worton 1995, Seaman and Powell 1996, Seaman et al. 1999), bobwhites often spent several consecutive days in the same location when they were nesting, and our home range estimates did not converge using this method. Instead, we used a single smoothing parameter (h) that was iteratively chosen based on successive trials to produce what visually appeared to be the most accurate home ranges. Accuracy was determined using several criteria: 1) inclusion of all observed locations, 2) no holes in the home range except in areas of open water, and 3) not excessively large. For example, given that we tracked the birds daily and bobwhites are not known to move large distances and return in a short amount of time, it would be unrealistic to include areas >500 m away from observed locations within a season. Bobwhite home ranges are commonly estimated for only those individuals with ≥25–30 relocations following the recommendations of Seaman et al. (1999) and Kenward (2001) (Terhune et al. 2010, Singh et al. 2011, McGrath et al. 2017). However, given that we did not use the LSCV method, we attempted to identify the minimum number of locations necessary to obtain an accurate home range estimate by graphing home range area curves to visually determine when each curve reached an asymptote (Odum and Kuenzler 1955, Bond et al. 2001). Bobwhite home ranges reached an asymptote with a minimum of 30 locations within study 1. Study 2 home ranges reached an asymptote with a minimum of 50–55 locations, but <10 individuals had enough relocations for home range estimation. In order to preserve sample size for greater statistical power, we chose to defer to the existing literature and analyzed data of individuals with ≥30 locations in both field seasons.

Along with treatment, we included covariates that would be likely to influence home range size such as sex (Taylor et al.

1999), reproductive status (with nest, with brood, or neither), and number of locations used in home range estimation (Macdonald et al. 1980). Both feeders and feedlines were placed unevenly across the property, and in 2019, 12 of the 92 feeders within the broadcast fed treatment were mistakenly overlooked and left full for a large portion of the field season. To quantify whether bobwhites had the potential to have been regularly using space that contained supplemental feed, we visually confirmed the appearance of any overlap between all 90% home range polygons and supplementally fed areas using ArcGIS (release 10.7; Esri, Redlands, CA, USA, 2019). All home range polygons within fed treatments overlapped with supplemental feed; however, home ranges of 2 bobwhite in the broadcast-fed treatment overlapped with both feed lines and filled feeders. As a result, we included whether an individual had been exposed to multiple feeding styles as an additional parameter in the home range analyses of bobwhite in the 2019 field season.

We performed a separate linear regression using a log-normal distribution within a Bayesian framework for each year. We used vague normal priors for fixed effects (mean = 0, precision = 0.001), and numerical predictors were scaled using the scale package of base R to standardize measurements and allow for comparison. The model was parameterized using the "effects" parameterization where the fixed effects represented the difference from either the unfed control treatment (year 2018) or the broadcast fed treatment (year 2019) as follows:

$$\mu_j = \beta_0 + \beta_{j,treatment} + \beta_{j,sex} \times X_{sex} + \beta_{j,nest} \times X_{nest} + \beta_{j,brood} \times X_{brood} + \beta_{j,loc_freq} \times X_{loc_freq},$$

Where $HRsize_i \sim dlnorm(\mu_j, \tau)$ is the model likelihood and

$$\tau \sim Gamma(0.1, 0.1);$$

$$\beta_k \sim Norm(\mu_k, \tau_k);$$

$$\mu_k \sim Norm(0, 0.001);$$

$$\tau_k \sim Gamma(0.1, 0.1)$$

are model priors. The model was fitted for $j = 1, 2, \ldots n$, where n denotes the number of individuals, and $k = 1, 2, \ldots$ represents the number of fixed effects. Here *HRsize* represents the home range size for individual *j*. β_0 represents the intercept. $B_{treatment}$ represents the effect of feeding treatment. B_{sex} characterizes the effect of sex. B_{nest} symbolizes the effect of nest status. B_{brood} symbolizes the effect of brood status. β_{loc_num} characterizes the effect of the number of locations used to estimate home range. *X* represents the response variable for each respective fixed effect noted.

Bobwhite Home Range Results

Study 1: feeder-fed treatment vs. unfed treatment.—Twenty-six bobwhite were included in our home range and core use area analyses. Fourteen individuals (8 F, 6 M) were within the unfed treatment while the remaining 12 (7 F, 5 M) were within the feeder-fed treatment. Bobwhite home ranges (90% KUDs) within the feeder-fed treatment were 16% larger than those in the unfed treatment (Bayesian *P*-value = 0.92, Tables A1, A2). Home ranges of nesting individuals and individuals that had broods were 63% and 43% smaller, respectively, than individuals that were recorded with neither (Bayesian *P*-value = 0.99, 0.97, respectively, Table A1). Male home ranges were 28% larger than female home ranges (Bayesian *P*-value =0.99, Tables A1, A3), and for every 6 locations included in home range estimates, home range size increased by 8% (Bayesian *P*-value = 0.86, Table A1).

Bobwhite core use areas (50% KUDs) within the feeder-fed treatment were 11% larger than those in the unfed treatment (Bayesian *P*-value = 0.86, Tables A1, A2). Core use areas of nesting individuals and individuals that had broods were 126% and 73% smaller, respectively, than for individuals that were recorded with neither (Bayesian *P*-value = 1.00, 1.00, respectively, Table A1). Male core use areas were 8% larger than female core use areas (Bayesian *P*-value = 0.79, Tables A1, A3). For every 6 locations included in core use area estimates, core use area size increased by 10% (Bayesian *P*-value = 0.92, Table A1).

Study 2: feeder-fed treatment vs. broadcast-fed treatment.—Thirty-five bobwhites were included in our home range analyses. Nineteen individuals (9 F, 10 M) were within the broadcast-fed treatment while the remaining 16 (9 F, 7 M) were within the feeder-fed treatment. Bobwhite home ranges were 31% smaller within the feeder-fed treatment than the broadcast-fed treatment (Bayesian *P*-value = 0.98, Tables A1, A2). Male home ranges were 39% larger than female home ranges (Bayesian *P*-value = 1.00, Tables A1, A3). No other parameters of interest were likely to have affected home range size, including whether individuals had a nest or brood (Bayesian *P*-value = 0.57, 0.61, respectively, Table A1), or the locations included in home range estimation (Bayesian *P*-value = 0.70, Table A1).

Bobwhite core use areas were 26% smaller within the feeder-fed treatment than within the broadcast-fed treatment (Bayesian *P*-value = 0.95, Tables A1, A2). Male home ranges were 28% larger than female home ranges (Bayesian *P*-value = 0.95, Tables A1, A3), and nesting individuals had 36% smaller home ranges than those that had neither nested nor had a brood (Bayesian *P*-value = 0.78, Table A1). No other parameters of interest had a clear effect on home range size, including whether individuals had a brood (Bayesian *P*-value = 0.63, Table A1), or the number of locations included in home range estimation (Bayesian *P*-value =0.58, Table A1).

Table A1. Mean linear regression output and credible intervals for northern bobwhite (*Colinus virginianus*) home range sizes in relation to feeder-fed and unfed treatments in 2018 and broadcast-fed and feeder-fed treatments in 2019. Intercept denotes the effect of the unfed (2018) or broadcast-fed (2019) treatment on females.

Year	Kernel %	Parameter	2.50%	25%	Mean	75%	97.50%	Bayesian *P*-value
2018	50%	Intercept	1.91	2.23	2.39	2.56	2.87	1.00
		Treatment	-0.10	0.04	0.11	0.18	0.33	0.86
		Nesting	-1.23	-0.93	-0.79	-0.64	-0.33	1.00
		Brood	-0.95	-0.69	-0.56	-0.42	-0.14	1.00
		Sex	-0.14	-0.01	0.06	0.13	0.29	0.79
		Location Freq	-0.05	0.05	0.09	0.14	0.24	0.92
	90%	Intercept	2.71	3.03	3.18	3.34	3.66	1.00
		Treatment	-0.06	0.08	0.15	0.22	0.37	0.93
		Nesting	-0.92	-0.63	-0.49	-0.35	-0.06	0.99
		Brood	-0.75	-0.49	-0.36	-0.23	0.03	0.97
		Sex	0.04	0.18	0.25	0.33	0.46	0.99
		Location Freq	-0.07	0.03	0.08	0.12	0.22	0.86
2019	50%	Intercept	1.55	1.93	2.12	2.32	2.70	1.00
		Treatment	-0.52	-0.32	-0.23	-0.14	0.05	0.95
		Nesting	-1.12	-0.57	-0.31	-0.04	0.50	0.78
		Brood	-0.45	-0.19	-0.06	0.07	0.32	0.63
		Sex	-0.02	0.16	0.25	0.34	0.52	0.96
		Location Freq	-0.33	-0.13	-0.03	0.07	0.28	0.58
	90%	Intercept	2.69	3.03	3.20	3.37	3.70	1.00
		Treatment	-0.53	-0.36	-0.27	-0.19	-0.02	0.98
		Nesting	-0.80	-0.30	-0.06	0.19	0.66	0.57
		Brood	-0.29	-0.07	0.05	0.16	0.38	0.61
		Sex	0.09	0.25	0.33	0.41	0.56	1.00
		Location Freq	-0.34	-0.16	-0.07	0.02	0.21	0.70

Table A2. Summary of northern bobwhite (*Colinus virginianus*) home ranges within each feeding treatment in 2018 and 2019; SD is standard deviation.

Year	Kernel %	Treatment	*n*	Mean	SD	Lower range	Upper range
2018	90	Unfed	14	25.27	6.87	15.48	38.87
		Feeder-fed	12	27.88	7.78	14.86	39.21
	50	Unfed	14	7.10	2.43	4.48	11.26
		Feeder-fed	12	7.45	1.98	3.61	12.43
2019	90	Broadcast-fed	19	41.63	12.10	21.92	64.21
		Feeder-fed	16	32.19	11.26	12.95	53.27
	50	Broadcast-fed	19	11.56	3.43	6.11	19.02
		Feeder-fed	16	10.14	3.88	3.70	16.27

Table A3. Summary of male (M) and female (F) northern bobwhite (*Colinus virginianus*) home ranges in 2018 and 2019; SD is standard deviation.

Year	Kernel %	Sex	*n*	Mean	SD	Lower range	Upper range
2018	90	M	11	30.17	5.91	21.28	39.21
		F	15	23.77	7.14	14.86	38.86
	50	M	11	7.54	1.98	5.28	11.41
		F	15	7.05	2.43	3.61	12.43
2019	90	M	17	43.84	11.18	20.15	64.21
		F	18	31.16	9.87	12.96	41.3
	50	M	17	12.65	3.60	5.49	19.02
		F	18	9.26	2.94	3.70	14.02

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SURVIVAL, MOVEMENT, AND HABITAT USE OF TRANSLOCATED NORTHERN BOBWHITE IN TEXAS

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ABSTRACT

For decades there has been a noticeable decline in northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) populations. Few studies have assessed the survival of translocated bobwhite. We evaluated the effectiveness of reintroduction of bobwhite into the Texas (USA) Parks and Wildlife Department's Gus Engeling Wildlife Management Area (GEWMA), where they had been extirpated but now have suitable habitat. Before reintroduction, GEWMA was surveyed (spring call counts) to make sure no bobwhite were present. Forty-six bobwhite were trapped from March–April 2019 in South Texas, banded, bled, radio-tagged, transported to GEWMA, and released. In addition, 17 bobwhite were trapped banded, bled, radio-tagged, and released back into the source population as a control for comparison of movements, reproduction, and survival estimate differences between the source and released bobwhite populations. During July 2019, 3 broods (24 bobwhite) were trapped and translocated from a South Texas ranch to the GEWMA. Survival for bobwhite released at GEWMA was 37.0% through 1 July 2019 and 70.6% for bobwhite left on the ranch in South Texas. Three nests were found at GEWMA while none were found on the ranch in South Texas. Movement distances between daily locations for males and females did not differ at GEWMA or at the ranch in South Texas; however, there was a significant ($P \leq 0.001$) difference in daily movement for bobwhite at GEWMA and the South Texas ranch. Female bobwhite at GEWMA moved 5.4 times the distance of female bobwhite in South Texas and male bobwhite at GEWMA moved 5.9 times the distance of male bobwhite in South Texas. Bobwhite at GEWMA were located in woody cover only 24.2% of the time, whereas bobwhite in South Texas were located in woody cover 76.1% of the time. The greater daily movement and less use of woody cover for bobwhite at GEWMA probably contributed to their lower survival.

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Northern bobwhite (*Colinus virginianus*; hereafter bobwhite) population declines have been acknowledged since the 1930s in Texas, USA and widespread declines across their historical range have been documented since the 1960s (Brennan 1991). Range-wide population decreases have been attributed to a variety of factors, including nonnative species such as red imported fire ants (*Solenopsis invicta*) and feral hogs (*Sus scrofa*) and weather events such as drought (Bridges et al. 2001), ice storms or heavy snow (Chavarria et al. 2012), and flooding events (Perotto-Baldivieso et al. 2011, Caldwell 2015). The 2 major reasons generally given by bobwhite biologists for the decline of bobwhite in Texas are lack of habitat and habitat fragmentation (Hernández and Peterson 2007). As bobwhite become isolated in fragmented populations, these small populations become vulnerable to local extinction through the occurrence of catastrophic events (Roseberry 1962). However, few if any management programs can completely offset the effects of catastrophic weather events. Although creation of favorable habitat can mitigate the impact of extreme weather events on bobwhite, these interventions are often prohibitively expense to undertake at a large scale.

As bobwhite have declined for decades across much of their range, local, regional, and statewide extinctions have occurred (Martin et al. 2017). Because of successful translocations of other gallinaceous birds, bobwhite enthusiasts increasingly call for use of the approach (Martin et al. 2017). Martin et al. (2017) concluded that bobwhite translocations were not a panacea for broad-scale restoration of bobwhite but stated the technique should remain at the forefront of bobwhite science so that a practical and reliable solution could be developed. Translocation can be used to supplement low-density bobwhite populations in some areas (Liu et al. 2000, 2002; Sisson et al. 2017) or to reestablish populations where bobwhite were extinct (Coppola et al. 2020).

The International Union for Conservation of Nature (IUCN) "Guidelines for the Re-introduction of Galliformes for Conservation Purposes" recommends defining success in 3 phases: 1) the survival of founders, 2) evidence of breeding by founders, and 3) long-term persistence of the translocated population (World Pheasant Association and IUCN/SSC Re-introduction Specialist Group 2009). Short-term goals may include survival of translocated bobwhite and successful reproduction. Long-term goals would include the persistence and growth of the population, to the point that it becomes self-sustaining and could withstand hunter harvest without significant reduction of the population size. This long-term condition defines the ultimate success for bobwhite population restoration.

Reintroduction of bobwhite entails the release of bobwhite into an area that was once part of its range, but from which it has since been extirpated (Seddon 2010, IUCN/SSC 2013). Dispersal from the release site has been observed in several translocations of gallinaceous birds (Lawrence and Silvy 1987, Coppola et al. 2020). Translocated sage grouse (*Centrocercus urophasianus*) also had increased movement, which led to lower survival (Baxter et al. 2008). Further complicating analysis, many of the bobwhite translocation studies (Liu et al. 2000, 2002; Terhune et al. 2010; Downey et al. 2017; Sisson et al. 2017) have released bobwhite into areas where current populations of bobwhite exist, making it difficult to measure the success of the translocation attempt.

There are a few examples of reintroductions of bobwhite in Texas (Liu et al. 2000, 2002), but no examples of long-term successful reintroductions of bobwhite in Texas. A major limitation to reintroductions of bobwhite in Texas is the difficulty in obtaining birds from appropriate (i.e., wild-caught individuals from similar habitats to the release area) source populations. Historically, few private landowners in Texas have been willing to allow wildlife managers access to their property to obtain birds, but it may be possible to obtain bobwhite from Texas wildlife management areas.

We assessed the survival of translocated bobwhite from South Texas to the Texas Parks and Wildlife Department's Gus Engeling Wildlife Management Area (GEWMA) to evaluate the feasibility of reintroducing and establishing a stable and self-sustainable population into areas where there are no longer bobwhite, but where the habitat was suitable for them. Our objectives were to 1) determine the survivability of reintroduced bobwhite, 2) compare nesting and brooding success between source and release populations, and 3) compare movements and habitat used by source site and reintroduced bobwhite.

STUDY AREA

Research was conducted from March 2019 through December 2019. Initially, this was to be a 2-year project, but the State of Texas would not allow travel during 2020 due to the coronavirus pandemic. Bobwhite were trapped in 3 different sites (Los Lazos Ranch, a Carrizo Springs ranch, and Santa Rita Ranch) for translocation (source sites) and then translocated to the reintroduction site, GEWMA. Los Lazos Ranch was located in the vicinity of the small community of Aguilares, Texas, about 48.3 km east from the border city of Laredo, Texas. This 145.7-ha ranch was in a predominantly arid region that contained mostly sandy clay loam and series of very deep, well-drained soils (U.S. Department of Agriculture 2010). The vegetation consisted of native brush, as well as native grasses, cacti, and buffelgrass (*Cenchrus ciliaris*). The ranch was used predominantly for white-tailed deer (*Odocoileus virginianus*) hunting, with no specific management plan except for corn feeding. Outside the hunting season, the ranch supported 20 head of cattle, which were restricted to a 129.5-ha area and had supplemental feeding and water troughs.

The other 2 source sites were a ranch near Carrizo Springs, Texas and the Santa Rita Ranch, located on the county line dividing Webb and Zapata counties southeast of Laredo (Figure 1). Both ranches were in a predominantly aridic region that contained mostly sandy clay loam and series of very deep, well-drained soils (U.S. Department of Agriculture 2010). The vegetation consisted of native brush, as well as native grasses, cacti, and buffelgrass. Both ranches were used predominantly for white-tailed deer hunting, The Santa Rita Ranch was an

80.9-ha low-fence ranch and had an effective control program for hogs and other predators.

The bobwhite reintroduction site (GEWMA) was a 4,435.5-ha area managed by the Texas Parks and Wildlife Department and was located near Tennessee Colony, Texas about 708 km northeast of the extraction locations (Figure 2). Several areas were being restored to bobwhite habitat. In these areas, the department had thinned post oak (*Quercus stellata*) trees or cleared the land of all trees. In all areas being restored for bobwhite, yaupon (*Ilex vomitoria*) was removed from the understory and little bluestem (*Schizachyrium scoparium*) grasses were reestablished to return these areas to their original native state. We selected an approximately 100-ha area being managed for bobwhite in the middle of GEWMA to release translocated bobwhite. A major difference between the source sites and GEWMA was soil type; the source sites were sandy clay loam, whereas GEWMA consisted of mostly light colored, rapidly permeable sands on the uplands. Prior to reintroduction, GEWMA was surveyed (spring call counts) to make sure no bobwhite were present.

Precipitation data for all study areas were obtained from U.S. Climate Data (2020). Precipitation during 2018 at the Los Lazos Ranch was below normal (53.6 cm) until September (Figure 3). With lack of precipitation during the normal bobwhite breeding season (May–July) bobwhite at the Los Lazos Ranch probably did not nest until September 2018 after the heavy rains that month. In 2019, monthly precipitation was closer to normal (Figure 3) and nesting started in May and continued through July 2019. Precipitation at the Santa Rita Ranch was probably similar to that of the Los Lazos Ranch due to their proximity to each other and to Laredo, Texas (the nearest weather station to both ranches).

Precipitation during 2018 at the Carrizo Springs ranch was below normal (yearly average was 50.1 cm) and similar to that of the Los Lazos Ranch. Rainfall at Carrizo Springs (Figure 4) from January–June 2018 (13.3 cm) and from July–August 2019 (21.5 cm) was close to normal for those periods.

Precipitation (yearly normal 111.3 cm) at GEWMA during 2018 averaged only 4.8 cm/month from January through June 2018 but averaged 8.6 cm/month from July through December 2018. During the same periods in 2019, GEWMA averaged 18.5 cm/month and 4.1 cm/month, respectively. A freeze (-5.6° C) on 7 March 2019 killed and then delayed forb production even with the abundant early rainfall.

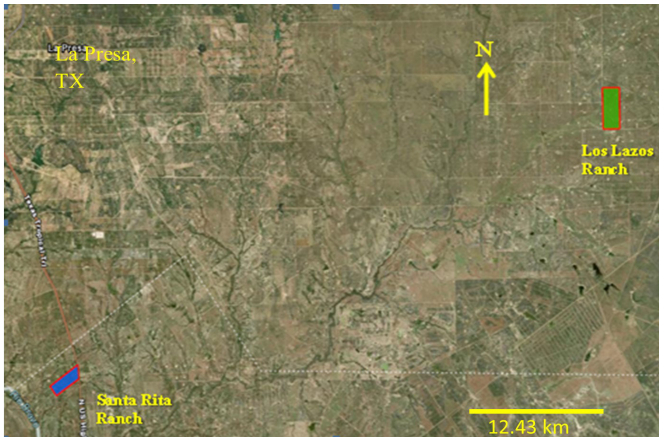

Fig. 1. Map location of Santa Rita Ranch (blue) in reference to Los Lazos Ranch (green), Texas, USA.

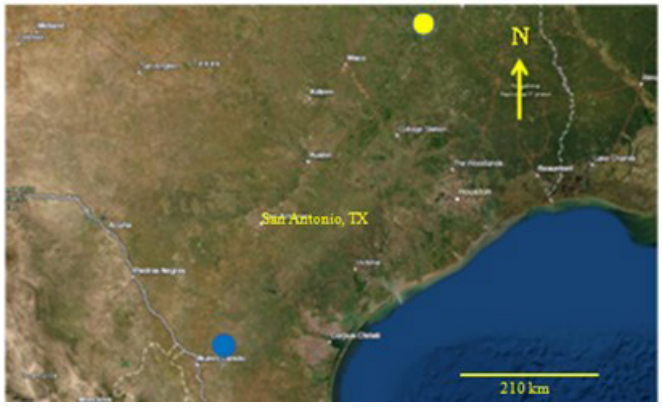

Fig. 2. Map location of Santa Rita Ranch (blue) in reference to Gus Engeling Wildlife Management Area (yellow), Texas, USA.

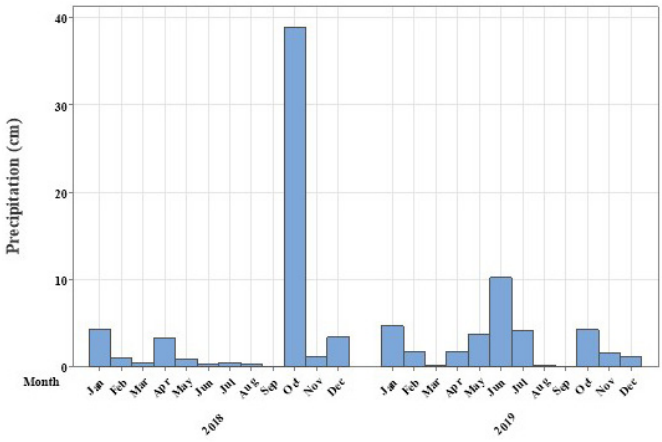

Fig. 3. Monthly precipitation (cm) totals for Laredo, Texas, USA during 2018 and 2019 (U.S. Climate Data 2020).

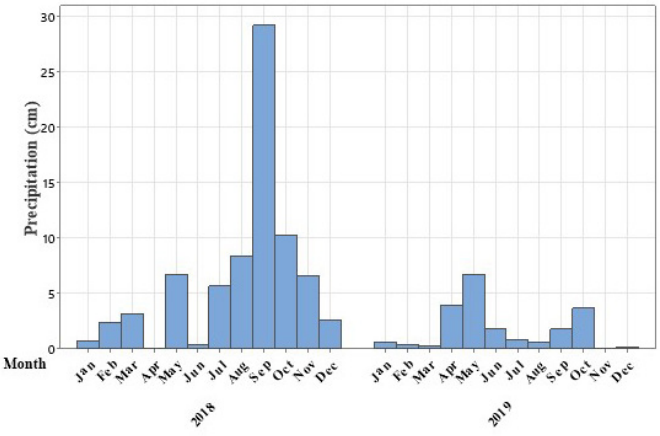

Fig. 4. Monthly precipitation (cm) totals for Carrizo Springs, Texas, USA during 2018 and 2019 (U.S. Climate Data 2020).

METHODS

Trapping and Marking

Trap sites were selected based on bobwhite sightings. Where we observed little or no bait disturbance between trapping days, we replaced those unproductive sites with new sites that had potential for successfully trapping bobwhite. Trap sites were baited regularly with commercial bird seed (Royal Wing Classic Mix Wild Bird Food, Tractor Supply, College Station, TX) starting in February so that when trapping was conducted (Mar–Aug 2019), bobwhite were already aware of these areas with readily available food and had become accustomed to frequenting the baited sites. Each trap location was supplied with approximately 0.5 kg of mixed grains including cracked corn, millet, milo, and black-oil sunflower seed once a week for the month leading up to trap placement. The use of a variety of grains for bait rather than using a single grain type allowed the bobwhite to selectively eat first the more palatable grains then gradually consume the less preferable grains, resulting in consistent access to a food source, even when the bait sites had been heavily utilized.

Bobwhite were trapped using Kniffin modified funnel traps (Reeves et al. 1968), a walk-in style trap similar to that originally described by Stoddard (1946) for trapping bobwhite. Traps were placed at the prebaited sites and baited with about 0.5 kg of mixed grains. Traps were checked once an hour to process captured animals. All bobwhite trapped were aged by primary covert color, sexed by head color (Lyons et al. 2020), weighed, and banded with a size 7 silver-colored band (National Band and Tag Company, Newport, KY, USA) on the right leg. Nontarget species captured were released and a tally was kept each trap day by species. Birds to be translocated were provided food and water while kept in a cardboard poultry container at room temperature and held for no more than 36 hours. Birds were transported by vehicle to GEWMA for release.

Bobwhite trapped at the source sites were fitted with an 8.8 g VHF (approximately 4% body weight) radio-transmitter with a mortality signal (150 MHz; Wildlife Materials, Carbondale, IL, USA; Figure 5) and bled for further genetic studies. Radio-tagged bobwhite were either translocated to GEWMA or released at the trap site. All radio-tagged bobwhite were monitored daily from March–July 2019 with each bird being located twice daily (morning and afternoon) using a handheld Yagi antenna to determine general location, movement, and survival status.

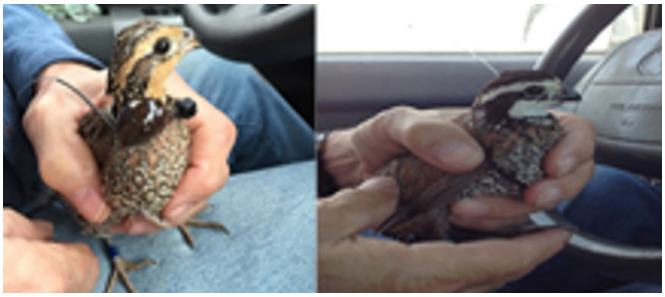

Fig. 5. Female bobwhite (left) fitted with bib-type radio-transmitter attached with zip tie. Before release, feathers are pulled through the zip tie to conceal the transmitter (male at right).

Bobwhite Survival

We estimated bobwhite survival using the nonparametric Kaplan-Meier estimation method (Distribution Overview Plot with **r**ight **c**ensoring, Minitab Statistical Software Package, 2019). We captured bobwhite from March through August and analyzed survival as a function of days since capture by entering the elapsed days at which individuals died or remained alive at the end of 100 days. We plotted survival and 95% confidence intervals as a function of days since survival and compared mean days of survival between groups with a log-rank Chi-square test. Because of the 7 March 2019 freeze at GEWMA and our observed lack of forbs following the freeze and insects, we compared survival of the first 12 radio-tagged bobwhite released (7–15 Mar 2019) at GEWMA to the second 12 radio-tagged bobwhite released (16–20 Mar 2019) on GEWMA for 100 days. By the time the second 12 bobwhite were released, small forbs where available as a bobwhite food source. We also compared survival for radio-tagged bobwhite left on the Los Lazos Ranch in South Texas and for radio-tagged bobwhite translocated to the GEWMA for 100 days.

Bobwhite Movements

To determine whether translocated bobwhite displayed movement similar to individuals from the source population, we plotted daily locations of radio-tagged bobwhite on base maps of the source and translocated study areas. We then measured the distance between successive daily locations of male and female bobwhite to obtain a mean-daily-movement distance (Silvy 1967, Robel et al. 1970) for the source and translocated populations. These mean-daily-movement distances for males and females from the source and translocated populations were then compared using a Student's *t*-test (Ott and Longnecker 2016) to determine whether they differed significantly.

Bobwhite Habitat Use

Vegetation types (grass, brush, and trees) on the Los Lazos Ranch and GEWMA were documented from aerial photographs (ground-truthed by personnel on the areas) and then compared to determine whether these vegetation types were used similarly by the source and translocated populations of radio-tagged bobwhite. We used a Chi-square test (Ott and Longnecker 2016) to determine whether vegetation type used by bobwhite was random or was being selected for at each area. To do this, each radio-tagged bobwhite at the Los Lazos Ranch and at GEWMA was located daily to determine location within a vegetation type. Vegetation-type use data were then compared for bobwhite left at the Los Lazos Ranch and bobwhite at GEWMA using a Chi-square test (Ott and Longnecker 2016) to quantify the use of grass, brush, and trees.

Bobwhite Reproduction

Radio-collared females at GEWMA were tracked with a handheld Yagi antenna ≥4 times/week. We walked in on female bobwhite once they had been found in the same location for 3–4 consecutive tracking sessions to determine whether the female was on a nest, and we took care to avoid flushing the female. If the female was found to be on a nest, a piece of flagging tape was tied to tall vegetation at least 10 m from the nest. This step allowed nests to be relocated once they hatched or were destroyed without attracting potential predators to the area. Once nesting, females were tracked 1–2 times daily and once a female was located off the nest for 3–4 consecutive tracking sessions, the nest was checked to determine whether the nest had hatched or failed.

For successful nests, we took notes on the location of the nest, the number of hatched eggs, the number of unhatched eggs, and the date of hatch. For unsuccessful nests, we noted location of the nest, the reason for failure, the number of unhatched or destroyed eggs, if possible to determine, and the date that it was destroyed. If a nest was successful, the female and brood were tracked twice daily and the number of chicks surviving in the brood was recorded if a female and brood were sighted along a road. Any transmitter that emitted a mortality signal was checked immediately. If a transmitter was recovered, the site was examined for probable cause of mortality (e.g., a pile of bobwhite feathers with a transmitter showing cuts in the rubber surrounding the antenna would indicate mortality by a raptor) and the female was then listed as deceased. A brood was considered to have survived if at least 1 chick remained at 3 weeks of age.

RESULTS

Trapping and Marking

Sixty-nine bobwhite, of which 62 were radio-tagged, were translocated to GEWMA. From 7 March–15 July, 33 bobwhite (9 adult males, 10 juvenile males, 2 adult females, and 12 juvenile females) were trapped and translocated from Los Lazos Ranch to GEWMA. During 17–20 March an additional 12 bobwhite (7 adult males, 1 juvenile male, 1 adult female, and 3 juvenile females) were translocated from Carrizo Springs to GEWMA. From 14–26 April 2019, 9 male (7 adults and 2 juveniles) and 8 female (6 adults and 2 juveniles) bobwhite were trapped, radio-tagged, and released at the Los Lazos Ranch. Last, 3 broods (24 bobwhite [4 adult males, 6 juvenile males, 2 adult females, and 12 juvenile females]) were trapped from 15–20 July and translocated from Santa Rita Ranch to GEWMA. Juvenile bobwhite in each brood were approximately ¾ adult size and were sexed by head coloration (Lyons et al. 2020). All adult bobwhite were radio-tagged when released at GEWMA; however, because of a shortage of transmitters, only 2 juvenile females were radio-tagged before release.

Bobwhite Survival

Ten of the first 12 bobwhite released at GEWMA were mortalities during the first 100 days, whereas 11 of the second 12 bobwhite released were mortalities during the first 100 days. However, the mean days of survival for the first 12 bobwhite released (7–16 Mar 2019) at GEWMA was 24.5 (± 9.59 SE) days through 100 days, whereas the mean days of survival for the second 12 bobwhite released (17–25 Mar 2019) was 54.2 (± 10.04 SE) days through 100 days (Figure 6); however, this difference was not significant ($X^2 = 2.062$, $df = 1$, $P = 0.151$).

Of the 45 bobwhite released at GEWMA, 33 were mortalities during the first 100 days. Of the 17 bobwhite trapped and released back on their capture site on the Los Lazos Ranch, only 5 were mortalities during the first 100 days. The mean days of survival for 45 bobwhite released at GEWMA was 50.4 (± 5.85 SE) days through 100 days compared to 76.0 (± 9.18 SE) days for 17 bobwhite left on the Los Lazos Ranch in South Texas (Figure 7); this difference was significant ($X^2 = 8{,}089$, $df = 1$, $P = 0.004$).

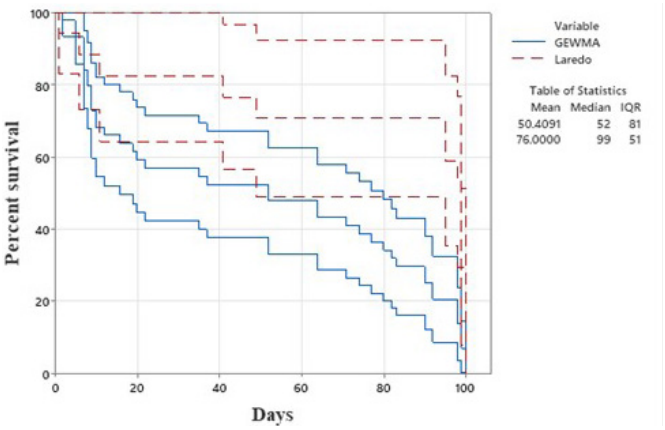

Fig. 6. Percent survival and 95% confidence interval and mean and median survival days for the first 12 bobwhite compared to the second 12 bobwhite released at Gus Engeling Wildlife Management Area, Texas, USA.

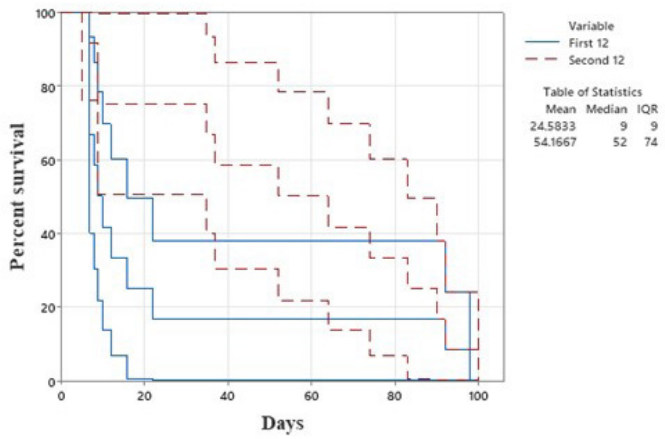

Fig. 7. Percent survival and 95% confidence interval and mean and median survival days of northern bobwhite from the source population (South Texas, USA) compared with the translocated population (Gus Engeling Wildlife Management Area, Texas).

Bobwhite Movements

Distances between daily locations for male (348 ± 84 SD) and female (270 ± 48 SD) bobwhite at GEWMA nor did male (59 ± 11 SD) and female (50 ± 11 SD) bobwhite distances between daily locations differ at the Los Lazos Ranch; however, there was a significant ($P < 0.001$) difference in daily movement for bobwhite at GEWMA and the ranch. Female bobwhite at GEWMA moved 5.4 times the distance of female bobwhite at Los Lazos Ranch and male bobwhite at GEWMA moved 5.9 times the distance of male bobwhite at the Los Lazos Ranch (Table 1).

Habitat Use

Bobwhite at GEWMA used the grass vegetation type more (75.8%) than was available (16.5%) and used the brush and tree vegetation types less than expected (Table 2). These differences were significant ($X^2 = 434.6416$, $n = 372$, $df = 2$, $P = 0.00001$). Bobwhite at GEWMA were located in woody cover only 24.2% of the time, whereas bobwhite at Los Lazos Ranch were located in woody cover 76.1% of the time (Table 2). Bobwhite at Los Lazos Ranch used the brush vegetation type more (76.1%) than expected (67.1%) and grass and trees less than expected (Table 2). These differences were significant ($X^2 = 6.8288$, $n = 403$, $df = 2$, $P = 0.032896$). Bobwhite at the GEWMA were located most often in areas dominated by little bluestem. Most bobwhite mortalities at the GEWMA were located in or near areas dominated by post oak trees.

Table 1. Mean distance traveled (m) between consecutive daily locations by northern bobwhite (*Colinus virginianus*) by age and sex at Gus Engeling Wildlife Management Area (GEWMA) in Texas, USA, and Laredo, Texas during July 2019.

Age/Sex[a]	Location	*n*	Mean	Standard deviation
AM	GEWMA	5	307	73
JM	GEWMA	2	451	113
All males	GEWMA	7	348	84
AF	GEWMA	2	217	37
JF	GEWMA	4	297	53
All females	GEWMA	6	270	48
AM	Laredo	5	57	9
JM	Laredo	1	66	22
All males	Laredo	6	59	11
AF	Laredo	4	49	10
JF	Laredo	2	53	13
All females	Laredo	6	50	11

[a] A: adult, J: juvenile, M: male, F: female.

Table 2. The percentage of bobwhite (*Colinus virginianus*) locations within 3 vegetation types on the Gus Engeling Wildlife Management Area (GEWMA) and a private ranch near Laredo, Texas, USA, during July 2019. Numbers in parentheses are the percentage of cover of each vegetation type on the study areas. Roads, ponds, and oil-well pads composed 2.8% of the Laredo ranch.

Area	*n*	Vegetation type		
		% Grass	% Brush	% Trees
GEWMA	12	75.8(16.5)	21.2(5.7)	3.0(77.8)
Laredo	13	23.9(28.9)	76.1(67.1)	0.0(1.2)

Reproduction

No bobwhite nests were located at the Los Lazos Ranch; however, 3 bobwhite nests were located at GEWMA. The first nest was located on 30 May 2019 and at that time contained 8 eggs and later 12 eggs. Feral hogs destroyed this nest on 3 June 2019. A second nest was located on 4 June 2019 and contained at least 13 eggs; it was destroyed by an unknown cause. The third nest, located on 14 June 2019, contained 15 eggs. This nest was destroyed on 17 June 2019 by a snake (3 eggs still in nest). All nests located at GEWMA were located in little bluestem clumps.

DISCUSSION

The lower survival of the first 12 radio-tagged bobwhite released on 7 March 2019 at GEWMA compared to the survival of the next 12 radio-tagged bobwhite released on 17 March 2019 was probably due to the lack of available food (forbs and the insects that feed on them) caused by the 7 March 2019 freeze. During this same time-period, availability of forbs and insects was not a problem on the South Texas ranches where bobwhite were trapped. Osborne (1993) suspected radio-transmitters on released bobwhite caused mortality. However, all bobwhite in our study were fitted with radio-transmitters; therefore, any additional mortality caused by the radio-transmitters should have been similar for the 2 populations. Scott et al. (2012), collaborating with the Texas Parks and Wildlife Department, translocated 550 bobwhite to 2 sites during 2004–2006. Radio-tagged, translocated bobwhite had lower (35%) survival compared to residents (56%). Scott et al. (2012) speculated that restoring bobwhite populations in fragmented landscapes with a few remaining declining bobwhite populations might be impractical.

The mean days of survival for 45 bobwhite released at GEWMA was 50.4 days, similar to a report by Downey et al. (2017). They translocated 409 wild bobwhite (186 radio-marked females) to supplement 2 sites in Shackelford and Stephens counties, Texas, during March 2013 and March 2014. Their spring–summer (Mar–Sep) survival ranged between 32% and 38%. Their translocation efforts failed to increase the bobwhite population beyond that of the control during this study. Downey et al. (2017) recommended that future translocation research should aim to increase translocation success by investigating methods for increasing survival during the first 4 weeks following translocation.

Although bobwhite on GEWMA moved more than those at the Los Lazos Ranch, movement was similar to that found by Terhune et al. (2006) for their translocated bobwhite in Georgia, USA. Bobwhite at GEWMA used limited areas (<100 ha) of suitable habitat. Bobwhite on GEWMA spent about

23.9% of the day in the grassland vegetation type. Terhune et al. (2010) suggested that 2 site-specific criteria should be met prior to instituting translocation. First, habitat management should be conducted to ensure that high-quality habitat exists. Second, the patch size should be ≥600 ha of high-quality habitat and poorer sites may warrant even larger patches. Both criteria were met at GEWMA as the release sites were managed for bobwhite reintroduction. Terhune et al. (2006) translocated bobwhite associated with other bobwhite present on their release area, which probably limited the movements of the translocated bobwhite.

Three of 5 (60%) juvenile bobwhite females translocated to GEWMA and still alive in June were able to establish and incubate nests. Of the 4 adult females translocated to GEWMA, none were observed to nest. Downey et al. (2017) reported that 74% of their translocated females that entered the nesting season produced a nest. They also found an apparent nest success of 46.1% and a nesting rate of 1.1 ± 0.1 (SE) nests per female. Scott et al. (2012) found the percentage of hens nesting (95% CI = 36 ± 16.4%) and nesting rate (95% CI = 1.1 ± 0.2 nests/hen) were lower for translocated bobwhite than for resident bobwhite (79 ± 12.4% and 1.6 ± 0.3 nests/hen, respectively).

MANAGEMENT IMPLICATIONS

Translocated bobwhite had greater daily movements than resident bobwhite. Because translocated bobwhite were introduced into a new habitat without any knowledge of available resources, we speculate that much of the movement can be attributed to searching for forage, nest sites, and shelter. We believe the translocation was somewhat successful as the translocated bobwhite attempted to nest and survival of the translocated bobwhite was similar to that of the bobwhite followed on the Los Lazos Ranch. Previous bobwhite translocation studies did not compare survival, reproduction, vegetation-type use, and movement of their translocated bobwhite to bobwhites followed at their source sites. Because we did so, results from our translocation shined a light on certain results that had been previously overlooked. For a bobwhite reintroduction to be fully successful (a self-sustaining population), founders should survive, founders should breed and produce young, and there should be long-term persistence of the translocated population. In addition, a larger number of bobwhite should be translocated and done so over several years for a successful translocation.

ACKNOWLEDGMENTS

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WINTER SURVIVAL AND RESOURCE USE OF TRANSLOCATED NORTHERN BOBWHITE IN THE MID-ATLANTIC UNITED STATES

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ABSTRACT

Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) in the Mid-Atlantic United States have been experiencing precipitous population declines due to a combination of habitat deterioration, urban and suburban sprawl, change in forest management regimes, and farming practices. In recent years, restocking of bobwhite through translocation efforts has gained interest to rebuild local populations. However, empirical studies are warranted to understand the limitations of translocation as it relates to its potential use for long-term population recovery and persistence in this region. Further, few studies nation-wide have evaluated resource use and survival during the non-breeding season on translocated sites. As such, we translocated 360 bobwhites from source populations from southern latitudes during March–April 2015–2017 into 2 different landscape types similar to the source population vegetative communities (agricultural cropland dominated in Maryland, USA versus pine forest dominated in New Jersey, USA) and tested the effects of habitat fragmentation on survival and habitat use during the subsequent non-breeding season. We found habitat fragmentation negatively affecting survival and resource use among translocated bobwhite on fragmented cropland-dominated sites as compared to larger unfragmented forested sites. Survival was lower on cropland sites compared to forested sites such that bobwhite in cropland-dominated landscapes were >125 times less likely to survive the winter than those on forested sites. In our examination of resource use, bobwhite in structurally complex forested sites used cut pine, early-successional woody, early-successional herbaceous, and thinned pine more than what was available on the landscape. On the cropland sites bobwhite used food plots, early-successional woody, and mixed woods more than what was available on the landscape and only food plots at the home range scale. While larger unfragmented forested bobwhite habitat ultimately provided a more successful translocation landscape, birds still had large home ranges and relatively low survival. Therefore, proper pine management may be necessary to optimize habitat availability during the non-breeding season. Our findings provide rare information on demographic resiliency and resource use for translocated bobwhite during the non-breeding season. Further, this research provides valuable information to improve future translocation efforts in the Mid-Atlantic.

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Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) are one of the most studied and managed game birds in the world (Brennan et al. 2014), yet their numbers continue to decrease throughout much of their distribution. Bobwhite populations have been experiencing precipitous distribution-wide declines and distribution contractions for more than 50 years (Sauer et al. 2017). The rapid declines in bobwhite populations are largely attributed to loss of habitat to urban and suburban sprawl, changes in farming techniques with increased mechanization and clean farming practices, removal of prescribed fire, and habitat fragmentation (Brennan 1991, Church and Taylor 1992, Roseberry and Sudkamp 1998, Peterson et al. 2002, Williams et al. 2004). The most dramatic declines can be observed in the Mid-Atlantic United States. For example, bobwhite populations declined at a rate of 11.2%/year in New Jersey and 9.5%/year in Maryland between 1966–2017 compared to the average distribution-wide decline of 3.4% per year (Sauer et al. 2017). Furthermore, an accelerated decline since the 1980s has led to the functional extirpation of wild populations in New Jersey (Chanda and Herrighty 2011) and Pennsylvania (McKenzie et al. 2015, Martin et al. 2017). This observation supports the "abundant center" hypothesis (Andrewartha and Birch 1954, Hengeveld and Haeck 1982) that as distribution-wide populations decline, peripheral populations are more likely to go extinct and geographic distribution will contract (Goel and Richter-Dyn 1974, Tracy and George 1992, Mehlman 1997, Vucetich et al. 2000), often due to density-independent stochasticity rather than density-dependent maintenance (Williams et al. 2003). This concept heightens the concern for the bobwhite populations in the Mid-Atlantic given that this region is currently in the northern extent of their distribution.

New Jersey is currently ranked as the state with the greatest human population density, averaging more than 386 people/km² (U.S. Census Bureau 2010). Because of the continued urban and suburban expansion, there is amplified competition between creating more human infrastructure and setting aside land for wildlife conservation. Because bobwhite often require multiple landscape types and are a relatively low-mobility species (Terhune et al. 2010, Scott et al. 2013), this increased habitat fragmentation makes bobwhite more vulnerable to predation (Rollins and Carroll 2001, Lyons et al. 2009). For example, Duren et al. (2011) found bobwhite populations in the Mid-Atlantic were most negatively affected by the cohesion of human development within 2.5 km of their potential occupied sites. New Jersey land use has transitioned from predominantly crop and livestock agricultural lands and forests to urban and suburban sprawl with nearly 5,665 ha converted each year (Lohr 2009, Chanda and Herrighty 2011).

In addition to human population expansion, changes in agricultural and forestry practices in New Jersey and elsewhere in the United States have amplified the loss of sufficient habitat. Traditionally, production agricultural land possessed numerous field borders and hedgerows between crops which served as escape or thermal cover for adults and optimal brood cover for bobwhite chick rearing as well as additional insect and seed food sources (Klimstra 1982, Moorman et al. 2013). However, as farming technology advanced and the average farm size increased, bobwhite habitat has been reduced in the landscape (Klimstra 1982, Brennan 1991). Forest management in New Jersey and the rest of the eastern United States has changed due to a reduction in both prescribed fire and forest thinning (Brennan 1991), increasing canopy closure and thus reducing sunlight to the forest floor for early successional plants. Maintaining pine (*Pinus* spp.) canopy closure of <50% paired with prescribed burning is essential in habitat management (Brennan 1999) and is one of the most effective and cost-efficient management tools for enhancing the growth of bobwhite plant foods, increasing biomass of insects for broods, and removal of thick understory growth (Stoddard 1931, Hurst 1972).

Decreasing trends in available habitat and increased fragmentation across the landscape reduce local populations of wildlife, limiting opportunities for colonization and population growth following habitat restoration. Because local sources of bobwhite are not available in the Mid-Atlantic region, long-distance translocations would be required for recolonization. Translocation of bobwhite has demonstrated promise for restoring bobwhite populations in the Southeast (Terhune 2008; Terhune et al. 2006*a*, 2010), but few studies have tested its efficacy in the Mid-Atlantic. Translocation can mitigate the behavioral and genetic problems associated with captive breeding programs, thus producing comparable survival rates, nest production, and nest survival to resident bobwhites (Terhune 2008, Terhune et al. 2006*a*). However, this outcome can be dependent on a few factors, including the number of birds translocated from one or multiple donor source populations and whether there are conspecifics present at the release site. Specifically, for social species such as bobwhite, the addition of conspecifics to the landscape may help to change translocated individuals' perceptual error of poor habitat by translocated individuals by signaling to dispersers that the habitat is suitable (Bayard and Elphick 2012, Andrews et al. 2015). However, translocated birds may also perceive habitat as inferior and disperse—leaving the site no better off than before translocation (Martin et al. 2017). Research by Terhune (2006*a*) indicated that translocating wild bobwhite prior to the breeding season can enhance the adult breeding population and subsequent fall population, making it a viable option for recolonizing bobwhite populations. Furthermore, reported numbers of coveys detected on release sites have more than doubled after translocation efforts in Georgia, USA (Terhune 2006*a*, Sisson et al. 2017). Despite these successes, long-distance translocations present additional challenges (e.g., extended holding times, increased stress, climate variability between source site and release site) for bobwhite, potentially hindering demographic performance and resource use post-release (Coppola et al. 2021).

The Northern Bobwhite Conservation Initiative identified regional focal areas for bobwhite habitat improvement and restoration efforts. Priority areas in the Mid-Atlantic included the southwestern agricultural lands and the south-central Pine Barrens of New Jersey and much of the western Delmarva Peninsula of Delaware and Maryland (Delmarva; Figure 1).

Because these focal areas historically had bobwhite populations and currently have areas of focused habitat management (Delmarva and southwestern New Jersey) or have large contiguous tracts of managed land (New Jersey Pine Barrens), these sites are ideal candidates for bobwhite translocation. However, empirical studies are warranted to understand the limitations of translocation as it relates to its potential use for long-term population recovery and persistence in this region, especially given the limited wild bobwhite resource.

Translocation research typically focuses on immediate demographic responses during the initial breeding season as negative effects are most severe during the first few months post-translocation (Ewen et al. 2010, Terhune et al. 2010, Coppola et al. 2021). Few studies, however, have evaluated resource use and survival during the non-breeding season on translocated sites. As such, we translocated bobwhite into 2 different landscape types (agricultural cropland dominated versus forest dominated) and tested the effects of habitat fragmentation during the non-breeding season. We predicted that no difference in survival would be observed between the cropland and forested sites for translocated birds given that the lack of site familiarity was equal among translocated birds and given equal time-opportunity to assimilate to their new surroundings. That said, we expected differential resource use would be observed among forested and cropland sites, whereby bobwhite would adaptively use resources beneficial to fitness.

STUDY AREA

We conducted this research during 2015–2017 on 3 privately owned properties within the Mid-Atlantic region of the United States, near the northeastern periphery of the current bobwhite distribution (Brennan et al. 2014): Pine Island Cranberry Company (Pine Island) in Burlington County, New Jersey; Turner's Creek Farm (Turner's Creek) in Kent County, Maryland; and Chino Farm in Queen Anne's County, Maryland (Figure 1). Releases occurred at 2 distinct sites on Pine Island, Home Farm and Sim Place, which were separated (~6 km) by Penn State Forest; therefore, 4 release sites (Home Farm, Sim Place, Chino Farm, and Turner's Creek) between the 2 states were designated for this study. All properties were within the Atlantic Coastal Plain physiographic region, though they differed in landscape composition, predator community, and existing bobwhite population prior to translocation. There were no conspecifics present on Home Farm, Sim Place, or Turner's Creek before the translocations described herein. Chino Farm had a small but recovering population at the time of initial release. We justify comparing these sites in this study because of their relative proximity, similarity in climate and local weather events, and the simultaneous translocations occurring among them.

Pine Island (~6,800 ha) is a working cranberry farm situated near the geographic center of the New Jersey Pinelands National Reserve (~39.740°N, –74.500°W; Figure

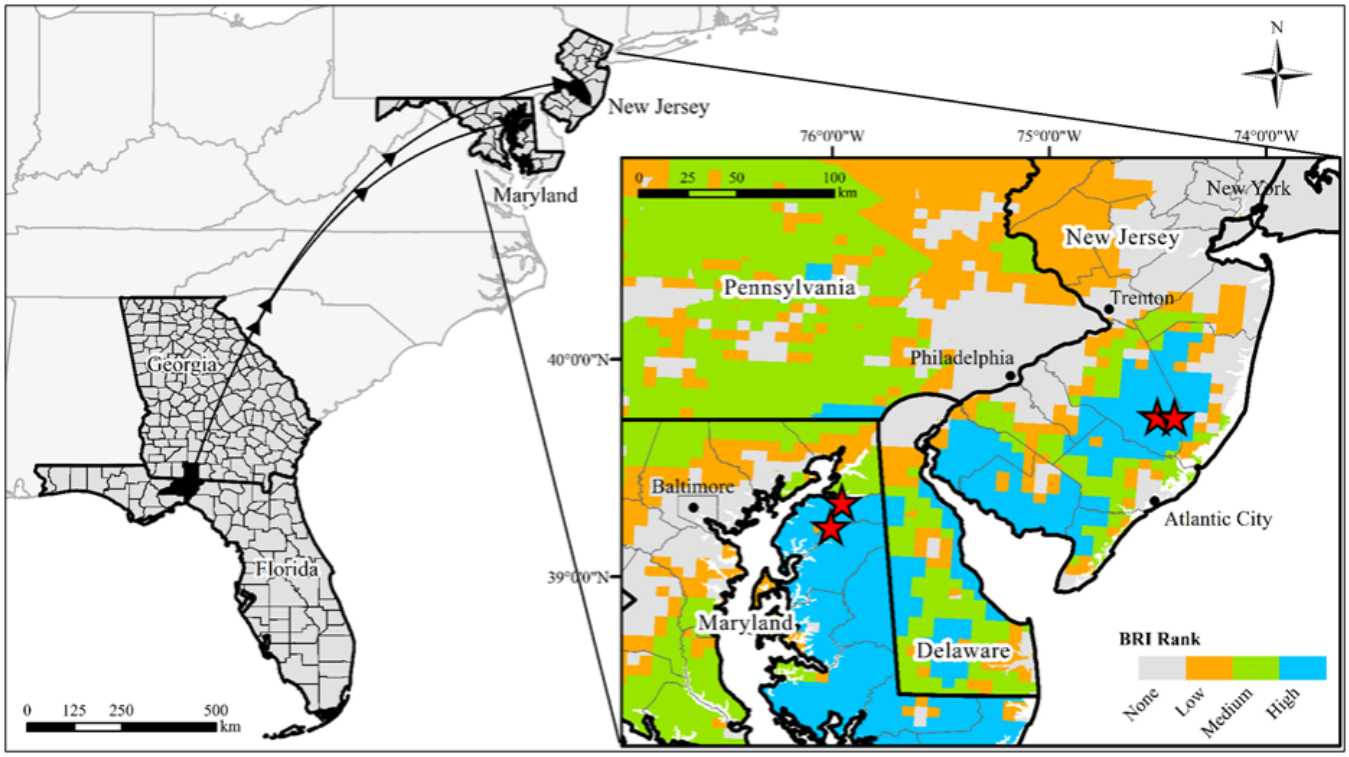

Fig. 1. Translocation sites (starred) in Kent and Queen Anne's counties, Maryland, USA and Burlington County, New Jersey, USA, overlaid on Bobwhite Ranking Information 2.0 classifications (BRI Rank; Palmer et al. 2011), 2015–2017. The source sites for translocated bobwhites were in Leon and Jefferson counties, Florida, USA and Thomas County, Georgia, USA; translocation and source site counties are black-shaded.

1), a 445,000-ha forest characterized by pine (*Pinus* spp.)-oak (*Quercus* spp.) and pine and shrub uplands transected by Atlantic white cedar (*Chamaecyparis thyoides*) swamps and emergent wetlands (Forman 1998). The landscape within a 15-km dissolved buffer around Home Farm and Sim Place was 68% forested, 24% wetland, 5% urban or suburban, 1% agriculture, 1% barren land, and 1% open water (New Jersey Department of Environmental Protection 2015). The mean temperature in southern New Jersey ranged from 0.17° C in January to 24.28° C in July, with an average annual precipitation of 114.43 cm (Office of the New Jersey State Climatologist 2019). The topography was principally low relief, gently rolling hills composed predominantly of acidic sandy soils (Rhodehamel 1998). The dominant canopy species included pitch pine (*P. rigida*) and shortleaf pine (*P. echinata*), with scattered black oak (*Q. velutina*), white oak (*Q. alba*), chestnut oak (*Q. montana*), post oak (*Q. stellata*), and scarlet oak (*Q. coccinea*). The understory was generally composed of scrub oaks, including dwarf oak (*Q. prinoides*), scrub (bear) oak (*Q. ilicifolia*), and chinquapin oak (*Q. muehlenbergii*); ericaceous shrubs, including northern highbush blueberry (*Vaccinium corymbosum*), lowbush blueberry (*V. angustifolium*), and black huckleberry (*Gaylussacia baccata*); and Pine Barren golden heather (*Hudsonia ericoides*). In areas where fire or mechanical treatment has been implemented, native herbaceous groundcover, including little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), broomsedge *(Andropogon virginicus*), and bracken fern (*Pteridium aquilinum*) had become established along with native forbs, including partridge pea (*Chamaecrista fasciculata*), tick-trefoils (*Desmodium* spp.), and bush-clover species (*Lespedeza* spp.). Some open areas contained bare substrate (coastal plain sands) and patches of juniper moss (*Polytrichum juniperinum*) and lichens (predominantly *Cladonia* spp.).

Forestry management had historically been limited on Pine Island, and when implemented it was principally intended for watershed management related to cranberry production. In 2005, managers in New Jersey approved a forestry stewardship plan for Pine Island that included prescriptions for timber thinning, burning, and roller-drum chopping (hereafter, roller chopping) in the upland portions of the property to support forest and watershed health. Between 2006–2012, dispersed retention cuts with planted pine regeneration occurred on 4 adjacent tracts (~50 ha each) within the Home Farm study area. Consequently, during the study period these tracts were largely dense young pine thickets, with scattered small patches of open shrubland. Timber thinning occurred across 155 ha of Home Farm to a basal area of 14–16 m^2/ha. The surrounding area was mature even-aged forests of uncut (≥18 m^2/ha) mixed species pine (*Pinus rigida* and *P. echinata*). Although uncut, these other forest stands were being managed with periodic prescribed burns as part of the property's Forest Stewardship Plan activities. Home Farm was fringed by agricultural fields (blueberry production), lakes, and impounded cranberry bogs. The Sim Place release site was centered on a 15-ha grassland dominated by warm-season grass species and surrounded by uncut, yet regularly burned, mature pine stands. These stands had an understory dominated by heath species—lowbush blueberry (*V. angustifolium*) and huckleberry (*G. baccata*) — and bear oak to the north and expansive cranberry bogs in the remaining 3 directions. A network of narrow canals (<10 m wide) transected the Sim Place study area, with the most centrally located canal running parallel to an abandoned bare ground airstrip. The perimeters of the canal system and airstrip areas were composed of native warm-season grasses (*Panicum virgatum, Schizachyrium scoparium, Andropogon virginicus*), greenbrier (*Smilax* spp.), winged-sumac (*Rhus copallinum*), running blackberry (*Rubus hispidus*), and native forbs, including partridge pea, tick-trefoils and bush-clovers, Additionally, both Home Farm and Sim Place had various sized (~1–8 ha) exposed substrate sandpits used for cranberry bog maintenance. These sandpits also contained a mosaic ("patches") of herbaceous growth as well as brush piles of discarded woody material from forestry activities or piles of discarded cranberry vines from bog restorations.

The assemblage of bobwhite predators at Pine Island was similar among sites. Common raptors included Cooper's hawk (*Accipiter cooperii*), sharp-shinned hawk (*A. striatus*), red-tailed hawk (*Buteo jamaicensis*), red-shouldered hawk (*Buteo lineatus*), northern harrier (*Circus cyaneus*), barred owl (*Strix varia*), and great horned owl (*Bubo virginianus*). Common mammalian predators or nest predators included coyote (*Canis latrans*), Virginia opossum (*Didelphis marsupialis*), striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), long-tailed weasel (*Mustela frenata*), gray fox (*Urocyon cinereoargenteus*), and red fox (*Vulpes fulva*). Snake species included northern black racer (*Coluber constrictor*), corn snake (*Pantherophis guttata*), black rat snake (*P. obsoletus*), timber rattlesnake (*Crotalus horridus*), and northern pine snake (*Pituophis melanoleucus*).

Chino Farm is 2,200 ha of mixed grassland and rotational cropland near Chestertown, Maryland (~39.230°N, –76.010°W) and Turner's Creek is a 304-ha rotational crop farm with native grassland buffers near Kennedyville, Maryland (~ 39.345° N, –75.955° W; Figure 1). The landscape within a 15-km dissolved buffer around Chino Farm and Turner's Creek was 58% agriculture, 19% forested, 14% open water, 8% urban or suburban, and 1% wetland (Maryland Department of Planning 2010). Crop fields over this landscape were planted primarily with corn, soybeans, and wheat. Forest canopy species were predominantly oak, hickory (*Carya* spp.), tulip poplar (*Liriodendron tulipifera*), Virginia pine (*Pinus virginiana*), and loblolly pine (*P. taeda*). Common understory and edge species were multiflora rose (*Rosa multiflora*), greenbrier, and Russian olive (*Elaeagnus angustifolia*). Common grasses included broomsedge, big bluestem (*Andropogon gerardi*), and orchard grass (*Dactylis glomerata*). Common forbs consisted of goldenrods (*Solidago* spp.), ragweed (*Ambrosia* spp.), and black-eyed Susan (*Rudbeckia hirta*). Raptor and mammalian species at these 2 sites were generally the same as those found at Pine Island; however, northern pine snakes and timber rattlesnakes were notably absent.

SOURCE SITES

Given the decline of bobwhite throughout its distribution and extirpation from many sites in the Mid-Atlantic region, source populations for translocation are not available. Therefore, long-distance translocation is required as the only viable option. Roberts (2018) indicated that long-distance translocation of bobwhite was feasible as translocated bobwhite had similar survival rates to resident bobwhite. We used private properties in Leon and Jefferson counties, Florida, USA and Thomas County, Georgia, as source sites for wild bobwhite. Two of the properties, Tall Timbers and Dixie Plantation, were owned and operated by Tall Timbers Research Station and Land Conservancy. These forested properties lay within the Red Hills geomorphic region, near the southwesternmost extent of the Atlantic Coastal Plain physiographic province. Landowners of each property had implemented intensive wild quail management for several decades, resulting in relatively high-density bobwhite populations (e.g., >2.5 birds/ha; Sisson et al. 2012, 2017). Management programs typically emphasized frequent fire application (<3-year fire return interval) and low timber density (2–15 m^2/ha) to promote and sustain early-seral stage groundcover vegetation communities (Palmer and Sisson 2017).

These properties were principally old field pine forests, characteristic of the Red Hills landscape. Common canopy species included longleaf pine (*Pinus palustris*), shortleaf pine, slash pine (*P. elliottii*), and loblolly pine, with scattered southern live oak (*Quercus virginiana*) and turkey oak (*Q. laevis*). Mid-story species included black cherry (*Prunus serotina*), scrub oak (*Quercus* spp.), sassafras (*Sassafras albidum*), common persimmon (*Diospyros virginiana*), and gallberry (*Ilex glabra*). Understory vegetation was predominantly broomsedge and other warm season grasses (*Andropogon* spp.), bracken fern, winged-sumac, blackberry (*Rubus* spp.), goldenrod, and partridge pea.

As a result of historical intensive quail management, these properties contained adequate habitat to sustain a variety of wildlife populations, including those of bobwhite predators. Common raptors included Cooper's hawk, sharp-shinned hawk, red-tailed hawk, red-shouldered hawk, northern harrier, barred owl, and great horned owl. Common mammalian predators included armadillo (*Dasypus novemcinctus*), bobcat (*Lynx rufus*), coyote, raccoon, gray fox, Virginia opossum, and red fox. Snake species included black racer, corn snake, gray rat snake (*Pantherophis spiloides*), eastern rat snake (*Antherophis alleghaniensis*), eastern diamondback (*Crotalus adamanteus*), coachwhip (*Masticophis flagellum*), and pine snake.

METHODS

As part of a larger translocation project, the New Jersey Audubon Society, University of Delaware, and Tall Timbers Research Station conducted 3 years of bobwhite translocation in late March and early April, prior to bobwhite breeding season, 2015–2017. We translocated bobwhites ($n \geq 120$) to Home Farm, Sim Place, Turner's Creek, and Chino Farm for 3 consecutive years (2015–2017), but we removed Chino Farm as a translocation site after year 1 because of logistical constraints. We focused capture timing to the period immediately preceding covey break-up in the South (Terhune et al. 2006*b*), as determined from field observations of bobwhite behavior on source sites, so that larger groups of bobwhites could be captured. By increasing capture efficiency, we thereby attempted to reduce the number of translocation trips within a given year. Additionally, this prebreeding period avoids interruption of reproductive behavior (e.g., nesting) and capitalizes on the high reproductive potential of bobwhite (Terhune et al. 2010, Sisson et al. 2012).

We captured bobwhites on source sites using baited (e.g., grain sorghum and cracked corn) standard walk-in funnel traps (Stoddard 1931). We placed traps in areas of dense cover and sheltered with brush to limit stress on captured birds and to conceal traps from predators. We attached unique aluminum leg bands (National Band & Tag Company, Newport, KY, USA) to all captured bobwhites and classified them by age (adult, juvenile) and sex (male, female, based on plumage) (Rosene 1969).

For each site and year, we translocated radio-collared bobwhites at an approximate 1:1 sex ratio. All captured birds for translocation were fitted with a radio-collar and leg band after capture at the source site. Radio-collars were 6.0–7.0 g very high frequency (VHF) pendant-style transmitters (Holohil Systems, Carp, Ontario, Canada) and were affixed to bobwhites weighing ≥132 g (transmitter ≤5% of body mass). This weight limit and transmitter style are common in contemporary bobwhite translocation research (Terhune et al. 2010, Scott et al. 2013, Downey et al. 2017) and do not influence physiology (in captive birds; Hernández et al. 2004) or survival (in wild birds; Palmer and Wellendorf 2007, Terhune et al. 2007) although capture and handling can negatively impact translocation (Abbott et al. 2005). Birds were health screened before being placed in transport boxes. Afterwards, we placed captured bobwhites into transport boxes in groups that did not necessarily reflect covey membership at the time of capture. In some instances, we combined partial coveys from different traps to form complete coveys (8–12 bobwhites) as capture success dictated. We provided a small amount of feed (cracked corn and milo) in transport boxes for consumption during transit. No water was provided in transit. We spread supplemental feed at release sites immediately before and after release to mitigate any stress placed on birds during transport and limit any immediate dispersal from release sites. Supplemental feed continued at the sites through the seasons, except during the summer months.

Translocations occurred over a 36-hour (2 night) period via motor vehicle. The straight-line translocation distance was 1,340 km to Pine Island (~1,600 km driven path) and 1,220 km to Chino Farm and Turner's Creek (~1,450 km driven path). Over the 3 years of the study only 2 birds died as a function of the radio antennae getting stuck in the seam of

the door, and no birds died of stress. We released bobwhites at centralized core locations on translocation properties using a hard release methodology (Martin et al. 2017). In 2016, low trapping success forced multiple translocations over 8 days (1–8 Apr) and we held 1 covey an additional night so we could translocate it with additional bobwhites captured the following day. In all other years, translocations occurred in ≤3 days.

To maintain sample size of radio-collared birds at the translocation sites during the winter, we trapped bobwhites with walk-in funnel traps baited with cracked corn and milo (Stoddard 1931). Because the Pine Island and Turner's Creek sites had no existing conspecifics, any bobwhite encountered after translocation was considered offspring from translocated birds. Chino Farms did have conspecifics so birds without tagging could have been from wild conspecific stock or offspring of translocated birds. All captured bobwhites were weighed, and classified by age and sex. If they were untagged, we fitted them with a unique aluminum leg band, and a pendant-style radio-collar following the protocol described earlier. If juveniles were caught that did not meet the weight requirement to be radio-collared, they were fitted with a unique aluminum leg band only. During the study we caught only 2 new birds on the New Jersey site and no birds in Maryland; thus, we assume that their impact was minimal in the analysis of the project. All trapping, handling, and marking procedures followed American Ornithologists' Union Report of Committee on the Use of Wild Birds in Research (American Ornithologists' Union 1999) and our protocol was approved by the University of Delaware Institutional Animal Care and Use Committee (AUP 1278).

We located individuals using a telemetry receiver (Model R4000, Advanced Telemetry Systems, Isanti, MN, USA) and a three-element Yagi antenna (Advanced Telemetry Systems) via the homing method (White and Garrott 1990) 3–5 times/week to estimate winter survival and habitat use October–March 2015–2018. We approached individuals within 25–50 m to minimize error in habitat classification. We marked individual locations using Avenza PDF Maps (Avenza Systems, Toronto, Ontario, Canada) for iOS mobile devices during radio-tracking while in the field. We determined the cause of mortality (avian, mammal, or unknown) by the condition of the transmitter and evidence at kill site (Dumke and Pils 1973, Curtis et al. 1988).

Individuals were allowed to adjust to radio-collars for 7 days before being included in survival analysis to reduce radio-collar bias (Tsai et al. 1999). We censored bobwhite because of unknown fate, collar loss, or survival beyond the end of the study season. If exact dates of collar loss or disappearance were unknown, we used the midpoint between the last unique location and the day the collar stopped moving or was not locatable as the censor date.

Survival Analysis

We estimated survival rates of bobwhites in relation to temporal and biological (group) effects using the known-fate data type in Program MARK (White and Burnham 1999). The known-fate model employs a binomial likelihood and permits incorporation of individual covariates (e.g., sex), temporal effects (e.g., year, linear and quadratic time trends, season, week), and groups (e.g., region, site) to evaluate their effect on survival. When the covariates were biologically relevant, we constructed *a priori* candidate models incorporating additive effects and interactions using a logit-link function. We computed weekly survival rates (WSR) and we specified the appropriate interval length in Program MARK to yield accurate estimates of survival and precision.

We used an information-theoretic approach (Akaike 1973, Guiasu 1977, Anderson et al. 2000, Burnham and Anderson 2002) to sequentially evaluate 2 sets of candidate models testing explicit hypotheses. The first set of models evaluated temporal (i.e., year, season, month, week, linear and quadratic time trends) effects, and we used the top-ranked, most parsimonious model as the baseline model for the second sequential model set evaluating region, site, and sex effects on survival. We used Akaike's Information Criterion adjusted for small sample bias (AIC_c; Akaike 1973, Wedderburn 1974, Burnham and Anderson 2002) to compare candidate models, and we considered the model with the lowest AIC_c to be the best approximating model, given the data. We assessed model fit (using evaluation of residual plots and cˆ) derived from the most general model. We assessed the relative plausibility of each model in the set of candidate models using Akaike weights (W_i; Anderson et al. 2000, Burnham and Anderson 2002), where the best approximating model in the candidate set has the greatest Akaike weight. We used model averaging (Akaike 1973, 1974; Burnham and Anderson 2002) to obtain weekly survival rates (WSR). To provide additional inferential power and to allow direct comparison of covariates, we evaluated and report beta coefficients, their standard errors (SEs), and 85% confidence intervals (CIs) for variables of interest (e.g., group; Arnold 2010).

Home Range Analysis

We used adehabitat in R (Calenge 2006) with a least-squares cross-validation as a smoothing parameter to calculate a 50% and 95% adaptive kernel home range (Worton 1989). We defined coveys as unique groups of bobwhites that remained together for >3 consecutive tracking days (Lohr et al. 2011). Coveys with <20 locations were excluded from analysis. This 20-telemetry location requirement to reduce estimation bias is lower than many other studies (Terhune et al. 2010); however, due to a small sample size, we felt it was necessary to get informative results from the model (Haines et al. 2009).

Resource Use Analysis

Second- and third-order habitat analysis was conducted for both the New Jersey and Maryland regions. Land cover classification was digitized for each site in ArcGIS version 10 (Esri Inc., Redlands, CA, USA) over spatial resolution (0.305 m) orthophotographs for the years of study (2015–2018). Due to the fundamental differences between the pine systems in the New Jersey sites and the agricultural landscape in Maryland sites, land cover categories were identified separately for the 2 regions.

The following 7 land cover categories were defined for the New Jersey sites: 1) pine woods (PNW), defined as mature closed-canopy pine-dominated upland within which no mechanical timber operations occurred with a basal area of >18 m^2/ha; 2) thinned pine (PNT), defined as partially open-canopy pine-dominated upland within which mechanical timber thinning and surface scarification occurred with a basal area of ~14–16 m^2/ha; 3) cut pine (PNC), defined as open-canopy pine-dominated upland within which clear cutting or dispersed retention cutting and roller chopping occurred 10–12 years preceding study period, as evidenced by mid-seral stage vegetation communities; 4) early-successional woody (ESW), defined as areas dominated by woody (e.g., shrub, scrub oak, pine saplings) vegetation and lacking any canopy; 5) early-successional herbaceous (ESH), defined as areas characteristically dominated by early stage herbaceous vegetation, including warm-season grasses and forbs; 6) wooded wetland (WTW), defined as closed-canopy wetlands dominated by hardwood trees; and 7) cedar woods (CDW), defined as wetlands dominated by Atlantic white cedar.

The following 6 land cover categories were defined for the Maryland sites: 1) cropland (CPS), defined as areas within which row crops were being cultivated; 2) cool-season grass drains (CSG), defined as areas covered by sod-forming cool-season grasses for erosion control; 3) early-successional herbaceous (see preceding paragraph); 4) early-successional woody; 5) food and cover plantings (FCP), defined as wildlife plantings meant to provide food and cover (e.g., bicolor lespedeza [*Lespedeza bicolor*]); and 6) mixed woods (MXW), defined as mature mixed-species woodlots, drains, and riparian areas bordering agricultural fields or other open land cover. For all sites, open water (including cranberry bogs) and manmade structures were classified as non-usable space.

On the New Jersey site only, we further evaluated telemetry locations for more in-depth microhabitat use assessment of pine management. Technicians in Maryland were not able to collect this information, so microhabitat analysis between pineland and agricultural management was not possible. We randomly selected 30 points/release site/year (n = 180) and collected 1) percentage of bare ground, litter, grasses, forbs, and woody debris in a 1-m^2 plot (Daubenmire 1959); 2) visual obstruction of location at 0.25 m and 1 m in height using a Nudds board (Nudds 1977); 3) basal density via a Jim-Gem® factor 10 prism (Doggett and Locher 2018); and 4) percentage of canopy closure via a convex spherical densitometer (Forestry Suppliers, Inc., Jackson, MS, USA). We further collected two randomized points (through randomized azimuths and paces taken from the telemetry location) to compare habitat preferences with availability. If the randomized point occurred within non-habitat (e.g., open-water, roadways), a new random point was selected from the point originally used.

We considered available resources at the second-order home range of the individual to be all the usable space within a 95% minimum convex polygon (MCP) of telemetry locations at each study site. Available resources at the third-order used within the home range were considered all usable space within the 95% adaptive kernal home range for each individual. To assess available use relative to telemetry locations of individuals, 5 random points were generated for each individual location within the second- and third-order available habitat. This provided a 5:1 available-to-use prevalence ratio for both second- and third-order analyses (Phillips et al. 2009). Fourth-order site-specific resource selection analysis compared field vegetation data at individual use points to those collected at randomized non-use points. This provided a 1:1 prevalence ratio for fourth-order analyses.

Mixed logistic regression models were used to estimate probability of use at the second, third, and fourth order. Land cover covariates were used at the second- and third-order analysis and vegetation covariates were used for the fourth-order analysis. All continuous covariates were centered on a mean of 0 and standard deviation of 1 to improve model convergence. We used Pearson's correlation tests to assess the degree of collinearity of model parameters and did not fit models when $r > 0.7$ (Coppola 2021). For second- and third-order analyses, we specified vague, normal priors with a mean of 0 and precision of 0.001 for all fixed effects (Royle and Dorazio 2008, Kéry and Shaub 2012). Three habitat variables—litter cover, canopy coverage, and visual obstruction at 2 m—all showed high correlation; thus, we removed litter and canopy cover and retained visual obstruction as the predicting variable in the fourth-order analyses.

R2Jags program in R (Su and Yajima 2015) was used to estimate posterior distributions using Markov chain Monte Carlo methods with 3 independent chains to assess habitat selection. Each chain ran 25,000 iterations, discarding the first 10,000 and saving every fifth iteration thereafter. We assessed convergence via visual inspection of trace plots and defined adequate convergence as Gelman–Rubin convergence statistics < 1.1 (Gelman et al. 2014). Regression coefficients whose 85% credible intervals (CrI) overlapped 0 were interpreted as indicating equal selection with availability.

RESULTS

In New Jersey, we followed 53 radio-tagged bobwhites between 2015–2017: 20 (10 male, 10 female) individuals in 5 coveys in 2015–2016, 15 (8 male, 7 female) individuals in 6 coveys in 2016–2017, and 18 (11 male, 7 female) individuals in 5 coveys in 2017–2018. Of those birds, only 2 were new captures (fall 2015) and all the remaining birds over the 3 years were from the original translocation population. In Maryland, we followed 18 radio-tagged bobwhites between 2015–2017: 4 (0 male, 4 female) individuals in 3 coveys in 2015, 4 (2 male, 2 female) in 2 coveys in 2016, and 10 (7 male, 3 female) individuals in 4 coveys in 2017. Because only 2 of the 71 birds were locally caught, we did not have the sample size to conduct any analyses that would compare survival and habitat use between translocated and local birds.

Survival

The most parsimonious model from the first sequential model set evaluating temporal effects included a quadratic time trend (W_i = 0.85; Table 1). This top-ranked model was >10 times more likely to explain temporal variation in survival than the second-ranked model, which included month (ΔAIC_c = 4.70, W_i = 0.08; Table 1). Although receiving no support, models including season (ΔAIC_c = 23.74, W_i = 0.00) indicated the season was biologically meaningful such that non-breeding survival was lower (β_{winter} = -0.512, CI = -0.871 to -0.065) during the winter period than the fall (Figure 2). Models incorporating year effects did not merit support based on Akaike weights and ΔAIC_c values > 10 (Table 1).

The most parsimonious model from the second sequential model set effects included region (AIC_c = 485.58, W_i = 0.62), which was >2.5 times more likely to explain variation in survival than individual site effects (ΔAIC_c = 1.93; W_i = 0.00; Table 2). Region and site effects were lower in cropland sites in Maryland (β_{region} = -0.815, CI = -1.263 to -0.367]) compared to forested sites in New Jersey (Figure 3a, 3b). Survival was lower during the winter in both Maryland and New Jersey, and individuals in cropland sites in Maryland were 125 times less likely to survive the winter than individuals in forested sites in New Jersey (Figure 4). Although models including sex received moderate support (ΔAIC_c = 4.48, W_i = 0.07; Table 2), its biological relevance was low (β_{female} = -0.353, CI = -0.721 to 0.261).

Table 1. Akaike's Information Criterion, adjusted for small sample (AIC_c), ranking temporal effects models for northern bobwhite (*Colinus virginianus*) survival (S) on 4 study areas in New Jersey, USA and Maryland, USA, October–March 2015–2018.

Model	AIC_c	ΔAIC_c	W_i	Model likelihood	k	Deviance
S (T + TT)[a]	489.94	0.00	0.85	1.00	3	483.92
S (Month)[b]	494.64	4.70	0.08	0.10	6	482.56
S (T)	494.89	4.94	0.07	0.08	2	490.88
S (Season)[c]	513.69	23.74	0.00	0.00	2	509.68
S (.)	515.87	25.93	0.00	0.00	1	513.87
S (Year)	518.28	28.33	0.00	0.00	3	512.25

[a] T and TT represent linear and quadratic time trends, respectively.
[b] Month evaluating individual monthly effects on survival.
[c] Season comparing fall and winter effects on survival.

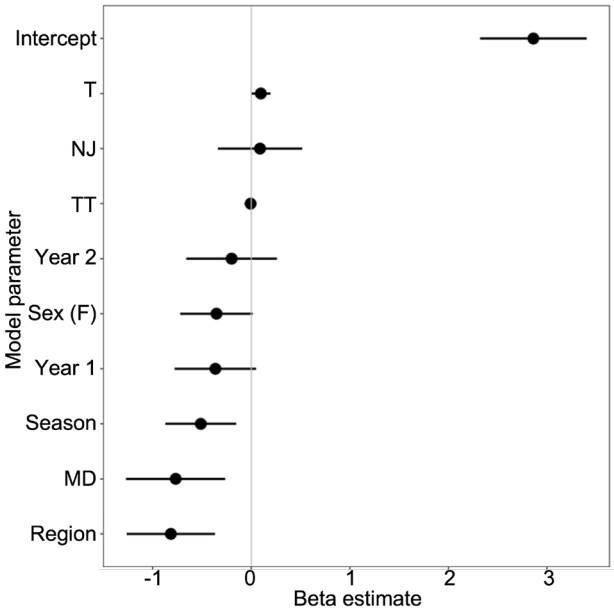

Fig. 2. Model average parameter estimates and 85% confidence limits for northern bobwhite survival during the fall and winter following spring translocation during 2015–2017 in the Eastern Shore of Maryland (MD), USA and Pine Island, New Jersey (NJ), USA. Models were developed *a priori* to evaluate temporal (T = linear time trend; TT = quadratic time trend; Season = Winter season compared to fall; year 1 = 2016 and year 2 = 2017 compared to 2015 as the baseline) and group (Region = cropland sites in MD compared to pineland sites in New Jersey; Sites = Sim Place and Home Farm in New Jersey and 2 sites in Maryland) effects on bobwhite survival.

Table 2. Akaike's Information Criterion, adjusted for small sample (AIC_c), ranking treatment group effects models for northern bobwhite (*Colinus virginianus*) survival (S) on 4 study areas in New Jersey, USA and Maryland, USA, October–March 2015–2018.

Model	AIC_c	ΔAIC_c	W_i	Model likelihood	k	Deviance
S (T + TT + Region)[a]	485.58	0.00	0.62	1.00	4	477.54
S (T + TT + Site)[b]	487.51	1.93	0.24	0.38	5	477.45
S (T + TT)	489.94	4.36	0.07	0.11	3	483.92
S (T + TT + Sex)	490.06	4.48	0.07	0.11	4	482.03
S (T)	494.89	9.31	0.01	0.01	2	490.88
S (Season + Region)[b, c]	513.15	27.57	0.00	0.00	3	507.13
S (Season)[c]	513.69	28.11	0.00	0.00	2	509.68

[a] Region comparing cropland sites in Maryland to forested sites in New Jersey.
[b] Site comparing individual study sites in Maryland and New Jersey.
[c] Season comparing fall weeks to winter weeks.

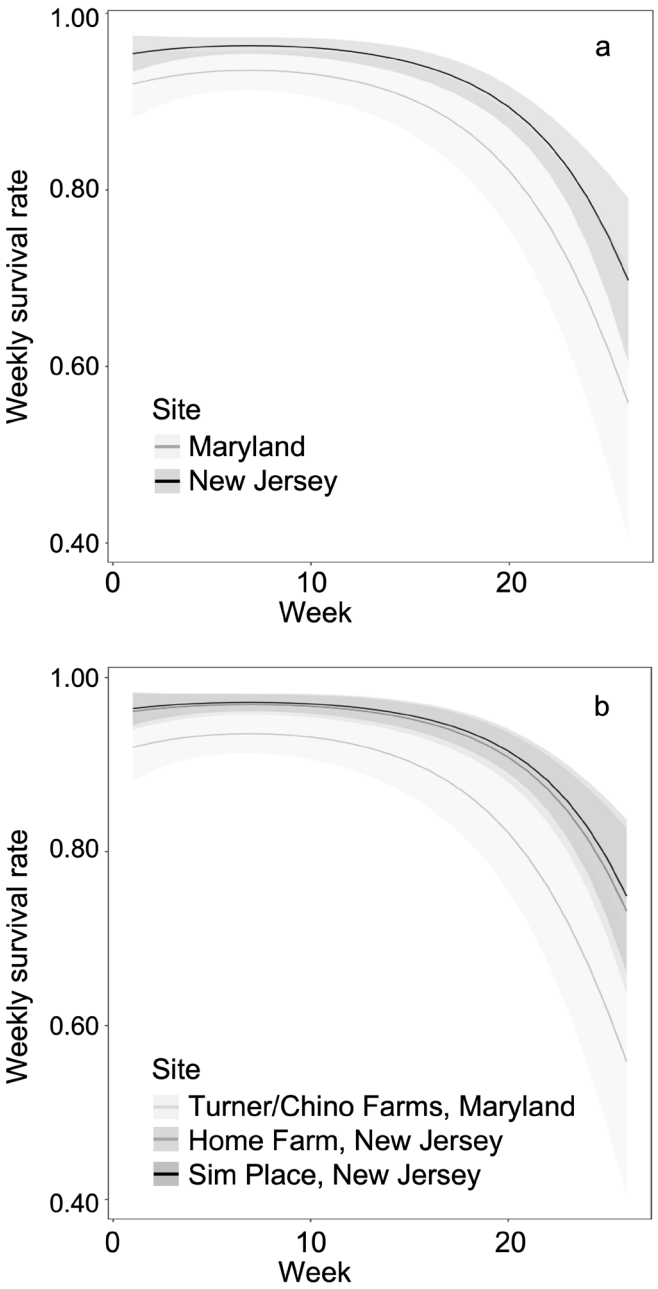

Fig. 3. Northern bobwhite weekly survival with associated 85% confidence limits for the over-winter season, October–March 2015–2017, derived for sites pooled by a) region (Maryland, USA and New Jersey, USA) using a linear and quadratic time trend model and b) site (TCF = Turner's Creek Farm in Maryland; Home Place and Sim Place in New Jersey).

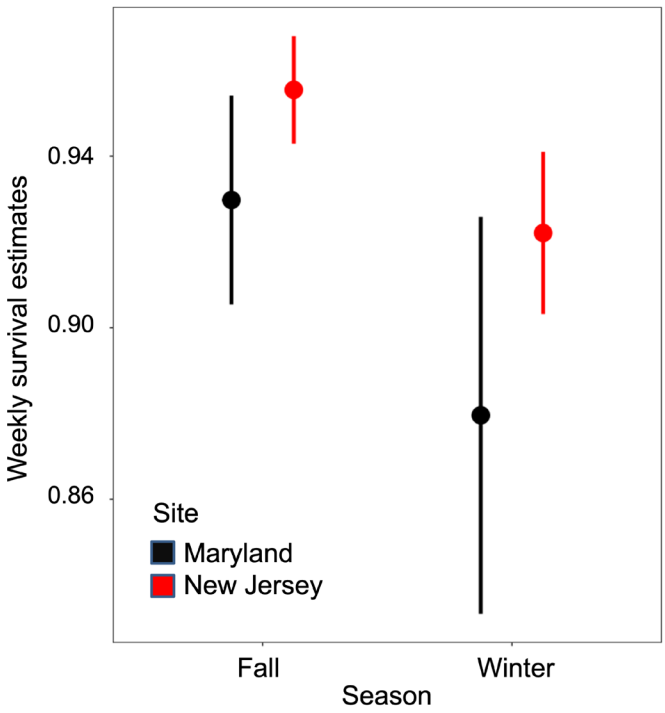

Fig. 4. Northern bobwhite weekly survival with associated 85% confidence limits during the fall and winter season, October–March 2015–2017, in Maryland and New Jersey, USA study sites.

HOME RANGE

Combining coveys across years, and removing any coveys with <20 telemetry locations, provided 54 covey locations on Home Farm, 108 covey locations on Sim Place, 53 covey locations on Turner's Creek, and 11 covey locations on Chino for analysis (note: Chino had bobwhites for winter analysis only in study year 1; Table 3). The 95% MCP home ranges were 81.01 ha (SE ±15.85) at Home Farm, 41.39 (SE ±5.09) at Sims Place, 22.74 (SE ±2.00) at Turner's Creek, and 10.31 (SE ±2.15) at Chino Farms. The 50% and 95% kernel densities, respectively, were 11.41 (SE ±1.55) and 54.32 (SE ±12.62) at Home Farm, 6.97 (SE ±0.53) and 31.52 (SE ±9.52) at Sim Place, 4.52 (SE ±0.59) and 20.44 (SE ±2.41) at Turner Creek, and 4.52 (SE ±0.59) and 20.44 (SE ±2.41) at Chino Farm.

RESOURCE USE

At the second-order scale for the Maryland sites, translocated bobwhites showed positive selection and probability of use for food and cover planting (β_{FCP} = 1.551, CrI = 0.973–2.141), early-successional woody (β_{ESW} = 0.711, CrI = 0.159–1.236), and mixed woods (β_{MXW} = 0.642, CrI = 0.123–1.136) land cover types, and negative selection for cool-season grass (β_{CSG} = -0.642, CrI = -1.356 to -0.012), cropland (β_{CPS} = -0.713, CrI = -1.170 to -0.251), and early-successional herbaceous (β_{ESH} = -1.535, CrI = -1.865 to -1.222) cover types (Figure 5a, 5b). At the third-order scale for the Maryland sites, translocated bobwhites showed positive selection and probability of use for food and cover planting (β_{FCP} = 1.187, CrI = 0.629–1.737) land cover types; equal selection for early-successional woody (β_{ESW} = 0.379, CrI = -0.157 to 0.913) and mixed woods (β_{MXW} = 0.066, CrI = -0.429–0.536) land cover types; and negative selection for cool-season grass (β_{CSG} = -0.818, CrI = -1.516 to -0.182), cropland (β_{CPS} = -0.573, CrI

Table 3. Mean home ranges (ha, 95% Minimum Convex Polygon [MCP]; kernel: 50% and 95%) for translocated, radio-marked northern bobwhites (*Colinus virginianus*) in 4 study areas in New Jersey (NJ), USA and Maryland (MD), USA, October–March 2015–2018.

Site (state)	Year	*n*	Locations, $\bar{x} \pm$ SD	95% MCP ha (SE)	50% Kernel ha (SE)	95% Kernel ha (SE)
Home Farm (NJ)	2015	24	47 ± 9	26.50 (3.72)	4.65 (0.96)	23.48 (19.96)
	2016	16	59 ± 16	151.32 (45.24)	20.05 (3.65)	92.01 (9.97)
	2017	14	57 ± 18	94.09 (19.24)	13.11 (2.09)	64.11 (16.86)
	Pooled	54	53 ± 15	81.01 (15.85)	11.41 (1.55)	54.32 (12.62)
Sim Place (NJ)	2015	15	44 ± 7	21.05 (3.06)	4.20 (0.47)	18.49 (16.43)
	2016	17	55 ± 14	84.34 (20.28)	12.68 (1.99)	56.66 (5.47)
	2017	22	58 ± 16	57.45 (14.83)	9.30 (1.28)	41.83 (12.93)
	2018	54	47 ± 14	26.97 (14.83)	4.98 (0.37)	23.02 (11.62)
	Pooled	108	50 ± 15	41.39 (5.09)	6.97 (0.53)	31.52 (9.52)
Turner's Creek Farm (MD)	2015	8	43 ± 16	18.40 (4.86)	1.77 (0.45)	9.53 (2.27)
	2016	9	43 ± 16	29.59 (3.91)	6.67 (1.75)	29.32 (7.08)
	2017	28	37 ± 8	22.81 (3.07)	4.98 (0.88)	22.04 (3.51)
	2018	8	53 ± 22	19.14 (3.85)	3.27 (0.74)	15.76 (3.92)
	Pooled	53	41 ± 14	22.74 (2.00)	4.52 (0.59)	20.44 (2.41)
Chino (MD)	2015	11	52 ± 15	10.31 (2.15)	2.20 (0.63)	10.66 (3.09)

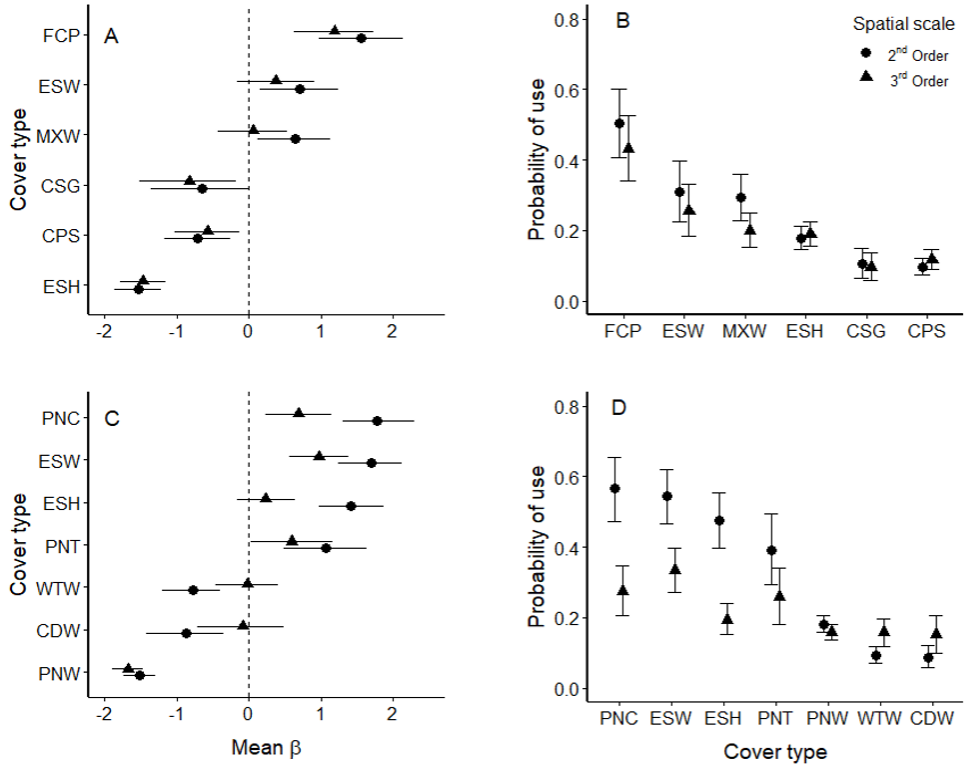

Fig. 5. Second- and third-order analyses for probability of use of various cover types (CDW: cedar woods; CPS: cropland; CSG: cool season grass; ESH: early-successional herbaceous; ESW: early-successional woody; FCP: food and cover plantings; MXW: mixed woods; PNC: cut pine; PNT: thinned pine; PNW: pine woods; WTW: wooded wetland) for translocated northern bobwhites in the Eastern Shore of Maryland, USA (A, B) and Pine Island, New Jersey, USA (C, D), during winter season (Oct–Mar 2015–2017).

= -1.036 to -0.125), and early-successional herbaceous (β_{ESH} = -1.468, CrI = -1.788 to -1.160) cover types (Figure 5a, 5b).

At the second-order scale for the New Jersey sites, translocated bobwhites had access to all vegetative types and showed positive selection and probability of use for cut pine (β_{PNC} = 1.783, CrI = 1.296–2.290), early-successional woody (β_{ESW} = 1.692, CrI = 1.242–2.130), early-successional herbaceous (β_{ESH} = 1.413, CrI = 0.966–1.871), and thinned pine (β_{PNT} = 1.063, CrI = 0.492–1.630) and negative selection for wooded wetland (β_{WTW} = -0.783, CrI = -1.199 to -0.392), cedar woods (β_{CDW} = -0.869, CrI = -1.420 to -0.350), and pine woods (β_{PNW} = -1.514, CrI = -1.731 to -1.297) land cover types (Fig. 5c, 5d). At the third-order scale for the New Jersey sites, translocated bobwhites showed positive selection and probability of use for cut pine (β_{PNC} = 0.689, CrI = 0.239–1.150), early-successional woody (β_{ESW} = 0.977, CrI = 0.565–1.379), and thinned pine (β_{PNT} = 0.560, CrI = 0.036–1.168); equal selection for early-successional herbaceous (β_{ESH} = 0.235, CrI = -0.168–0.641), wooded wetland (β_{WTW} = -0.016, CrI = -0.459 to 0.402), and cedar woods (β_{CDW} = -0.081, CrI = -0.711 to 0.482); and negative selection for pine woods (β_{PNW} = -1.678, CrI = -1.901 to -1.462) land cover types (Figure 5c, 5d).

Of the 6 vegetation variables considered as predictors of fourth-order habitat selection at the New Jersey sites, the most influential variables were grass cover, which showed a strong positive effect (β_{grass} = 0.643, CrI = -0.302 to 1.583), and visual obstruction at 1 m, which showed a strong negative effect (β_{vor1} = -0.235, 85% CrI = -0.611 to -0.138). The next most influential variables were woody groundcover (β_{woody} = 0.478, CrI = -0.048 to 1.01) and visual obstruction at 0.25 m (β_{vor025} = 0.294, CrI = -0.366 to -0.948. Probability of use decreased linearly with horizontal visual obstruction at 1 m (Figure 6). In contrast, probability of use for horizontal visual obstruction at 0.25 m, percent grass cover, and percent woody cover all increased linearly (Figure 6); however, it is important to recognize woody groundcover and visual obstruction at 0.25 m both overlapped with zero, so it is likely their selection effects were nominal.

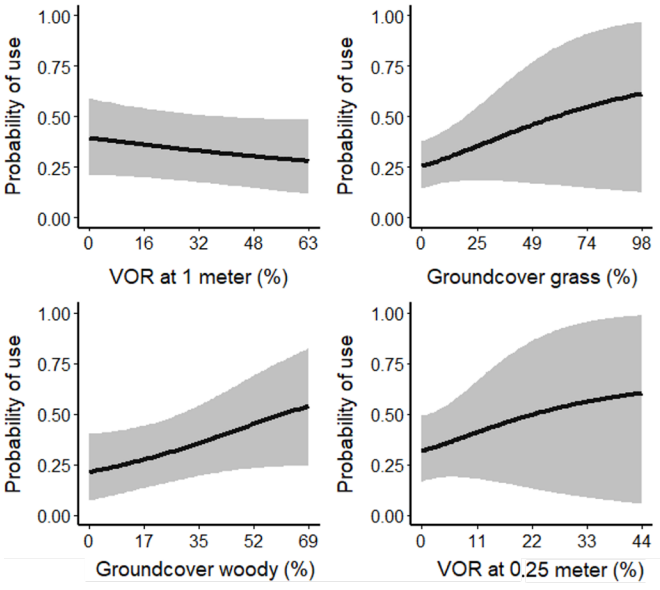

Fig. 6. Fourth-order analysis of probability of use as a function of visual obstruction (VOR) at a height of 1 m, percentage of groundcover in grass, percentage of groundcover in woody vegetation, and visual obstruction at 0.25 m for translocated northern bobwhites in Pine Island, New Jersey during winter season (October–March 2015–2017).

DISCUSSION

We found that survival and resource use differed among translocated bobwhite on cropland-dominated (fragmented) sites compared to forested sites. Survival was lower on cropland sites compared to forested sites such that bobwhite in cropland-dominated landscapes were >125 times less likely to survive the winter than those on forested sites. We observed differential resource availability among sites and use among bobwhites translocated to forested sites and cropland sites during the non-breeding season that were not as evident during the breeding season (Coppola et al. 2021).

Non-breeding season survival was low on all study sites, but especially on cropland-dominated sites. Lohr (2009) found wild bobwhite in New Jersey had a daily survival rate of 0.9934 and a cumulative non-breeding season survival rate of 0.30. Population models for bobwhite in the Mid-Atlantic predicted that bobwhite populations need a daily survival rate of 0.9968, which equates to an average weekly survival rate of 0.9778 (i.e., non-breeding, overwinter survival rate of 0.556) to maintain a stable population (Williams et al. 2012). Non-breeding season period survival was lower on both sites (New Jersey = 26.2% and Maryland 11.1%) than the predicted winter survival rate required for population stability in the Mid-Atlantic states. Furthermore, average weekly survival rates in our study were lower (WSRNJ = 0.9498 and WSRMD = 0.9189) for translocated bobwhites compared to average weekly survival (0.9728) of their origination (source) sites (Terhune et al. 2007, Sisson et al. 2017). Although our sample size was low, especially on the Maryland sites, these winter survival rates are cause for concern. However, they underscore the importance of resource availability needed in the Mid-Atlantic states to overcome challenges in the states in the northern periphery of bobwhite distribution during the non-breeding season and the opportunity for improvement of habitat conditions on our study sites.

Harsh winters are known to negatively impact wildlife and bobwhite survival (Janke et al. 2015, McLaughlin et al. 2019). We found that weekly survival rates on both cropland and forested lands were similar during the fall to other bobwhite studies (Terhune et al. 2007, 2010; Sisson et al. 2017) but much lower during the winter months (see Figure 4). However, bobwhite translocated to cropland sites experienced extremely low winter weekly survival rates, even compared to forested sites in this study. This is likely a result of a habitat pinch point on cropland landscapes where during the non-breeding season much of the available cover

(~70%) present during the breeding season is removed due to late-summer and early-fall annual harvest of crops. As such, birds are forced to use resources in a more concentrated area, potentially increasing predation risk and reducing food availability. While it is well established that broad-scale patterns of abiotic and biotic conditions affect organisms' distributions and population fluctuations, discrete events may be important drivers of space use, survival, and persistence. Discrete extreme climatic events can constrain populations and space use at fine scales beyond what is typically measured in ecological studies. Recently, a growing body of literature has identified thermal stress as a potential mechanism in determining space use and survival (Tanner et al. 2016). Although not directly assessed in this study, snow events could have contributed to reduced non-breeding season survival during the winter months and could elucidate our findings (Janke et al. 2015, 2017). Multiple snow events did occur on our study sites, but the magnitude of their impact is uncertain. That said, nutritional supplementation is known to improve survival during harsh winter weather and potentially help to mitigate but not eliminate habitat deficiencies (McLaughlin et al. 2019). Future translocation research should evaluate the interactive relationships between thermal cover and necessary food resource availability during the non-breeding season to support necessary survival.

Differential resource use by bobwhite on cropland compared to forested sites was evident at multiple spatial scales. On the forested sites, bobwhite used cut pine, early-successional woody, early-successional herbaceous, and thinned pine more than what was available on the landscape, but at the home range scale bobwhite only used cut pine, thinned pine, and early-successional woody higher than their availability. On the cropland sites, bobwhite used food plots, early-successional woody, and mixed woods more than what was available on the landscape and only food plots at the home range scale. Bobwhite on both landscapes used early-successional woody resources at all spatial scales, which has been shown to directly impact non-breeding season survival in other studies in northern U.S. states (Janke et al. 2015, 2017). This use of the woody resources and higher survival at the New Jersey forested site appears to run counter to some research that suggests that, although bobwhites generally select areas with greater understory cover, they avoided uplands when pine or hardwood basal area exceeded 20 m^2/ha or 12 m^2/ha, respectively; a plausible explanation is the association of high basal area with increased shading and subsequent loss of understory cover (Kroeger et al. 2020). However, in the New Jersey Pinelands ecosystem, the forest contains a high basal area with an intact understory consisting of low woody shrubs that provide not only winter thermal cover but also escape cover and forage opportunities from both soft and hard mast through the seasons. On cropland sites, however, bobwhite used food and cover plots most frequently and much higher than expected at both the landscape and home range scales. Food and cover plots and much of the early-successional woody cover were established several years before translocation. Considering bobwhite's high use of artificial plantings, other limiting resources such as forested lands (e.g., pinewoods, thinned pine) potentially indicate insufficient availability of resources conducive to adequate non-breeding season survival on these sites. In contrast, bobwhite on the forested landscapes in New Jersey had abundant, non-fragmented native resources available but still experienced large home ranges and relatively low survival. This may indicate that the resources are still limiting or are available, but habitat management modifications are needed to improve survival during the non-breeding season. For example, the high use of cut pine, early-successional cover (woody and herbaceous), and thinned pine may reveal a limitation of those resources within the forested landscape. The presence or absence of woody understory cover has been demonstrated repeatedly to be a stronger influence on bobwhite habitat selection than herbaceous cover during the non-breeding season, and managers should provide woody understory cover on the landscape (Cram et al. 2002, Lusk et al. 2006, Janke et al. 2013, Brooke et al. 2015, Rosche et al. 2019, Kroeger et al. 2020). Because forest management is not common in the New Jersey pine barrens, implementation of an intentional timber thinning and prescribed fire plan could improve all these habitat conditions (i.e., increase preferred fourth-order habitat availability and reduce home range size) on the New Jersey sites.

Resource availability is a precursor to demographic performance and a necessity for translocation success (Martin et al. 2017). Most translocation studies, to date, have focused on survival during the breeding season and did not assess non-breeding season survival and resource use. Our study demonstrates that non-breeding season survival can limit translocation success and subsequent population growth, which could elucidate why some studies show short-term success during the breeding season but do not find long-term population growth and stability (Scott et al. 2013, Downey et al. 2017). Habitat deficiencies and stress incurred by translocated bobwhite will undoubtedly influence reproductive effort and fall recruitment immediately after translocation (Coppola et al. 2021). Fewer individuals are expected to survive until fall, and insufficient non-breeding season habitat conditions will result in even fewer individuals making it through the winter. Sandercock et al. (2008) indicated the importance of adult survival, particularly non-breeding season survival, to bobwhite population stability. Whereas translocations in the southeastern United States have had widespread success, translocation in the northeastern United States poses additional constraints (e.g., limited local source populations) and challenges to population stability and growth.

MANAGEMENT IMPLICATIONS

Our findings provide rare information on demographic resiliency and resource use for translocated bobwhite during the non-breeding season. We recommend that translocation preferentially focus on forested landscapes as a priority over fragmented, cropland landscapes unless sites could potentially meet the minimum of 1,500 acres (607 ha) of year-round

available quail habitat (Palmer et al. 2011). Further, in New Jersey, our research supports the New Jersey Bobwhite Action Plan recommendation that the Pinelands probably represents the greatest potential growth area for wild bobwhite within their former distribution in New Jersey. In addition, intentional management plans employing appropriate management activities such as prescribed fire and timber thinning on an annual basis prior to, during, and after translocation, and at a spatially relevant scale, will improve breeding and non-breeding season habitat conditions and the overall likelihood of success.

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HIGHLY VARIABLE AUTUMN CALLING RATES OF NORTHERN BOBWHITE FOLLOWING TRANSLOCATION

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ABSTRACT

Fall covey counts are a popular index for monitoring population trends of northern bobwhite (*Colinus virginianus*; hereafter, bobwhite), but their utility is tenuous under different scenarios. Detecting an individual covey is the product of the probability that the covey's activity center is located within the sampling frame, the probability the covey is located within the sampling frame during the sampling periods, the probability of the covey vocalizing, and the probability an observer will detect a calling covey. Researchers attempt to maximize detection or account for these potential sources of error using standardized protocol of limiting counts to certain weather conditions, replication, and distance sampling. Variation in calling rates across a range of bobwhite densities could lead to tenuous inference of population abundance from fall covey counts, particularly at low densities. Our objectives were to assess fall calling rates at 2 sites with low bobwhite density during population restoration. Our study sites were located in Erath County, Texas, USA and Leon County, Florida, USA and received translocated bobwhite during 2019 and 2020. We hypothesized calling rates would be influenced by the number of adjacent coveys that called, and thus, would be low for our sites. Although we did not estimate bobwhite density on our study sites, we surmised that their respective populations were <1 bird/3 ha. Calling rate at the Erath County site was 0 in 2019 (n = 10 counts) and increased to 0.79 (standard error [SE] = 0.07, n = 34 counts) in 2020. Calling rate was assessed only in 2020 at the Leon County site and averaged 0.13 (SE = 0.07, n = 23 counts). Detection rate at count stations was 0 in 2019 and 0.78 (SE = 0.08, n = 27 calling coveys) in 2020 at the Erath County site. In 2020, detection rate at count stations was 0 (n = 3 calling coveys) at the Leon County site. We documented high annual variation in calling rates among low-abundance sites, suggesting researchers should seek to empirically estimate this parameter rather than applying arbitrary correction factors based on previous literature. Low and variable calling rates limit detection and can bias inference.

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Key words: calling rates, *Colinus virginianus*, detection, northern bobwhite, point counts, translocation

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Fall covey counts are a popular index for monitoring population trends of northern bobwhite (*Colinus virginianus;* hereafter, bobwhite), but their utility is tenuous under different scenarios (DeMaso et al. 1992, Wellendorf et al. 2004, Wellendorf and Palmer 2005, Rusk et al. 2007). Despite concerns of accuracy, wildlife managers and researchers often use covey counts to index bobwhite populations (Kubečka et al. 2019). Covey counts are advantageous because they can cover large areas and provide data on post-recruitment population abundance (DeMaso et al. 1992). However, one critical assumption of covey counts is that calling rate is constant over time and space. Constant calling rates lead to more consistent detection probability when detectability is not empirically estimated. It is imperative that detection probability is consistent to reliably estimate population trends. Researchers maintain consistency in survey methodology to standardize effects that may lead to differential calling rates and detection. Researchers conduct surveys in the fall approximately 45 minutes before sunrise until sunrise because calling rates are highest during this period (Guthery 1986, DeMaso 1992). Additionally, observers ensure consistency in detection probability by using 1) standardized protocol that limits surveys to optimal weather conditions (e.g., low wind, no precipitation) and 2) replication. Nevertheless, bobwhite exhibit antiphonal calling, that is, density-dependent calling activity (Stokes and Williams 1968), which may violate the assumption of constant detection probability and lead to erroneous abundance estimates.

Researchers have also used covey counts to assess bobwhite population responses to various treatments, such as translocation (Scott et al. 2013, Downey et al. 2017, Palarski 2021). Translocation of wild bobwhite has gained popularity as a conservation tool to combat population decline over the last 2 decades. Some of these efforts seek to evaluate specific research questions like effects of source population (Palarski 2021) or landscape connectivity (Coppola et al. 2021) on key demographic rates, such as survival, reproduction, and dispersal. However, many studies attempt to evaluate translocation success or efficacy using call counts in order to assess abundance in addition to demographics (Sisson et al. 2012, Downey et al. 2017, Sisson et al. 2017, Palarski 2021). Although call counts are often used, inference may be tenuous because they are often poor predictors of density at smaller scales (Kubečka et al. 2019).

Bobwhite translocations typically occur in areas with low abundance and densities (<1 bird/3 ha; Terhune et al. 2010, Downey et al. 2017, Palarski 2021), or in areas where bobwhite have been extirpated (Scott et al. 2013). As a result, calling rates may vary due to low populations before and during translocation. These low populations may negatively influence calling rates, and thus render covey call counts poor predictors of actual abundance. As a result, researchers may draw inaccurate conclusions on short-term success. Our objectives were to assess fall covey calling rates at sites with low bobwhite density (<1 bird/3 ha) during translocation. Specifically, we used our data to 1) quantify calling rates for known coveys and 2) calculate detection rate at predetermined call count stations.

STUDY AREA

We conducted this study in 2 locations: Erath County in Texas, USA, and Leon County in Florida, USA. Both study sites were actively managed for bobwhite and were undergoing translocation during the study period. We estimated that fall bobwhite density was <1 bird/3 ha on both study sites based on anecdotal observations, number of birds translocated to each site, and demographic rates from radio-marked bobwhite. Following a second year of translocation in 2020, fall populations likely increased from 2019 but remained low for both sites (<1 bird/3 ha).

Erath County

The first study area was a 1,011-ha private property located in western Erath County near De Leon, Texas (Figure 1). The area was in the Cross Timbers ecoregion, which was defined by forest (primarily *Quercus* spp.) intermixed with patches of grassland prairies (DeMaso and Dillard 2007). Herbaceous vegetation was dominated by little bluestem (*Schizachyrium scoparium*), while woody vegetation consisted of elbowbush (*Forestiera pubescens*), sandplum (*Prunus angustifolia*), and oak (*Quercus* spp.) mottes. Long-term (30-year) average annual precipitation for the area was 86.2 cm; maximum monthly precipitation occurred bimodally, peaking in May and September (PRISM Climate Group 2020). Average monthly temperatures ranged from 7–28° C (PRISM Climate Group 2020). We translocated 167 and 236 bobwhite to this study site in 2019 and 2020, respectively. A subset of these individuals (n = 111 and n = 110 in 2019 and 2020, respectively) were radio-marked with very high frequency (VHF) transmitters (American Wildlife Enterprises, Monticello, FL, USA). Bobwhite abundance in both study years was low (< 1 bird/3 ha) during covey counts.

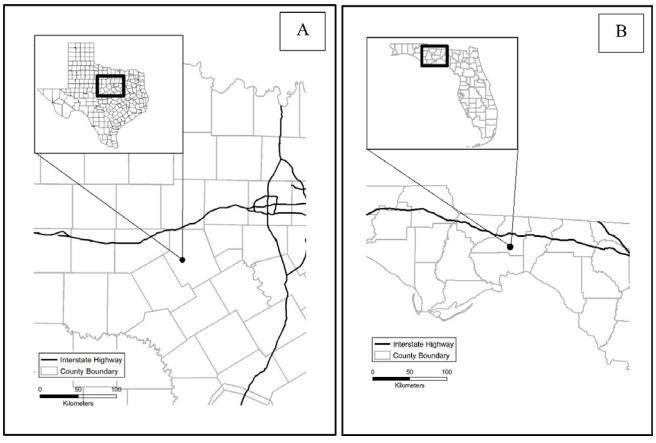

Fig. 1. Location of northern bobwhite (*Colinus virginianus*) translocation sites in A) Erath County, Texas, USA and B) Leon County, Florida, USA. The black dot represents the location of the release sites within each county.

Leon County

The second study area was a 1,538-ha unit of the Apalachicola National Forest in southern Leon County near Tallahassee, Florida. The area was located within the Munson Sandhills region distinguished by predominantly upland longleaf pine ecosystem and dry, well-drained sandy soils. Long-term (30-year) average annual precipitation for the area was 151.3 cm, peaking between June and August (PRISM Climate Group 2020). Average monthly temperatures ranged from 10–27° C (PRISM Climate Group 2020). Dominant woody cover consisted of bluejack oak (*Quercus incana*), sand post oak (*Quercus margarettae*), longleaf pine (*Pinus palustris*), dwarf huckleberry (*Gaylussacia dumosa*), and darrow's blueberry (*Vaccinium darrowii*). Herbaceous vegetation primarily consisted of wiregrass (*Aristida stricta*), pineywoods dropseed (*Sporobolus junceus*), bluestem (*Andropogon* spp.), witchgrass (*Dichanthelium* spp.), pineland pinweed (*Lechea sessiliflora*), silkgrass (*Pityopsis* spp.), gopher apple (*Geobalanus oblongifolius*), and saw greenbrier (*Smilax bona-nox*). This site was also included in an active translocation program during 2019 and 2020. We translocated 80 and 81 individuals to this study site in 2019 and 2020, respectively. We trapped 11 and 28 resident bobwhite on the study site during February 2019 and February 2020, respectively. We radio-marked all translocated and resident individuals with VHF transmitters.

METHODS

Field Methods

We conducted covey counts from 27 September–24 November in 2019 and 2020. The night before each formal call count, observers located the radio-marked covey's roost. Roost locations were determined approximately 1 hour after official sunset the night prior to counts to minimize disturbance near the roost site during the morning of counts. Observers located radio-marked coveys via VHF radio-telemetry by homing to approximately 30 m (White and Garrot 1980). At the Erath County site, we conducted covey counts using 2 observers. One observer was stationed at predefined call count stations used for long-term data collection at varying distances from the marked covey. This observer was used to estimate detection probabilities. The second observer was positioned approximately 125 m from the marked covey (Wellendorf et al. 2004). We chose this distance because we believed that likelihood of detection of calls at this distance was approximately 1 and minimized the effects that observers had on calling rate. Thus, the second observer served to estimate calling rate.

At the Leon County site, we obtained roost locations the night preceding call counts by homing to approximately 30 m. To estimate calling rates, we placed a Song Meter SM3 acoustic recording device (Wildlife Acoustics Inc., Maynard, MA, USA) on a nearby tree approximately 1.5 m above ground level during the roost visit. We assumed likelihood of detection by the device was 1 at a distance of 30 m from the covey (Wilhite et al. 2020). Similar to the Erath County site, the following morning, observers were positioned at predefined listening stations within the radius of audibility of the marked coveys; we assumed that observers could detect coveys up to 600 m (Reyna et al. 2012).

Observers arrived at listening stations at least 45 minutes before official sunrise and recorded whether the radio-marked covey called and, if so, the time it called. The survey stopped at sunrise if no calls were heard, or 20 minutes after the first call was heard (DeMaso et al. 1992). Observers replicated covey counts ≥3 times for each radio-marked covey. All observers were trained prior to conducting call counts. Training trials occurred beforehand until trainees achieved similar estimates for the number of coveys heard (Kubečka et al. 2019). Call counts were not conducted when wind speeds exceeded 16 km/hr or if it was raining.

Acoustic recordings from the Leon County site were manually reviewed by 1 observer. At both study sites, calling rate was calculated by dividing the number of radio-marked coveys that called by the number of radio-marked coveys monitored at each study site. Detection rate was calculated by dividing the number of radio-marked coveys heard at the established call count station by the number of radio-marked coveys that called.

RESULTS

We monitored 2 coveys in 2019 and 8 coveys in 2020 at our Erath County site. Calling rate at the Erath County site was 0 in 2019 (n = 10 counts) and increased to 0.79 (standard error [SE] = 0.07, n = 34 counts) in 2020. Detection rate, conditional on calling, was 0 in 2019 and 0.78 (SE = 0.08, n = 27 calling coveys) at the Erath County site. We monitored 8 coveys at the Leon County site in 2020. Calling rate at the Leon County site averaged 0.13 (SE = 0.07, n = 23 counts), but detection rate was 0 (n = 3 calling coveys). At the Erath County site, the mean distance from the covey to observer when coveys called but were not detected was 446 m (range = 409–515, n = 6 counts). At the Leon County site, the mean distance from the covey to observer when coveys called but were not detected was 362 m (range = 143–612, n = 3 counts). At the Leon County site, average calling time for radio-marked coveys was 4 seconds (range = 1–7, n = 3 calling coveys). Average number of calling events was 3 (range = 2–7, n = 12 events). Calling time and number of events were not assessed at the Erath County site.

DISCUSSION

Calling rate estimates for our Erath County site were highly variable between years. This variability can limit inference from fall covey counts and thus bias estimates. We caution researchers using covey call counts to assess population response from translocation.

Although we did not empirically estimate density, we surmised that bobwhite populations were low (<1 bird/3 ha) on both study sites. Since we did not compare calling rates across bobwhite density values, we acknowledge that attributing calling rate variability to low density is tenuous. We believe that low bobwhite density on our study sites resulted in highly variable calling rates between years (Stokes and Williams 1968, Lituma et al. 2017) though that relationship is speculative. Yeiser et al. (2021) sought to evaluate precision and bias of bobwhite density estimation via covey call counts under various scenarios. They suggested that a large number of call count stations (n = 35) over multiple years (n = 5) can produce unbiased estimates of bobwhite density. However, these recommendations are often untenable for both land managers and researchers. To survey 35 call count stations ≥3 times/year would require 105 total surveys. This sampling regime would also require a minimum area of approximately 4,000 ha assuming a 600-m radius of audibility for each call count station. The need for high intensity sampling coupled with large area size would preclude many areas from having unbiased estimates as proposed by Yeiser et al. (2021). Furthermore, simulations conducted by Yeiser et al. (2021) assumed bobwhite densities greater than estimates for our study sites (≥0.62 bird/ha). As a result, surveys would likely need to be repeated more than 3 times/season to reduce bias and increase precision on smaller areas. To mitigate logistical constraints surrounding human observers, acoustic recording units (ARUs) could be used to meet high demand from surveys (Wilhite et al. 2020). Although further development is needed, ARUs may provide a mechanism to achieve high intensity surveying.

Documenting a population response from translocation, and thus defining short-term success, is a primary objective of many translocation efforts. Prior translocations in Texas have been designated as failures because of the inability to document substantial increases in call counts on the release site (Scott et al. 2013, Downey et al. 2017). Notably, Downey et al. (2017) reported demographic rates of translocated bobwhite in the Rolling Plains ecoregion of Texas comparable to stable populations but failed to document a population response on the release site compared to a control site after 2 years of translocation. The population response was partially assessed by fall covey counts. It is possible that variability in calling rates, lack of precision in indices, and variation in detection could have affected abundance comparisons.

Rusk et al. (2007) documented that covey call counts consistently underestimated bobwhite density and did not reflect changes in population abundance. With a calling rate of 0.70, similar to the rate we reported from 2020 in Erath County, bobwhite density estimates were still biased low compared to distance-based aerial (helicopter) surveys (Rusk et al. 2007). Results from Rusk et al. (2007) and our data suggest that using covey call counts to designate translocation success in the short term may be unreliable unless paired with estimates of detection and calling rate.

Mean distances from radio-marked coveys that called but were not detected at a call count station were within the 600 m radius of audibility at both study sites. We assumed a 600-m radius of audibility under ideal conditions, but topography, vegetation, and observer acuity may limit distances where calls can be heard. These factors can produce inconsistent and reduced detection probabilities. Our data may also be partially explained by results from Seiler et al. (2005), who estimated a mean measurement error of 75 m between known calling covey locations in rolling terrain. Additionally, we documented short calling durations and few calling events at our Leon County site, which may further limit detection at long distances (>400 m) from the observer.

The effects of conspecifics on calling behavior are well documented in the literature such that birds are known to increase calling activity in response to the presence of conspecifics (Penteriani et al. 2002, Sexton et al. 2007). It is plausible that use of playback calls may increase calling rates; however, use of this technique has yielded mixed results among songbirds and bobwhite. Lituma et al. (2017) found that the number of bobwhite conspecific calls and individual calling rate of conspecifics increased the likelihood of detection and an individual's detection availability during the breeding season. Other studies have shown that the use of playbacks to stimulate calling activity using the assembly call increased detection during the breeding season (Bailey 1978, Coody 1991) and non-breeding season (Wellendorf et al. 2001) under varying conditions. At low-density sites, the availability of a covey to be detected is low because of the ostensible lack of conspecifics present or high vulnerability to predation risk (or both) (Lima 1993, Bleicher 2017, Gaynor et al. 2019). Wellendorf et al. (2001) documented no difference between natural calling rates and stimulated calling rates during good weather conditions (<50% cloud cover and <16 km/hr wind speeds) but did detect an increase in stimulated calling rates during poor weather conditions (>50% cloud cover and >16 km/hr wind speeds); however, their study was conducted on moderate-density sites. Additionally, playbacks may not provide the necessary call frequency or magnitude needed to simulate a wild covey and elicit a response by unobservable coveys (DeMaso 1991, DeMaso et al. 1992, Rusk et al. 2009). Although there was an increase in calling rates using the playback device during poor weather conditions, we standardized our protocol to not conduct counts during these conditions. Regardless, when using call counts with or without playbacks, collecting data to decouple detection components by using time-of-detection and dependent double-observer methods is important to provide reasonable estimates of availability and detection given availability (Riddle et al. 2008, 2010). However, few studies have been conducted on low density (<1 bird/3 ha) sites for bobwhite using playbacks. More research is warranted to understand how playbacks at low densities influence calling rate and availability of detection.

Similarly, more research is needed to understand variability in peak covey calling spatially and temporally as well as alternatives to obtaining population estimates

for assessing population growth, particularly germane to translocation success. We used a standardized protocol that provides guidance on when to conduct counts; it incorporates weather conditions and time of year to capture peak calling activity. However, peak calling could also be assessed temporally and spatially by monitoring number of calling coveys heard and determining when calling rates peaked post hoc. For example, calling rates in Erath County during the first week (1 Oct–8 Oct) was 0.13, but increased to 1 for all subsequent weeks of the survey. Additionally, automated recording devices could be used to ascertain peaks in calling activity and to increase sampling area and frequency (Wilhite et al. 2020). Call count data could then be used during this peak to further reduce variation in calling rates. Last, our study focused on design-based methods to minimize variability in detection probability. Abundance estimates can also be improved by using statistical models that may further reduce bias and increase the likelihood of detecting population trends (Yeiser 2021). Modeling detection by incorporating distance-to-observer, time-of-removal information, or repeat visits or observers can be an effective method to estimate abundance (Thompson 2002).

MANAGEMENT IMPLICATIONS

In light of the unreliability of covey call counts at low population densities, we suggest utilizing alternative approaches to determine short-term success of translocation. We suggest integrating appropriate detection estimation procedures such as the dependent double-observer and time-of-detection method. When using covey call counts as a means to document population response, we recommend that researchers empirically estimate calling rate rather than applying arbitrary correction factors based on previous literature. Further refinement of acoustic recording units could provide a possible remedy for determining calling peaks, obtaining sufficient sample sizes, and reducing observer bias.

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TRANSLOCATING WILD CALIFORNIA VALLEY QUAIL TO TEXAS: AN EVALUATION OF SURVIVAL, DISPERSAL, TRACKING EFFICACY, AND ROOST PREFERENCE

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ABSTRACT

Quail translocations are becoming increasingly popular in regions of suitable habitat where local quail populations have declined. In northeastern Texas, USA, northern bobwhite (*Colinus virginianus*) populations have drastically declined for over a century and have reached undetectable levels in many areas. As a result, the number of quail hunters and quail conservation funding have also declined. California valley quail (*Callipepla californica*; hereafter, valley quail) have increased across their range and have been translocated to many states and countries. Thus, the goal of this study was to determine whether translocating wild valley quail to Texas was feasible, and evaluate their survival, dispersal, roost location preference, and potential predator impacts. We translocated 748 wild valley quail from Idaho, USA to northeastern Texas in 2019 and 2020. We collected quail location data from very high frequency (VHF) and digital transmitters. Motion-triggered cameras, scent stations, simulated nests, and raptor transects were used to record predator presence and potential predator impacts. Survival of birds with tracking devices was 63% (VHF) in 2019, and 38.8% (VHF) and 92.5% (digital tag) in 2020. Survival was greater for quail with digital transmitters. Median dispersal distance was 633.5 m in 2019 and 246.6 m in 2020 for valley quail with VHF transmitters, and 310.4 m for quail with digital transmitters. Minimum convex polygon area medians were 4.3 ha in 2019 and 3.1 ha in 2020 for quail with VHF transmitters, and 16.1 ha in 2020 for quail with digital transmitters. Roost sites were primarily in young stands of oak trees. Median simulated nest survival was 2 days (minimum [min] = 1, interquartile range [IQR] = 2–5.4, maximum [max] = 23) in 2019, and 7.5 days (min = 2, IQR = 4.5–15.2, max = 23) in 2020. The most frequent mammalian predators observed were raccoons (*Procyon lotor*), feral hogs (*Sus scrofa*), and white-tailed deer (*Odocoileus virginianus*). Red-tailed hawks (*Buteo jamaicensis*) were the most frequent aerial predator. We completed the first documented translocation of wild California valley quail to Texas, demonstrating it is feasible. Future translocation may benefit from translocating more birds over a longer period of time, with more consistent methodology. The establishment of a sustainable population may require ≥7 years of translocation at a rate of 500 birds per year with >2,000 ha of suitable habitat.

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Key words: California valley quail, *Callipepla californica, Colinus virginianus*, dispersal, mesomammal, nest camera, nest predation, northern bobwhite, predator-prey, radio-telemetry, radio handicap, survival, scent stations, translocation, Texas

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Quail translocations are becoming increasingly popular in regions of good habitat where local quail populations have declined (Martin et al. 2017). Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) populations in the United States have declined 3.1% annually since 1966 (Sauer et al. 2020). Bobwhite populations have declined to undetectable levels in northeastern Texas, USA, the focal region of this study. With declining quail populations, quail hunter numbers in Texas have decreased from 127,451 in 1999–2000 to 49,752 in 2017–2018 (Purvis 2018). Fewer hunters results in less funding for quail conservation (Brennan 2015). Thus, landowners and wildlife agencies are looking for novel approaches to restore quail and quail hunter numbers.

Population restoration techniques (PRTs) are used to restore quail populations in areas of restored habitat where resident populations do not exist. Landowners have implemented PRTs, such as releasing captive-reared bobwhites and translocating wild birds, with little documented long-term success (Whitt et al. 2017, Reyna and Newman 2018, Reyna et al. 2021). The failure of bobwhite PRTs has been attributed to bad source stock (Reyna and Newman 2018), poor timing of releases (Sisson et al. 2012), stress (Martin et al. 2017), severe weather (Chavarria et al. 2012*b*), and improper predator response (Stephenson et al. 2011, Reyna and Newman 2018). Additionally, predators are major stressors for newly translocated bobwhites and can adversely impact survival and translocation success (Martin et al. 2017). Predation losses are responsible for ≥89% of nest failures and 93% of adult mortalities (DeVos and Mueller 1993). Recent studies have investigated methods to improve bobwhite translocation success, and recommend release just prior to breeding season, a large area of high quality habitat on the recipient site, and short handling and transport times (Liu et al. 2002; Terhune et al. 2006*b*, 2010; Sisson et al. 2017; Reyna et al. 2021).

Bobwhites are not the only quail species to have been widely translocated. California valley quail (*Callipepla californica*; hereafter, valley quail) have been successfully translocated to ≥8 U.S. states and to Canada, New Zealand, Australia, Chile, Germany, and France (Phillips 1928, Schwartz and Schwartz 1950, Williams 1952, Leopold 1977, Pietri 1995). Many of these translocations resulted in increased hunting opportunity and revenue (Leopold 1977). While bobwhite populations have declined range-wide, valley quail populations have increased, particularly in regions where they were introduced (Sauer et al. 2020). Valley quail inhabit temperate to subtropical regions and have demonstrated high adaptability to new environments and tolerance of anthropogenic influences (Leopold 1977). Valley quail are less dependent on insects than bobwhites (Glading et al. 1940, Crispens et al. 1960, Hurst 1972) and are considered "suburban adaptable" (Blair 1996). Unlike most quail, which roost at ground level, valley quail roost in trees or elevated positions at night (Sumner 1936, Leopold 1977). There is a dearth of scientific literature on the utility of these adaptations to improve translocation success. For example, roost site selection is in part due to predator avoidance (Weatherhead 1983), and roosting in trees could decrease night predation. Because of their previous long-term translocation successes, ability to adapt to a wide variety of new environments, and increasing population numbers, valley quail appear to be good candidates for translocations to restored habitat.

We investigated the feasibility of translocating wild valley quail to Texas. A recent attempt by James et al. (2017) to translocate valley quail was unsuccessful. Therefore, our objectives were to translocate wild valley quail from Idaho, USA to Texas and evaluate their survival, dispersal, roost site selection, and potential predator impacts.

STUDY AREA

We focused on a ~500 ha privately owned ranch in Fannin County, Texas (Figure 1). Surrounding private land was also evaluated as translocated quail dispersed. The study area was in the Blackland Prairie ecoregion (Griffith et al. 2004) and was a mixture of grasslands interspersed with densely wooded areas. Average annual rainfall for Fannin County was 117 cm and mean annual temperature was 17° C (Arguez et al. 2011). The study area was managed primarily for white-tailed deer (*Odocoileus virginianus*), ducks (family Anatidae), and quail, although no quail were known to be present prior to the study. Predator control consisted of trapping and shooting, which, for this study, began in July 2019 and continued through the end of this study. Grasslands were interspersed with supplemental food plots, including oats (*Avena sativa*), legumes (family Fabaceae), and *Sorghum* spp. to attract and support deer and other wildlife. The ranch was managed through mechanical means (e.g., disking, mowing), prescribed burning, and periodic grazing of cattle to maintain early-successional grasslands and woodlands. The grasslands on the study area were mostly tallgrasses (*Panicum* spp., *Schizachyrium* spp., *Sorghastrum* spp.) intermixed with sections of briars (*Rubus* spp., *Smilax* spp.) and stands of young trees (*Quercus* spp.,

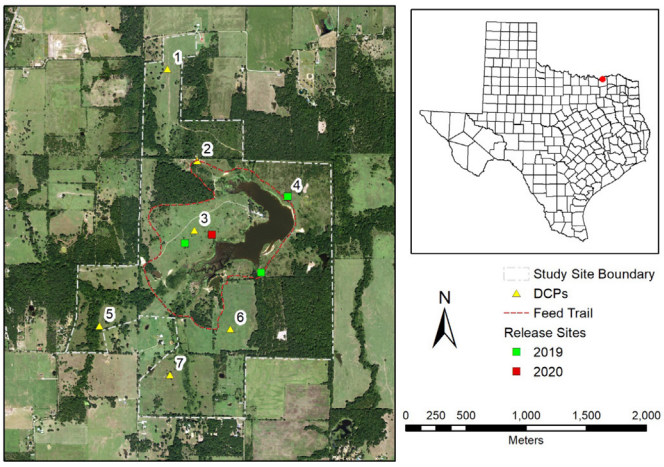

Fig. 1. California valley quail (*Callipepla californica*) translocation study area with data collection points (DCPs), feed trail, and quail release locations for 2019 and 2020.

Ulmus spp., *Juniperus* spp.) that provide cover and shelter for quail (Stoddard 1931, Leopold 1977). Water sources included 4 small creeks that flow into a ~16 ha reservoir near the center of the property, along with 9 small ponds (≤0.4 ha) around the perimeter of the study area.

Seven data collection points (DCPs) were established within the study area (Figure 1). They were marked by a numbered plate on a T-post, placed at the center of an understood 800-m diameter circle (Hansen and Guthery 2001, Whitt 2019), considered the data collection area (DCA).

METHODS

All animal handling methods were approved by the institutional animal care and use committee at Texas A&M University-Commerce (Animal Use Protocol P18-018). Birds were collected under Idaho Department of Fish and Game Wildlife Collection Permit #181220.

Trapping

We captured wild valley quail with modified Stoddard (1931) funnel traps (Smith et al. 1981) baited with a seed mixture (Deluxe Dove and Quail Blend, Chuckanut All Natural Products, Jefferson, OR, USA), which included white millet (*Panicum miliaceum*), safflower seed (*Carthamus tinctorius*), canola seed (*Brassica napus*), canary seed (*Phalaris canariensis*), wheat (*Triticum aestivum*), and cracked corn (*Zea mays*). Trapping occurred during February–March 2019 and 2020. Traps were checked daily and captured valley quail were transferred to the processing site, <10 km away, using a transport coop (COOP-6-Q; KUHL Corp., Flemington, NJ, USA).

Processing

We banded quail with numbered leg bands (1242-8; National Band and Tag Co., Newport, KY, USA) and recorded bird weight, sex, age (juvenile or adult), and general health. We extracted ≤100 µL of blood from the brachial vein of each bird (Owen 2011) using a lancet and 75 µL heparinized microhematocrit capillary tubes (51608; Pulmolab, Northridge, CA, USA) for disease testing.

Disease Testing

Prior to translocating valley quail to Texas, the Texas Animal Health Commission required that 10 birds/flock test negative for avian influenza (Influenza A virus subtype H5N1), and all birds test negative for pullorum disease (*Salmonella enterica* subsp. *enterica* serovar Gallinarum biovar Pullorum) and fowl typhoid (*S. enterica* subsp. *enterica* serovar Gallinarum biovar Gallinarum). A certificate of flock health from a veterinarian was also required. For avian influenza testing, ~50 µL samples of blood from 10 birds/flock were sent to the Idaho State Department of Agriculture Animal Health Laboratory in Boise. For pullorum disease and fowl typhoid testing, 20 µL of the extracted blood was applied to the rapid whole-blood plate test with pullorum typhoid antigen (Charles River Laboratories, Wilmington, MA, USA). Remaining blood samples were stored on labeled blotter cards (Whatman WB120205; Sigma-Aldrich®, St. Louis, MO, USA; Smith and Burgoyne 2004) for future genetic testing. When all tests were returned negative and a veterinarian's health certificate was received from a visiting veterinarian, the Texas Animal Health Commission issued an import permit.

Translocation

We placed birds in shipping boxes (16-Bird Shipping Box; Boxes for Birds, Conway, AR, USA) and shipped them to Texas using Priority Mail Express™ via the U.S. Postal Service. Each bird was supplemented with a ~30–50-g cucumber slice for nutrition and hydration during the 2-day shipping period (L. Webster, Oklahoma Quail Ranch, personal communication) in 2019, and millet sprays in 2021 (Currier 2021).

Quail were transported from the post office in Texas to the study area (~75 km) in the cargo area of a pickup. Shipping boxes were brought into a screened enclosure (Tailgaterz; Wenzel, Boulder, CO, USA) to prevent translocated birds from escaping. Birds were weighed, all demographic data confirmed, and notes made of any injuries or debilitating conditions. In 2019, 100 of the 250 quail were randomly selected and outfitted with very high frequency (VHF) radio transmitters as a necklace (Pip Ag393; Lotek Wireless Inc., Newmarket, Ontario, Canada). For 2020, 50 of the 500 quail were fitted with VHF transmitters as a necklace (A1070; Advanced Tracking Systems, Isanti, MN, USA), and 100 were fitted with a solar-powered digital transmitter (LifeTag™; Cellular Tracking Technologies, Rio Grande, NJ, USA) as a backpack. All birds in each shipment were released on the same day and within 1 week of capture. Quail in 2019 were released in separate locations within the study area. In 2020, all quail were released in the same location near the center of the study area (Figure 1).

In addition to habitat and predator management, the release site was prepared by establishing a ~5.8 km (3.6 mile) supplemental feed trail prior to release, to provide immediately accessible food and reduce mortality (Figure 1; Sisson et al. 2000). Feed was scattered along the feed trail biweekly using an electric feeder (55-Gallon Classic Game Feeder; One and Done Pro, Garland, TX) mounted in the bed of a utility task vehicle (Ranger Crew 570-4; Polaris®, Medina, MN). Feed consisted of ~226 kg (500 lbs) of hen scratch, a mixture of cracked corn, milo (*Sorghum bicolor*), and wheat. Release locations were also supplied initially with a small amount (~10 kg) of hen scratch on the day of release.

Monitoring

We tracked birds with VHF and digital transmitters to determine survival, dispersal, and roost locations. We located birds with VHF transmitters at least once per week. The digital transmitters sent a unique digital ID every 2 seconds in full sun, and every ~30 seconds in partial shade. Signals were relayed by nodes to a base station that recorded time and relative signal strength to estimate location. We also tracked

digital transmitters by hand using a digital receiver and Yagi antenna. We located VHF transmitters using a combination of triangulation and direct tracking (Millspaugh et al. 2012). While triangulation was the primary method, direct tracking was often more practical when quail were unlikely to flee (Millspaugh et al. 2012), for example, while roosting. We completed direct tracking by walking using a hand-held Yagi antenna to scan for VHF or digital transmitters within the study area. When a VHF or digital transmitter could not be detected within 1 week, we expanded the search radius for the bird from the point it was last recorded. We searched for missing digital transmitters using mobile nodes attached to vehicles. We attempted to locate VHF transmitters from all roadsides in a 2-km radius from the last known point as well as from private land, if permission could be obtained. If the VHF or digital transmitter was not located for 3 weeks, it was considered lost (Liu et al. 2000) and weekly attempts were made to relocate it. If a VHF or digital transmitter did not move for >1 week, the associated quail was flushed to determine status. Recovery dates and locations were recorded and marked with a hand-held Global Positioning System (GPS) device (GPSMap 64st; Garmin Ltd., Olathe, KS, USA).

Indirect quail counts were performed during spring and early summer seasons as an index of breeding potential and to record population trends (Smith and Gallizioli 1965). We conducted call counts at 7 DCPs across the study area (Figure 1). We placed DCPs in locations that did not restrict the observer from effectively hearing calls and avoided areas that were heavily wooded while still remaining ~800 m apart, to avoid double detection (Hansen and Guthery 2001). Call counts were performed starting at sunrise and continued until all DCPs had been visited. We recorded the number and estimated distance of calls, temperature, dew point, wind velocity, and percent cloud cover. Probability of detection was estimated using the double observer method (Nichols et al. 2000). Call counts and visual observations were used as indices for studying population trends.

In addition to radio-telemetry, a hand-held forward-looking infrared device (FLIR; Scout III, FLIR Systems, Wilsonville, OR) was used in combination with a Yagi antenna to detect quail on roost after sunset (Chavarria et al. 2012*a*). Once roosting quail were located, roost locations were marked with GPS coordinates and revisited for evaluation during the day. We recorded roost tree species, estimated age, diameter at breast height using a diameter tape, and estimated height using a tangent height gauge.

Simulated Nests

Simulated nests were created to mimic valley quail nests and to identify and estimate relative abundance of nest-predator species in the study area (Pietz et al. 2012, Dyson et al. 2020). Nests were constructed under a clump of bunchgrass (e.g., little bluestem; *Schizachyrium scoparium*) >0.3 m in diameter by kicking the toe of a boot under the bunchgrass and creating a nest bowl (Rollins et al. 2005). Each nest contained 14 Coturnix quail eggs (*Coturnix japonica*) since they were readily available and resemble valley quail eggs (Figure 2). Simulated nests were active for 23 days, the incubation period for valley quail, and nests were considered successful at day 23. Nests were terminated either once all eggs had been depredated or after 23 days. Nests were checked weekly for predation. Eggs were replaced at 2 weeks if undisturbed to avoid attracting predators to rotten egg odors (Major and Kendal 1996).

In 2019, simulated nests were placed in random clusters. Clusters consisted of 6 nests inside a 40-m × 40-m area. Four clusters were placed in locations typical of valley quail habitat, determined by the presence of adequate bunchgrass (Arredondo et al. 2007), cover, and proximity to food and water (Leopold 1977), along with radio-telemetry data or visual detection of coveys. Clusters were active on a rotating basis 1 May 2019–20 June 2019. When all nests in a cluster were terminated, the next cluster was initiated. Motion-triggered cameras (Model 119874C; Bushnell Corp., Overland Park, KS) were placed <2 m from each nest, and an orange flag placed behind the camera <1 m away. We checked nests every 1–2 days for predation and checked cameras for battery life and media storage.

Fig. 2. A simulated California valley quail (*Callipepla californica*) nest to determine nest predator impacts on translocated valley quail in Fannin County, Texas, USA, June 2019.

In 2020, simulated nests were placed in DCAs 1–5 along 300-m transects. We omitted DCPs 6 and 7 due to lack of suitable nesting habitat and lack of quail recorded in the area. We placed transects on DCPs in a randomly selected cardinal direction (Reyna et al. 2012). Six simulated nests were placed per transect, one every 50 m. We placed motion-triggered cameras <2 m from each nest, with remote flagging located ~7 m from a nest (Major and Kendal 1996). Simulated nests were active 1 May 2020–20 June 2020 as cameras were available. Transects 1 and 2 were initiated simultaneously. Transects 3–5 were initiated once 6 cameras were available from earlier transects. We checked nests weekly for predation and checked cameras for battery life and media storage.

We used photographs from simulated nests to identify nest predators and calculate nest survival. Predators returning to simulated nests could be determined by looking at unique markings (Heilbrun et al. 2003), size comparisons, and specific behavioral traits (Bridges and Noss 2011).

Predator Scent Stations

Relative abundance of predator species was assessed using predator scent stations, modified from Sargeant et al. (1998). We constructed predator scent stations at all 7 DCPs, ≥800 m from one another. A predator scent station consisted of a motion-triggered camera and a fatty acid scent tablet (Predator Survey Disks; Wildlife Control Supplies, East Granby, CT, USA) placed ~2 m from the camera and enclosed in a wire mesh envelope (5 cm × 5 cm). Mesh envelopes were secured with cable ties attached to a 10-cm metal stake driven into the ground. Scent stations were active for 5 consecutive days 1 May–20 June 2019 and 2020. We replaced tablets after rainfall.

Evaluation of Raptor Presence

To determine raptor presence and relative species abundance, a ~5.8-km transect was established along the existing supplemental feed trail (Figure 1). Two technicians with binoculars walked the transect twice, once clockwise and once counterclockwise, between 0600 and 1000 or 1600 and 2000 and recorded the date, time, weather conditions, location, quantity, and species type of each raptor observed. Raptor identification experience varied among individuals, so those with little experience reviewed the Merlin Bird ID phone application (version 1.8.2; Cornell Lab of Ornithology, Ithaca, NY, USA) to differentiate raptor appearances, songs, cries, and calls. We conducted surveys only on calm days (Craig 1978) and did not conduct surveys during active precipitation. Surveys were conducted twice monthly in 2020, beginning in February and continuing through June, with the exception of March 2020 due to COVID-19 restrictions and weather conditions (Schlater 2019). Raptors presenting themselves in the same spot every day were not counted each time as an incidental observation, but were counted if present during a raptor survey. We compiled data from raptor surveys with incidental observations.

Motion-triggered Cameras

We activated motion-triggered cameras along the supplemental feed trail (Whitelaw et al. 2009), and at an existing gravity feeder (Quail feeder, 1,000lb; Outback Wildlife Feeders, Gilmer, TX) to record predator presence and prevalence, and to monitor translocated quail. Camera locations were adjusted based on sightings of quail coveys and radio-telemetry location estimates. Cameras were identified by deployment location and date.

Data Analysis

Maximum survival was estimated using confirmed deaths from located tracking devices. Quail and simulated nest survival were analyzed with the Kaplan-Meier (Kaplan and Meier 1958) procedure with a log-rank test to compare survival data between groups (Bland and Altman 2004). Dispersal was quantified by: 1) measuring the maximum linear distance each quail traveled (Terhune et al. 2006*a*), and 2) using GIS software (ArcGIS 10.6.1; Esri Inc., Redlands, CA) to compute minimum convex polygon home ranges (MCPs) and center points (Jones 1999). We created a MCP for each quail that had ≥4 recorded locations. Convex polygons are an estimate of the range that the quail traveled over the study duration. Dispersal data were compared across each group of released birds using Mann-Whitney U test. A chi-square test was used to compare predator frequencies recorded from predator scent stations and simulated nests between years. Relative abundance of visits at scent stations was reported as a scent station index (SSI; Reyna et al. 2012), defined as (total station visits/total station operating nights) × 100. All motion-triggered cameras were checked at least once every 2 weeks. We entered image date and time, predator species, number of individuals present, and camera ID in a spreadsheet (Excel® 16.0; Microsoft® Corp., Redmond, WA, USA). Individuals photographed on a motion-triggered camera could be identified based on coat pattern or behavior and were not counted twice if identified twice on the same day, defined as the 24-hour time period beginning at 0000. Image capture times for the 5 most common predators were visualized in a scatterplot.

RESULTS

Translocation

We translocated 748 wild valley quail from Idaho to Texas (>2,000 km): 248 in 2019 and 500 in 2020. Valley quail were in transit for ~48 hours. All translocated valley quail tested negative for avian influenza and pullorum typhoid disease.

Survival

Due to short battery life and failures of VHF transmitters in 2019, survival estimates were determined at 6 weeks post-release. Maximum survival of quail with tracking devices (without censoring) was 63% (VHF) in 2019, and 38.8% (VHF)

and 92.5% (digital tag) in 2020; Kaplan-Meier estimates were lower (Figure 3). Survival was greater for translocated valley quail with digital tags than VHF transmitters in 2020 (log-rank test, df = 1, $\chi^2 = 9.71$, $0.001 < P < 0.01$).

Among birds without tracking devices, survival rate was less certain. At 60 days following the 2019 release, we estimated the number of surviving birds without transmitters in the study area at ~30 individuals, based on observations and assembly calls. At 120 days after our first release, 5–6 valley quail were regularly observed on the site. However, on 21 August 2019, a separate covey of ~15 birds was flushed and appeared to include at least 2 juveniles, indicating ≥1 successful nesting event by the translocated birds. More birds were observed in October, with ≥20 valley quail, including ≥2 juveniles ~6 months after release, with an unknown number outside the study area.

In April 2020, one translocated quail from the 2019 release was found 30.5 km (18 miles) away in Bells, Texas. In June 2021, 2 males were recorded on video chasing a hen on a neighboring property. As of August 2021, residents still observe translocated valley quail in the region of the study area.

Dispersal

Median dispersal for translocated valley quail with VHF transmitters was 633.6 m (minimum [min] = 36.3 m, interquartile range [IQR] = 397.5–833.4, maximum [max] = 2,029.2) in 2019, and 246.6 m (min = 12.6, IQR = 149.8–628.6, max = 1,696.3) in 2020. Median dispersal for translocated valley quail with digital transmitters in 2020 was 310.4 m (min = 34, IQR = 176.6–538.6, max = 975.9). Median dispersal in 2019 was greater for birds with VHF transmitters than in 2020 (Mann-Whitney U, $P < 0.001$) and for birds with digital transmitters (Mann-Whitney U, $P < 0.001$). There was no difference in dispersal distance between quail with VHF and digital transmitters in 2020 (Mann-Whitney U, $P = 0.24$).

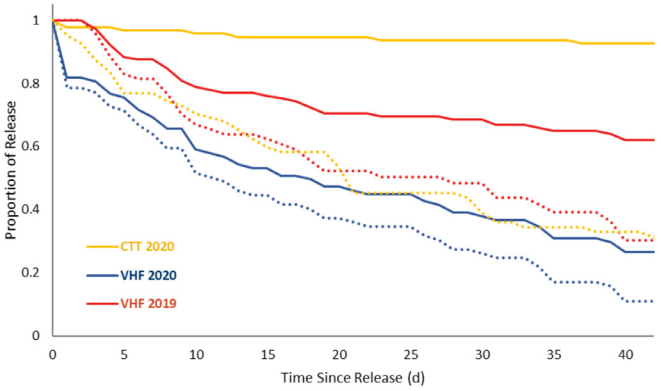

Fig. 3. Estimated survival for California valley quail (*Callipepla californica*) translocated from Idaho, USA to Texas, USA with very high frequency transmitters in 2019 (red) and 2020 (blue), and digital transmitters in 2020 (gold) based on recovered tags (top solid line) and Kaplan-Meier survival estimations, in which tags with an unknown location are censored (bottom dotted lines).

Sufficient location estimates were obtained to generate MCPs for 35 translocated valley quail with VHF transmitters in 2019 and 24 quail in 2020. There were 82 MCPs generated for translocated valley quail with digital transmitters in 2020. Median MCP area was greater for valley quail with digital transmitters than for birds with VHF transmitters in 2019 and 2020 (Mann-Whitney U, $P < 0.001$). Median MCP area for translocated valley quail with VHF transmitters was 4.3 ha (min = 0.1, IQR = 0.9–12.2, max = 44.1) in 2019, and 3.1 ha (min = 0.1, IQR = 0.7–12.5, max = 42.8) in 2020. Median MCP area for translocated valley quail with digital transmitters was 16.1 ha (min = 1.4, IQR = 7.6–26.9, max = 78.5) in 2020. There was no statistical difference in median MCP area for translocated valley quail with VHF transmitters between 2019 and 2020 (Mann-Whitney U, $P = 0.99$). There was no difference in MCP area of male and female quail (Mann-Whitney U, $P = 0.14$).

One quail from 2019 was found 30 km away from its release site. This datum was considered an outlier and excluded from dispersal analysis. In 2019, there were ~300 quail locations recorded from VHF transmitters. In 2020, there were 144 quail locations recorded from VHF transmitters, and >25,000 quail locations from digital transmitters.

Spring Call Counts

We conducted two call counts in June 2019 and recorded 0 quail. In 2020, we recorded 2 calls in May and 2 calls in June. Both observers reported the same number of calls.

Fig. 4. An oak tree (*Quercus* sp.) used as a roost site for California valley quail (*Callipepla californica*) translocated from Idaho, USA to Fannin County, Texas, USA. Surrounded by cover for quail and partially covered with briars (*Smilax* sp.), this tree is representative of the majority of roost sites for the translocated quail.

Roosts

We documented 27 roost sites, >60% in oak (*Quercus* spp.) and elm (*Ulmus* spp.) trees. Of the 14 roosts in 2019, 9 consisted of multiple young trees that grew close together, providing dense cover for the birds (Figure 4). Tree mean diameter at breast height (DBH; ±standard error) was 9.0 ± 2.9 cm, with a mean height of 5.5 ± 1.6 m. The remaining roosts for 2019 included single eastern redcedars (*Juniperus virginiana*; $N = 2$) and ground roosts ($N = 3$). For 2020, 10 roosts were recorded in trees with a mean height of 8 ± 1.5 m and DBH of 22.7 ± 7.6 cm. All sites were <15 m from escape cover, such as *Rubus* spp. and *Smilax* spp. At least 3 roost sites were used ≥1 night.

Simulated Nests

Median simulated nest survival time in 2019 was 2 days (min = 1, IQR = 2–5.4, max = 23). Median simulated nest survival time in 2020 was 7.5 d (min = 2, IQR = 4.5–15.2, max = 23). Nest survival time was greater in 2020 than 2019 (Figure 5; $\chi^2 = 7.95$, df = 1, $P = 0.005$). One nest (4%) survived 23 days in 2019. Four nests (16%) survived 23 days in 2020.

Predator Scent Stations

Predator scent station cameras recorded 7 mammalian and 1 avian species (Table 1). In 2019, the most common visitors were raccoons (SSI = 48.6), followed by feral hogs, white-tailed deer, and armadillos (please see Appendix A for scientific names of predator species). In 2020, the most common visitors were feral hogs (SSI = 31.4), white-tailed deer, and raccoons. Species frequencies did not differ between years ($\chi^2 = 11.296$, df = 7, $P = 0.126$).

Evaluation of Raptor Presence

Nine species were detected during 8 raptor surveys conducted 16 February 2020–30 June 2020 (Figure 6). March was excluded due to weather and COVID-19 exposure protocols. Sixty percent of raptors were recorded during raptor surveys, and 40% were recorded from incidental observations. Species could not be determined for 6 raptors.

Motion-triggered Cameras

Motion-triggered cameras recorded ≥20 species of quail predators (13 mammalian, 6 avian, and 1 reptile). The most common nest predators were raccoons (33%), feral hogs (24%), and white-tailed deer (20%). Including species not considered quail predators, 45 vertebrate species were recorded on the study area through motion-triggered cameras and visual detection by technicians (Appendix A). Of note, 2 quail were photographed during copulation in 2019 (Figure 7).

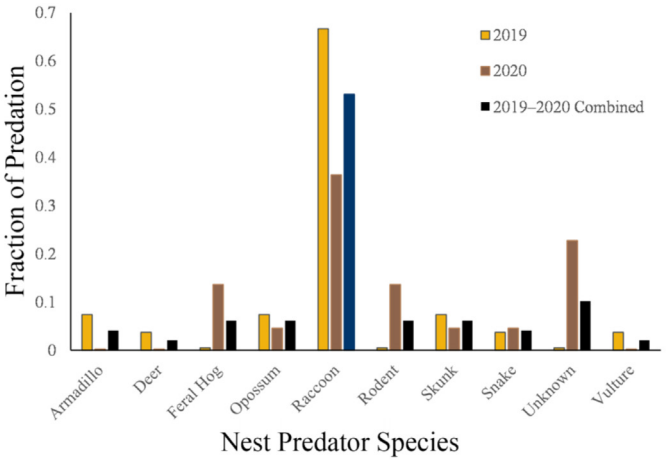

Fig. 5. Proportion of simulated California valley quail (*Callipepla californica*) nest predations per species within a quail translocation study area in Fannin County, Texas, USA, May–June 2019 and 2020.

Table 1. Scent station index (SSI) for species identified on motion-triggered cameras deployed at predator scent stations in Fannin County, Texas, USA, May–June 2019–2020.

Species	Scent station index[a]	
	2019	2020
Raccoon	48.6	14.3
Feral hog	20.0	31.4
White-tailed deer	11.4	17.1
Armadillo	11.4	2.9
Coyote	8.6	5.7
Bobcat	5.7	0.0
Skunk	2.9	2.9
Roadrunner	0.0	2.9

[a] Scent station index estimates number of predator visits (total station visits/total station operating nights) × 100.

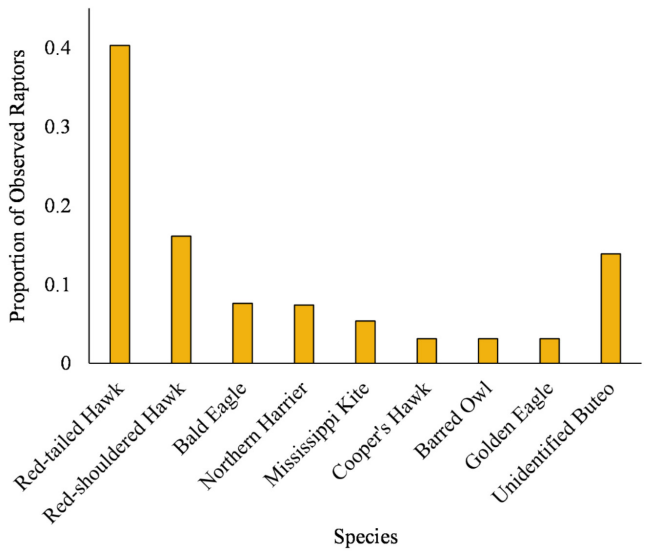

Fig. 6. Proportions of raptors recorded during raptor surveys and incidental observations within a California valley quail (*Callipepla californica*) translocation study area in Fannin County, Texas, USA, February–June 2020.

Fig. 7. Wild California valley quail (*Callipepla californica*) copulating in Fannin County, Texas, USA, 2019, after translocation of birds to the region.

DISCUSSION

This was the first documented translocation of wild California valley quail to Texas, demonstrating that translocating wild valley quail to Texas is feasible. This study improved on previous efforts by James et al. (2017) by: 1) translocating wild birds; 2) selecting a release area with a sufficient quantity and quality of escape, loafing, and nesting cover; 3) preparing the release area for translocations; and 4) recording roost selection.

Survival

Comparable survival estimates >6 weeks were difficult to obtain due to the lack of performance of tracking devices. The longer life of quail with digital transmitters was likely due to the difference in mass between digital and VHF transmitters (Guthery and Lusk 2004). Digital transmitters weighed ~0.45 g, and VHF transmitters weighed ~3.3 g. However, we are unclear if some of this advantage was offset by harness type. Digital transmitters were attached as a backpack to allow exposure for the solar power source, whereas the VHF transmitters were attached as a necklace. Pheasants (family Phasianidae) with backpack harnesses had a lower recovery rate through shooting or trapping than those with a necklace of equivalent mass, suggesting a lower survival rate (Marcström et al. 1989).

The 2020 translocation was more successful than the 2019 translocation in terms of number of birds recorded on the study area >5 months and in the region >12 months after release. This may be due to the increased number of birds released in 2020, conspecifics in the area (Martin et al. 2017), or the introduction of lighter transmitters.

In the first year of the study, birds copulating were captured in a photograph, and a fertilized egg was found in front of a camera in early June. Despite evidence of at least one successful reproductive event, no valley quail nests were located in this study. This could be due to a majority of quail with tracking devices being censored or depredated prior to nesting season. Expected breeding times for valley quail are from April to August (Raitt 1960).

The study area in Texas was different in both climate and vegetation than the Idaho trapping site. In Boise, Idaho, summer months have average daily high temperatures above 28 °C. The warmest month, July, has average high temperatures of 34 °C and lows of 17 °C. In July in Bonham, Texas, ~10 km from the study area, the average high is 35 °C and the average low is 23 °C (Arguez et al. 2011). There is some evidence that valley quail eggs may be more susceptible to extreme heat than bobwhite eggs (Reyna and Burggren 2012, Moser 2021), and it is not known how well valley quail will survive in a drought year in Texas. Future studies would benefit from evaluating the impacts of Texas drought conditions on the development and survival of valley quail and determining lethal and sublethal temperatures (Reyna and Burggren 2012, 2017; Tomecek et al. 2017; Reyna 2019).

Dispersal and Detection

The 3.1–4.3 ha MCP for quail with VHF transmitters was likely biased low, since we used few location (≥4) to generate the MCPs. Other studies used ≥25 (Coppola et al. 2021) or ≥30 locations (Terhune et al. 2006*a*). Our MCP size for birds with digital transmitters was 18.7 ha, comparable to home ranges of 3.9–22.1 ha for wild valley quail in Oregon (Kilbride et al. 1992), 17.4 ha for translocated bobwhites in Georgia, USA (Terhune et al. 2006*a*), and 20.40–20.85 ha for translocated bobwhites in Texas (Yancey 2019). The larger MCP size for translocated valley quail with digital transmitters is likely due to more locations recorded (~260 per bird), allowing for more complete estimates of movement. While the digital transmitters produced more locations, the location data were not as accurate as those recorded from quail with VHF transmitters. Mean difference between estimated and recovery locations of digital transmitters was 85.9 ± 16.2 m (n = 11).

Some studies incorporate detection in addition to location (Downey et al. 2017). Tracking data are lacking for quail that left the study area, especially in areas where vegetation was thick and impenetrable. The grid of nodes that detected digital transmitters covered ~390 ha. However, the system required line-of-sight and, in some regions of the study area, vegetation was too thick for digital transmitter signals to be consistently detected. Additionally, a quail with a digital transmitter outside of the grid's range could be detected only by a technician with a hand-held Yagi antenna or a portable node. Due to dense forest vegetation along roads, these efforts produced <10 additional locations. Most off-site observations were reported by nearby residents. Coveys of translocated quail were frequently recorded outside the perimeter of the study area. Future studies using VHF transmitters would benefit from obtaining more location points for each bird. For future use of digital transmitters, deploying more nodes and base stations is likely to improve detection range. A digital transmitter that

is both solar and battery powered could alleviate some of the detection difficulties of solar-powered digital transmitters.

Spring Call Counts

Few valley quail were heard during spring call counts. Unlike bobwhites, which produce audible calls 15–45 minutes prior to sunrise (Wellendorf et al. 2004), translocated valley quail call times were inconsistent. Some days, no quail were detected in the morning, but quail were heard in the same location later in the day; thus, this method of census was not a reliable metric representation of the local quail population. Future studies may be able to reduce the potential for false negatives at low densities by increasing detection time (Delaney and Leung 2010, Riddle et al. 2010). Quail calls did help determine whether quail were present in a given area.

Simulated Nests

Mesomamamals accounted for 70% of simulated nest predation. A camera study of bobwhite nests in North Florida, USA and South Georgia (Thornton 2003) showed mesomammals responsible for 11–53% of nest depredations, with raccoons, armadillos, and opossums the most common predators. The landowner began predator control July 2019 and continued through the end of this study, resulting in the removal of ~25 raccoons, 2 otters, and >60 feral hogs prior to the 2020 simulated nest predation experiment. While nest survival was greater in 2020 than 2019, it cannot be conclusively attributed to predator control. The change in nest placement methods in 2020 meant that simulated nests were both less common in high quail activity areas as measured by radio-telemetry and less densely spaced, which can influence predation rate (Reitsma 1992).

This ambiguity is common in predator control studies. Predator control did reduce predator activity and improve bobwhite nest success in an 8-year study in Florida, Georgia, and Alabama, USA (Jackson et al. 2018). However, predator control efforts had no impact on simulated nest survival in the Rolling Plains of Texas (Lyons et al. 2009), and inconsistent effects on chick production rates in north-central Texas (Jackson 1951). Thornton (2003) also found predator control efforts had inconsistent results on bobwhite nest predation in North Florida and South Georgia.

Two unexpected nest predators were photographed: turkey vultures and white-tailed deer. Vultures have been recorded predating nests of iguanas, crocodiles, and sea lions (Sexton 1975, Pavés et al. 2008, Platt et al. 2014). Likewise, white-tailed deer are opportunistic eaters and have been reported predating northern bobwhite nests (Pietz and Granfors 2000, Thornton 2003, Ellis-Felege et al. 2008). Khanal et al. (2006) reported 22% of bobwhite nests were depredated by white-tailed deer in an area with heavy predator control.

Predator Scent Stations

Raccoons and feral hogs represented 40 of 65 (61.5%) of our scent station visits and had indices of 31.4 and 25.7 SSN (Table 1). In contrast, feral hogs were the third most common and raccoons the fifth most common predators recorded at scent stations in South Texas (Haines et al. 2004), and coyotes were the most common visitor, with an SSI of 2.9–12.5. While their mean of 7.5 was comparable to our SSI values for coyotes (5.7–8.6), coyotes represented 57% of all scent station visitors over 3 years in South Texas, and their frequencies for all predators combined were lower (SSI = 5.7–20.5) than the 2-year mean frequencies of raccoons alone (SSI = 31.5) in our study. Total predator visit frequencies in this study (SSI = 77.2–108.6) were 3.8–19.1 times higher than those for Haines et al. (2004). This may be interpreted as supporting the mesomammal release hypothesis (Crooks and Soulé 1999). The landscape immediately surrounding the study area is fragmented, with a mean parcel size of ~27 ha, compared with ~179 ha in the Rio Grande Plains in 2003 (Brewster 2005). Lower fragmentation combined with coyotes being relatively more common in South Texas may explain the much lower mesomammal predator numbers in the study by Haines et al. (2004).

Raptor Observations

The most commonly recorded raptors—red-tailed hawks, red-shouldered hawks, Cooper's hawks, and barred owls—are all common, year-round residents in Fannin County, Texas. Bald eagles, golden eagles, and northern harriers are winter residents. Mississippi kites are primarily migrants, but have been observed as summer residents (Dunne et al. 1988, Sullivan et al. 2009).

Motion-triggered Cameras

Raccoons decreased and feral hog populations increased from 2019 to 2020. However, motion-triggered cameras were primarily used for monitoring quail and, as such, were placed along the feed trail and near locations where translocated quail were observed. Four cameras failed in April–July 2020 and were not replaced. Thus, predator observations could not be accurately compared between years.

Skunks, male white-tailed deer, and select feral hogs were the most identifiable species during the study. In general, it was easier to identify individuals from video than from still images, despite the lower resolution, as characteristics like gait and other movements could be observed. In many cases, individual identification was hindered by camera blur, environmental obstructions (e.g., tall grass), or distance from the motion-triggered camera. Probability of identification could be improved by minimizing obstructions, or through use of higher resolution cameras. In some locations, wind-blown vegetation regularly caused motion-triggered cameras to activate without the presence of an animal. Future studies should attempt to keep vegetation trimmed near cameras and consider prevailing winds from multiple directions.

Bobwhites and valley quail share most of the same predator species (Leopold 1977, Rollins and Carroll 2001, Staller et al. 2005). It is reasonable to assume that any predator management and avoidance techniques that work for

bobwhites in northeast Texas should work for valley quail. One possible exception is that valley quail often roost in trees (Leopold 1977) and may encounter different predators, or the same predators at different rates than bobwhites.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

We showed that it is feasible to translocate wild valley quail to Texas, but the duration of our project was not sufficient to establish a sustainable population. For example, the establishment of valley quail in New Zealand was completed over ≥10 years (Williams 1952). Nearby sightings of quail >1 year following translocation show there is potential for annual overlap, potentially increasing survival rates for future translocations (Martin et al. 2017).

Northern bobwhites have a population threshold of ~800 birds with 1–2 ha/individual needed for a population to become sustainable (Guthery et al. 2000). Assuming a similar threshold for valley quail, it would take ≥7 years to reach the 800-quail threshold with 500 birds translocated annually, 10% annual survival, and replacement-level reproduction of the surviving 10%. In addition, any sustainable population would have to make use of land outside the study area. Attempts to create a sustainable population through translocation would be best attempted on sites with >2,000 ha managed for quail.

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APPENDIX A

Appendix A. Predator and nonpredator species photographed during 2019–2020 on the valley quail translocation site in Fannin County, Texas, USA. Entries of 0 represent species' presence recorded by technician sightings.

Animals observed	Scientific name	Number of photos
Raccoon	*Procyon lotor*	738
Striped skunk	*Mephitis mephitis*	89
Virginia opossum	*Didelphis virginiana*	50
White-tailed deer	*Odocoileus virginianus*	491
Feral hog	*Sus scrofa*	1630
Nine-banded armadillo	*Dasypus novemcinctus*	15
Coyote	*Canis latrans*	221
Eastern gray squirrel	*Sciurs carolinensis*	0
Eastern flying squirrel	*Glaucomys volans*	0
Fox squirrel	*Sciurus niger*	3
Eastern cottontail	*Sylvilagus floridanus*	>20
Bobcat	*Lynx rufus*	30
River otter	*Luntra canadensis*	1
North American beaver	*Castor canadensis*	0
Cattle	*Bos taurus*	>20
Red-tailed hawk	*Buteo jamaicensis*	5
Red-shouldered hawk	*Buteo lineatus*	3
American crow	*Corvus brachyrhynchos*	>40
Black vulture	*Coragyps atratus*	>50
Road runner	*Geococcyx californianus*	3
Turkey vulture	*Cathartes aura*	>50
Waterfowl	*Anatidae* spp.	0
White-throated sparrow	*Zonotrichia albicollis*	>300
Barn owl	*Tyto alba*	2
Wild turkey	*Meleagris gallopavo*	6
Northern flicker	*Colaptes auratus*	2
Painted bunting	*Passerina ciris*	2
Northern cardinal	*Cardinalis cardinalis*	>50
Cooper's hawk	*Accipiter cooperii*	0
Northern harrier	*Circus cyaneus*	0
Barred owl	*Strix varia*	0
Golden eagle	*Aquila chrysaetos*	0
Bald eagle	*Haliaeetus leucocephalus*	0
Mississippi kite	*Ictinia mississippiensis*	0
Green heron	*Butorides virescens*	0
Great blue heron	*Ardea herodias*	3
Ornate box turtle	*Terrapene ornata ornata*	0
Three-toed turtle	*Terrapene carolina triunguis*	0
Snapping turtle	*Chelydra serpentina*	0
Northern cottonmouth	*Agkistrodon piscivorus*	0
Rough green snake	*Opheodrys aestivus*	0
Eastern copperhead	*Agkistrodon contortrix*	0
Black rat snake	*Pantherophis obsoletus*	3
Ribbon snake	*Thamnophis sauritus*	0
American green tree frog	*Dryophytes cinereus*	0
American bullfrog	*Lithobates catesbeianus*	0
Southern leopard frog	*Lithobates sphenocephalus*	0
Woodhouse's toad	*Anaxyrus woodhousi*	0

STRESS AND PREDATION IMPACTS ON NORTH AMERICAN QUAIL TRANSLOCATIONS

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ABSTRACT

Translocations have been used in attempts to bolster or restore native quail populations for >150 years, often with little success. However, with some northeastern United States quail populations undetectable or extirpated, and others across the United States on the extreme decline, translocation as a tool for quail population restoration is becoming increasingly popular. Two factors contributing to translocation failure are physiological stress and predation. Chronic stress associated with translocations can result in weight loss, reduced immune system function, suppressed reproduction, and an altered fight-or-flight response. These stress-induced responses increase vulnerability to predation, the primary cause of quail mortality. Here, we review the relationship between quail translocations, stress, and predation, and recommend future research and best practices to mitigate the impacts of stress and predation on translocated quail. To improve future translocation outcomes, more research is needed on stress mitigation throughout the translocation process (capture, handling, transport, and release). While capture and handling are unavoidably stressful, there is greater potential to reduce stress levels during holding and transport. Recent validation of fecal corticosterone metabolites as a non-invasive method to quantify stress in quail offers a useful tool for testing stress reduction protocols. Preliminary experimental results regarding nutritional supplements and stress levels are inconclusive, but enrichment during temporary holding and access to travel rations may help improve survival in long-distance (>800 km) translocations. We also recommend predator control at release sites, particularly for raccoons (*Procyon lotor*) and other mesomammals.

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Key words: California quail, *Callipepla californica, Colinus virginianus,* corticosterone, ethology, northern bobwhite, population restoration, predation, reintroduction, stress, translocation, wildlife management

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EVALUATING RELEASE STRATEGY FOR TRANSLOCATED NORTHERN BOBWHITES IN THE CROSS TIMBERS ECOREGION OF TEXAS: A PILOT STUDY

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) population decline is largely driven by the loss, fragmentation, and degradation of grassland habitats. Translocation is used to reintroduce or augment populations in fragmented landscapes where natural dispersal is inhibited. Northern bobwhites have been successfully translocated in the southeastern portion of their range, but outcomes of translocations in western ranges have been mixed. Our objective was to conduct a pilot study to test the feasibility of translocating northern bobwhites to a restored, but isolated, habitat in the Cross Timbers ecoregion of Texas, USA and to evaluate the influence of release strategy for improving northern bobwhite site fidelity and survival post-release. The release property was restored through brush management, native species seeding, and proper grazing management. We trapped and translocated 84 northern bobwhites from source populations in the Rolling Plains and Edwards Plateau ecoregions during March 2015. Coveys were assigned to either delayed or immediate release treatment. We radio-collared all hens (n = 40; 11 adults; 29 juveniles) and evenly divided the sample between delayed and immediate releases. Delayed release coveys were held on the release site for 4 weeks in a Surrogator® (Wildlife Management Technologies, LLC). We trapped and radio-collared resident hens (n = 15) in March and monitored all hens through breeding season (March–August; 180 days). We implemented a 2-state (alive or dead) multistate model in Program MARK to analyze survival as a function of the release treatment, resident status, and age. We found no evidence that survival differed between translocated and resident hens (β = 0.48, standard error [SE] = 0.38), release treatments (β = 0.10, SE = 0.40), or age (β = -0.16, SE = 0.54). Daily survival for all hens was 0.99 (SE = 0.009) and breeding season survival was 0.19 (SE = 0.08). Four (20%) immediate, 2 (10%) delayed release, and 0 resident hens dispersed off-property. Translocated and resident hens survived at similar rates, indicating that translocation may be a feasible management strategy for augmenting a northern bobwhite population on restored habitats in the Cross Timbers ecoregion although overall survival was low. We did not find evidence that delayed release improved daily survival post-release, but our small sample size may have prevented us from detecting a difference. However, delayed release birds were effectively sheltered from predation during peak raptor migration. Additional research is needed to fully understand population dynamics and implications of release strategy for translocated northern bobwhite.

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Key words: *Colinus virginianus*, northern bobwhite, release strategy, survival, Texas, translocation

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MONITORING SCALED QUAIL OCCUPANCY AND COLONIZATION POST-TRANSLOCATION ON A LARGE LANDSCAPE

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ABSTRACT

Large landscapes are important for sustaining quail populations in semiarid climates where annual variation in vital rates, and thus population volatility, tends to be larger than in subtropical climates. Translocations may need to be conducted on a similar scale to ensure long-term success. Large landscapes pose challenges for monitoring release sites in terms of costs and logistics. However, large landscapes also provide an excellent opportunity to evaluate habitat preferences and suitability because they inherently hold more variation in habitat type. Multiseason occupancy surveys are a potential monitoring tool for translocations where population persistence is a benchmark for success. Occupancy (i.e., presence–absence) data for quail are relatively easy to collect compared to more intensive surveying (i.e., mark-recapture or distance sampling) and can be analyzed in a framework that allows for the estimation of detection, colonization, and extinction as functions of spatial or temporal covariates. We used a multiseason occupancy survey to monitor a reintroduced population of scaled quail (*Callipepla squamata*) on a large landscape. Our objectives were to: 1) evaluate occupancy post-translocation, and 2) determine how landscape characteristics and distance from release points influenced colonization and extinction. Over 800 scaled quail were translocated to a >40,000-ha study area of contiguous rangeland in Knox County, Texas, USA from 2016–2017. We collected presence–absence data during a 10-day period in March just prior to release (2016) and for 2 years after first release (2017–2018). We sampled 73 locations on a 1.5-km × 1.5-km grid 3 times per year. We were unable to estimate true occupancy and thus any influence of covariates, because of low detection probability ($p = 0.05$, standard error = 0.02). However, we found that naïve occupancy based on detection within and outside of surveys increased from 1% in 2016 to 23% and 10% in 2017 and 2018, respectively. We recommend that monitoring programs prioritize survey methods that increase detection, such as sampling only during peak calling and call-back surveys, and using more than one method of detection.

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POPULATION DENSITY ESTIMATES OF THE MONTEZUMA QUAIL IN WEST TEXAS

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ABSTRACT

In Texas, USA, populations of Montezuma quail (*Cyrtonyx montezumae*) can be found scattered across mountain ranges in the Trans-Pecos region, including the Davis and Guadalupe, and farther east into the Edwards Plateau region. Abundance and distribution information to assist land managers in the enhancement of Montezuma quail populations is scarce due to the species' secretive behavior and unknown abundance. We aimed to provide population density indices to fill this information gap by using a search path technique. We searched for quail in the winter of 2018–2019 in West Texas at 6 study sites: 5 private ranches and Elephant Mountain Wildlife Management Area (EMWMA). We chose survey locations based on previous quail sightings and our perception that an area contained suitable Montezuma quail habitat. We searched small watersheds using at least 2 dogs while walking along contours. The average search path length was 1.82 km (range = 0.80–4.30). We produced a hexagonal grid with a cell size of 1 ha such that no pair of coveys can be encountered on the same cell. The area associated to each search was the sum of the areas of all hexagonal cells intersected by the search path. For density index, we directly used the definition of density (birds encountered divided by area searched). Mean covey density was 1.51 ± 2.53 (± standard error) coveys/km^2 (range = 0.50–4.17), although abundance data were overdispersed. The highest density estimate was for EMWMA. Mean covey size was 6.55 ± 0.61 birds/covey. These data yielded an estimate of 10.07 ± 17.45 birds/km^2. As we did not account for imperfect detection, our quail density estimates are lower bounds of actual density. These quail density estimates are lower than estimates for Arizona, USA but higher than density estimates reported for the Edwards Plateau and central Mexico. A prevailing concern regarding the harvest of the Montezuma quail among some wildlife professionals and the public in Texas is the perception that Montezuma quail are scarce. Therefore, our density estimates suggest that abundance of Montezuma quail in West Texas may not be as low as perceived and that Montezuma quail populations may be appropriate for an open hunt season.

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Key words: abundance, *Cyrtonyx montezumae*, Montezuma quail, population density, west Texas

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MONTEZUMA QUAIL IN THE EDWARDS PLATEAU OF TEXAS: DETECTION, OCCURRENCE, AND HABITAT

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ABSTRACT

Montezuma quail (*Cyrtonyx montezumae*) were historically found throughout nearly every county in the Edwards Plateau region of Texas, USA. Over the last century, shifting land use, reduction of fire on the landscape, and the subsequent encroachment of woody vegetation have constricted the distribution of Montezuma quail to a few counties in the southern portion of the Edwards Plateau. A renewed interest in management for Montezuma quail over the last decade has been met with a lack of information regarding their habitat requirements in this region. This lack of general information and increased sightings of this elusive species in areas where Ashe's juniper (*Juniperus ashei*) had been removed led to the initiation of this study to identify detection and site use. During April–August of 2015 and 2016, biweekly call-back surveys were conducted at 60 randomly stratified locations distributed across 9 properties in Edwards and Kinney counties, Texas. During each survey, weather conditions were recorded. Additionally, vegetation at each of the 60 survey locations was quantified. Montezuma quail were detected at 46% (28 of 60) of the survey locations during 6.7% of the total site visits during 2015 and 2016. Detection of Montezuma quail during call-back surveys was mostly explained by temperature. When temperatures exceeded 25 °C, probability of detection dropped below 70%. Site use by Montezuma quail was best explained by bunchgrass density as probability of site use exceeded 50% when bunchgrass density exceeded 0.63 plant/m^2. Future researchers may be more successful searching for Montezuma quail with an understanding of the environmental conditions under which they are most detectable. Furthermore, since relatively dense stands of bunchgrass were associated with site occupancy, this metric gives managers a management target to shoot for when restoring Montezuma quail habitat in the region.

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Key words: *Cyrtonyx montezumae,* Edwards Plateau, Mearns quail, Montezuma quail, Texas

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Montezuma quail (*Cyrtonyx montezumae*) are an elusive gamebird found throughout the montane regions of the southwestern United States and Mexico in oak-juniper (*Quercus* and *Juniperus* spp., respectively) savannahs (Leopold and McCabe 1957, Brennan et al. 2017). Montezuma quail are found in the Trans Pecos and Edwards Plateau regions of Texas, USA and are classified as a game species without an open hunting season. However, much of what we know about this species has come from populations in Arizona and New Mexico, USA; Mexico; and to a lesser extent, the Trans Pecos of Texas (Leopold and McCabe 1957, Brown 1982, Stromberg 1990). There is little information available to biologists, land managers, and quail enthusiasts in the Edwards Plateau of Texas regarding the habitat requirements of Montezuma quail. Once found in nearly every county throughout the Edwards Plateau, Montezuma quail populations have been constricted over the past century to an area encompassing portions of a few counties (Oberholser and Kincaid 1974, Harveson et al. 2007). This reduction in distribution has been attributed to antagonistic land use practices, the reduction of fire on the landscape and subsequent encroachment of Ashe's juniper (*Juniperus ashei*), red-berry juniper (*Juniperus pinchotii*), escarpment live oak (*Quercus fusiformis*), and other woody species (Leopold and McCabe 1957, Weniger 1988, Baccus and Eitniear 2007). Previous research has indicated that typical Montezuma quail habitat is characterized by a woody canopy of 25–50% (Brown 1982, Albers and Gehlbach 1990, Bristow and Ockenfels 2004). Today, much of the eastern portion of the ecoregion is dominated by juniper species with little herbaceous understory, presumably rendering large swaths within this region unusable. Across their entire geographic range Montezuma quail have suffered the greatest declines in the Edwards Plateau, underpinning the importance of understanding site use and habitat requirements in this area (Baccus and Eitner 2007).

During the 1970s and 1980s there was a renewed interest in Montezuma quail inhabiting the Edwards Plateau. Research conducted by Oberholser and Kincaid (1974), Sorola (1986), Albers and Gehlbach (1990), and Holderman (Texas Parks and Wildlife Department, personal communication) reported Montezuma quail in 5 counties: Edwards, Val Verde, Kinney, Uvalde, and Real counties. With sparse information regarding the general ecology and habitat requirement for Montezuma quail in this region, landowners, state biologists, and quail enthusiasts have been challenged when attempting to developing management strategies. In addition, the species' secretive nature has made study difficult. Monitoring such an elusive species with low detectability requires innovative methods. Call-back surveys during the breeding season have been useful in sampling elusive avian species (Johnson et al. 1981, Sanders 2012). To further our understanding of Montezuma quail in the Edwards Plateau of Texas, we attempted to 1) estimate site occurrence, 2) identify variables affecting the detection and site use of Montezuma quail in the Edwards Plateau, and 3) quantify the bounds of vegetation composition at sites where Montezuma quail were found.

STUDY AREA

We conducted this study on 9 properties in the Edwards Plateau ecoregion of Texas (Figure 1) (Gould 1975). These properties consisted of 8 privately owned ranches and 1 state park ranging in size from 40–5,754 ha located in Edwards and Kinney counties. The Edwards Plateau is centrally located in the state. Temperatures range from 18–31 °C in the warm season (Apr–Sep) and from 6–20 °C during the cool season (Oct–Mar; NOAA 2015). Average annual rainfall is 66.7 cm; this precipitation primarily occurs in a bimodal pattern during May–June and September–November. Ranging in elevation from 182 m to 1,638 m, the Edwards Plateau consists largely of limestone formations, covered by oak-juniper woodlands, upland savannahs, and native grass and shrublands (Gould 1975, Amos and Gehlbach 1988). Since the mid-1800s the Edwards Plateau has been utilized for livestock production including cattle, sheep, and goats. However, of the properties included in this study only 2 of the private ranches had domestic livestock (cattle and horses) grazing during the entire study. The primary soil types on the study sites were Dina, Eckrant, Ecktor, Oplin, Rio Diablo, and Tarrant series (NRCS 2009). These soil series are representative of relatively shallow soil horizons (<10 cm) with surface organic matter present. Sideoats grama (*Bouteloua curtipendula*), slim tridens (*Tridens muticus*), Hall's panicum (*Panicum hallii*), green sprangletop (*Leptochloa dubia*), purple threeawn (*Aristida purpurea*), silver bluestem (*Bothriochloa laguroides*), little bluestem (*Schizachyrium scoparium*), and King Ranch bluestem (*Bothriochloa ischaemum*) were common grasses on the study sites. Common forbs (in order of dominance) included Drummond's woodsorrel (*Oxalis drummondii*), one-seed croton (*Croton monanthogynus*), ten-petal anemone (*Anemone berlandieri*), knotweed leaf-flower (*Phyllanthus polygonoides*), and mealy sage (*Salvia farinacea*). Dominant woody and succulent species included Ashe's juniper, live oak,

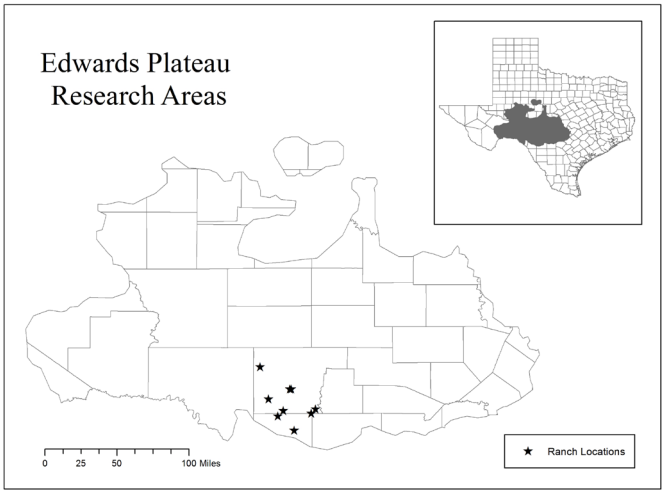

Fig. 1. Montezuma quail (*Cyrtonyx montezumae*) study area distribution in the southern Edwards Plateau ecoregion of Texas, USA.

Texas persimmon (*Diospyros texana*), Texas sotol (*Dasylirion texanum*), various pricklypear species (*Opuntia* spp.), Texas mountain laurel (*Sophora secundiflora*), Texas oak (*Quercus buckleyi*), Mexican piñon (*Pinus cembroides*), evergreen sumac (*Rhus virens*), guajillo (*Senegalia berlandieri*), and Texas kidneywood (*Eysenhardtia texana*). Individual study sites were unique in their topographic diversity, soil series, and plant compositions.

METHODS

Call-back Surveys

We conducted call-back surveys at 60 stratified locations distributed across the 9 properties during April–August 2015 and March–August 2016. We created an 800 m × 800 m grid of points in ArcMap 10.5.1 (Esri Inc., Redlands, CA, USA) to guide selection of survey locations. These dimensions were modified from Sanders (2012), who used a 400-m × 400-m grid, and Bishop's (1964) finding that a Montezuma quail buzz call is generally audible to humans up to 200 m away. The larger grid was selected to reduce the probability of double sampling. Each location in the grid had a unique elevation, slope, relative juniper density, and topographic position. Selected survey locations were stratified between high, medium, and low elevation (low: <156 m; medium: 156.1–180 m; high: >180 m), slope (low: 0–7°; medium: 7.1–13.9°; high: ≥14°), relative juniper density coverage (low: 0–24%; medium: 25–49%; high: ≥50%), and between hill tops, hill sides, and valleys to ensure that a wide range of conditions were sampled. The 60 locations were also partitioned proportionally with the size of the property (i.e., smaller properties had fewer locations).

We surveyed locations 2 times per month between sunrise and 1200 hours on a rotational schedule so that the first location surveyed in period 1 was the last location surveyed during period 2. This rotation was implemented to ensure that survey locations were visited during all periods of the morning. At each survey location, prior to beginning the call-back survey, percent cloud cover, wind speed (km/hr) and direction (N, NE, E, SE, S, SW, W, and NW), temperature (°C), barometric pressure (mm Hg), and relative humidity (%) were recorded using a Kestrel 4500 hand-held weather station (Nielsen-Kellermen Co., Boothwin, PA, USA). Following this period, the call-back survey was conducted for 10 minutes based on a pilot study conducted by Grahmann and Moore (2013–2014; personal communication) using a recording of a male Montezuma quail buzz call and a descending 9-note covey call. Calls were played using a Bose SoundLink Mini speaker (Bose Corp., Framingham, MA, USA) and volume was calibrated so the recording of the buzz call could be heard from 200 m away on a calm day, on level terrain and with no woody cover. During each survey, we recorded 1) the presence of a Montezuma quail and noted if the observation was made visually or audibly, 2) the type of call heard (male buzz call or 9-note descending whistle), 3) the number of calls heard, and 4) the approximate distance and direction the call came from. All surveys were conducted by the same individual throughout the duration of this study.

Habitat Characterization

We measured vegetation at each of the 60 call-back survey locations at 1) plot (at the survey location) and 2) pasture-wide scales during May–June and October–November during both 2015 and 2016. At each location, 4 10-m transects radiated in the cardinal directions. During the May–June sampling period, percent exposed litter, bare ground, rock, and percent cover of forbs, subshrubs, and grass (by species) were estimated by using a 20-cm × 50-cm sampling frame at 5 m and 10 m along each of the 4 10-m transects (Daubenmire 1959). Additionally, bunchgrass density and food plant (*Allium* spp., *Oxalis drummondii*, *Cooperia* spp., *Nothoscordum* spp. and *Cyperus* spp.) densities were estimated using a 1-m^2 sampling frame at 5 m and 10 m centered on each of the 4 transects (Bishop and Hungerford 1965). Bunchgrass was tallied if it exceeded 22.4 cm wide by 22.4 cm tall in accordance with the minimum size preferred by northern bobwhite (*Colinus virginianus*) in the region (Arredondo et al. 2007). Woody plant cover at each of the call-back locations was estimated along the 4 10-m transects by species using the line intercept method to 5 cm (Canfield 1941). Herbaceous and woody canopy height were measured at the 5-m and 10-m marks along the 4 transects. During the October–November sampling period, only food plants were estimated following the same protocol as the May–June sampling.

At the pasture scale woody cover was estimated from 2016 National Agriculture Imagery Program imagery using an unsupervised classification in the program to identify 1) woody cover, 2) herbaceous cover, 3) rock and bare ground, and 4) water cover classes within a 200-m buffer from each of the call-back locations.

Analyses

We examined means with standard errors (SE) and ranges of the weather variables affecting the detection of Montezuma quail and the vegetation characteristics at sites which showed use by Montezuma quail. To determine the effect of weather variables on detection and plant community effects on site use, stepwise logistic regressions were used with *a priori* selected variables. We ran a Pearson correlation analysis on all variables *a priori* to identify collinearity. Due to low observations, the data were pooled across years for analyses. The probability of observation was calculated using all site visits, while probability of detection was estimated following the occupancy when detection is less than 1 framework described by MacKenzie et al. (2006).

RESULTS

Observation

During the entire study 780 (2015: 360; 2016: 420) call-back surveys were conducted; of these, only 6.7% (52) of the surveys resulted in observation of at least 1 Montezuma quail. Detection was similar during the 2015 and 2016 survey season with 6.1% and 7.1% of surveys, respectively, resulting in observations. Of the locations where Montezuma quail were detected ≥ 1 time, the average probability of detection across both years was 17.9% during a single stand-alone survey.

Probability of detection was most influenced by temperature ($P < 0.0001$). As temperatures rose above 25 °C, the probability of detection dropped below 70% (Figure 2). While Montezuma quail were surveyed in a wide range of conditions, they were observed within distinct windows of environmental conditions. For example, wind speeds ranged from 0–14.7 km/hr during all surveys, while Montezuma quail calls were only observed within a window of 0.5–9.6 km/hr. Mean (± SE) wind speed averaged 3.4 ± 0.5 km/hr during visits resulting in observations. Temperature during all surveys conducted ranged from 4.5–36.3 °C, while Montezuma quail were observed during periods with temperatures ranging from 10.6–24.8 °C. Mean temperature during observations was 19 ± 0.5 °C. Humidity during surveys ranged from 41.3–100%, while observations were made when humidity was 61.4–100% and mean humidity during observations was 72.9 ± 5.4%. For cloud cover and barometric pressure, Montezuma quail responded to the call-back reel or were detected across the entire ranges sampled. For example, barometric pressure was 934.2–966.7 mm Hg during surveys and Montezuma quail responded from 934.4– 966 mmHg. Barometric pressure averaged 950.2 ± 1 mm Hg during sampling periods where a response was heard. Montezuma quail were observed during the full range of cloud coverages (0–100%); however, average cloud cover during observations was 72.9 ± 5.4%.

Site Use

During the 2015 and 2016 sampling periods, Montezuma quail were recorded at 30% (18 of 60 survey locations) and 43% (26 of 60 survey locations) of sites, respectively. Over the entire study 46% (28 of 60 survey locations) of the survey locations were used at least once and 27% (16 of 60 survey locations) were used during both years of the study. Due to a low sample size, site use data were pooled across years. Over this period, bunchgrass density ($P = 0.016$) was the most influential variable on site use by Montezuma quail. Probability of use exceeded 50% as bunchgrass density increased above 0.63 plant/m^2 (Figure 3).

The ranges of litter cover, bare ground, forb cover, grass cover, and bunchgrass density sampled at locations where Montezuma quail were observed represented the complete range that was sampled across all sampling locations regardless of site use. Litter coverage ranged from 2.3–90% with a mean of 30.8 ± 3.1% at used sites. Bare ground ranged from 0–34.4%, with a mean of 5.8 ± 0.9% used sites. Forb coverage ranged 0–61.6% with a mean of 11.5 ± 1.65% at used sites. Grass cover ranged from 0–87.5% with a mean of 29.8 ± 3% at used sites. Bunchgrass density ranged from 0 –1.1 plants/m^2, with an average abundance of 0.3 ± 0.04 plant/m^2 at used locations. Rock coverage was similar at used (0–66.9%) and unused sites (all-sites range: 0–77.1%) with an average of 27.4 ± 2.4% at used sites. Subterranean food plant density ranged 0–16.8 plants/m^2 among all locations; used locations had a mean of 1.1 ± 0.31 plants/m^2 with a range of 0–8.6 plants/m^2. Montezuma quail were detected at locations with a wide range of woody cover. Among all locations regardless of site-use status, woody cover ranged 5.8–82.6%. The mean woody coverage at used sites was 49.3 ± 3.1% with a range of 5.8–74.8%. Woody height among all locations ranged 0–5.8 m, while at used locations average woody height was 1.4 ± 0.2 m with a range of 0–5.1 m. Herbaceous height ranged 0–36.9 cm at all surveyed locations, while at used locations the mean

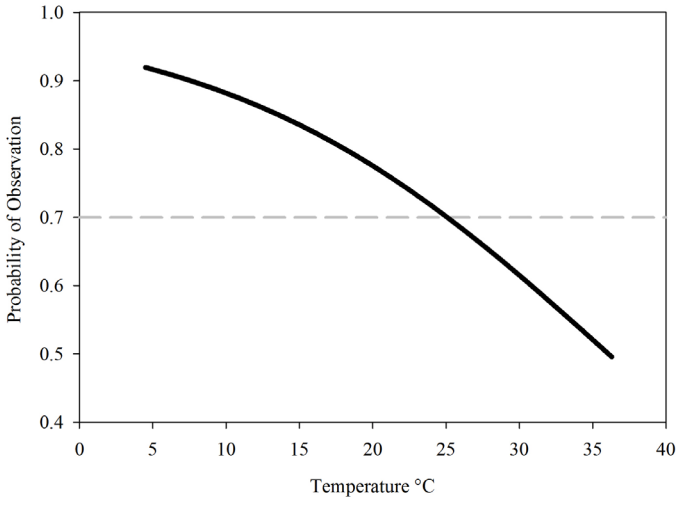

Fig. 2. Probability of observation of Montezuma quail (*Cyrtonyx montezumae*) in relation to temperature in the Edwards Plateau, Texas, USA.

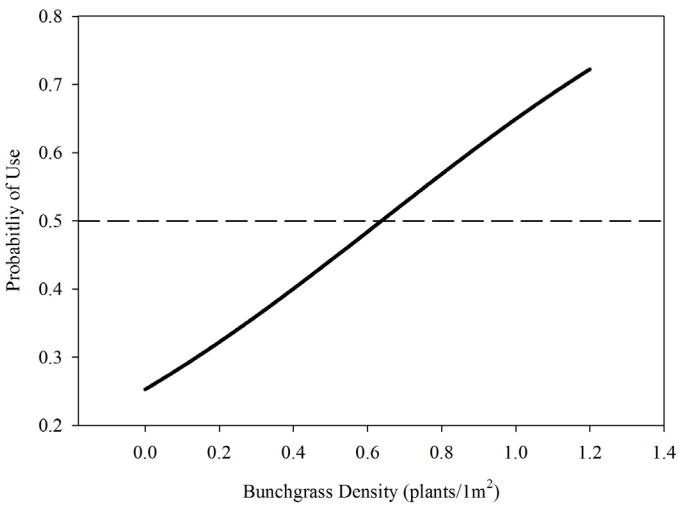

Fig. 3. The relationship between the probability of use by Montezuma quail (*Cyrtonyx montezumae*) and bunchgrass density (plants/m^2) in the Edwards Plateau, Texas, USA.

was 12.1 ± 1.4 cm and ranged 0–31.3 cm. Regardless of site use, juniper coverage varied greatly, from 0–87.5%, with an average of 26.8 ± 4.2% at used locations. Woody coverage estimated using remotely sensed imagery within the 200-m buffer was estimated among all locations and ranged 5.8–82.5%, while at used locations it ranged 8–81.3% with a mean coverage of 45.2 ± 4.7%.

DISCUSSION

The elusive behavior of Montezuma quail makes them a difficult species to study, especially in areas of relatively low abundance like that experienced in the Edwards Plateau region of Texas. In this study we experienced a low probability of detection (18%) across both years of sampling. Rates of detection were similar between the 2 consecutive years, even with increased sampling effort from 2015 to 2016. Sanders (2012; mean call/point on 2 routes: 0.01 and 0.18) and Stewart et al. (2021; 0.06 detection/hour) found similar results in the Edwards Plateau, with higher rates of detection and relative abundance of Montezuma quail in the Trans Pecos ecoregion of Texas. The low levels of detection and observation may support the idea that Montezuma quail populations exist at lower levels in the Edwards Plateau than in other areas of their Texas distribution. To give insight into the probability of detection at a single location without prior sampling, we estimated the probability of observation. This rate is what could be expected in an exploratory search where occupancy is unknown. The probability of observation was most associated with temperature; however, wide ranges and small standard errors of environmental conditions in which Montezuma quail were observed suggest that it was likely a collective influence of different environmental conditions. This result differs from the findings of Sanders et al. (2017) as they found no correlation between calling rate and maximum daily temperature in the Edwards Plateau. Optimal conditions to sample for Montezuma quail during exploratory searches may be described as having moderate temperatures and barometric pressures, higher cloud cover percentages, lower wind speeds, and higher humidity. Other quail scientists have previously described this range of conditions on searches for Montezuma quail in the Edwards Plateau while conducting call-back surveys (Holderman, personal communication, Texas Parks and Wildlife; E. Grahmann, personal communication, Caesar Kleberg Wildlife Research Institute).

The history of overgrazing by sheep (*Ovis* spp.), goats (*Capra* spp.), cattle (*Bos* spp.), and nonnative wildlife in the Edwards Plateau exceeds a century. This pattern of intense herbivory has been suggested as a direct factor contributing to the decline of Montezuma quail in the Edwards Plateau (Texas Game, Fish, and Oyster Commission 1945, Baccus and Eitner 2007). Lockwood (2001) suggested intensive herbivory that removes 40–50% of tall grass cover leads to extirpation of Montezuma quail. The study sites used in this investigation had low to no grazing pressure by domestic livestock for at least 5 years prior to the study. We found bunchgrass density to be the most influential habitat feature on occupancy of Montezuma quail, with occupancy increasing as bunchgrass density increased. However, similar to patterns influencing detection, site use by Montezuma quail can likely be explained by a combination of habitat variables. At the local scale, sites with the highest rates of occupancy were savannah shrublands and grasslands, and on hillsides. Sampling the habitat variables at the sampling point may not have been the best method to identify fine-scale patterns in site use. Occupancy status was determined if a Montezuma quail was detected, audibly or visually, in ≥1 sampling period. Bishop (1964) suggested the male buzz call can be heard from up to 200 m away. Thus, the sampling location which was defined by the 4 10-m transects was not completely representative of the area actually used by the birds. Trapping, radio-telemetry, and associated vegetation sampling at quail locations were not possible using current technology and known means of capture under the low densities of birds found in the area.

Another attribute regarding habitat variables at occupied sites is the wide range used for each variable or metric sampled. For example, Montezuma quail were found in areas near the extremes of each sampled metric. These findings may suggest that at least some level of habitat plasticity exists in their site use. This potential conclusion conflicts with the commonly cited notion of Montezuma quail being habitat or site specialists (Leopold and McCabe 1957).

MANAGEMENT IMPLICATIONS

Renewed interest in management for Montezuma quail by landowners and scientists is hampered by a lack of general information on the species. We recommend the maintenance of savannah-like shrublands and grasslands, especially along hillsides, through the select removal of juniper and reduction of grazing pressure to ensure adequate amounts of bunchgrasses for cover.

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NESTING OF MONTEZUMA QUAIL IN MEXICO

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ABSTRACT

Although Mexico has the greatest diversity of quail of any New World country, basic information on the ecology and life history of Mexican quails remains unknown. Our objective was to describe nest characteristics of the Montezuma quail (*Cyrtonyx montezumae montezumae*) in central Mexico. We searched for Montezuma quail nests within 8 counties in the state of México, Mexico during May–September 2003. We conducted nest searches along 66 transects (3–5 km × 40 m) distributed across 17 study sites. We recorded vegetation community, elevation, and nesting substrate for each nest. We measured nest characteristics: height, depth, nest entrance diameter, and orientation. If eggs were found, we recorded clutch size and egg mass, texture, color, and shape. We observed 324 quail and located 6 nests along a 254-km route. Nests were located at elevations ranging from 2,568–2,692 m above sea level. Mean (± standard deviation) nest height and depth were 122.2 ± 7.7 mm and 195 ± 61.8 mm, respectively. Nest entrance orientation for 5 of 6 nests was toward a southerly direction. Mean nest egg mass was 9.9 ± 0.1 g. Our study provides basic and descriptive information on a poorly known quail species in Mexico.

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Key words: central Mexico, clutch, *Cyrtonyx montezumae*, egg, Montezuma quail, nest

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Mexico has the greatest quail diversity of any country in the New World, with 15 quail species, 5 of which are found in the state of México. This high diversity is due in part to the latitudinal location of the state, which is at the intersection of the Nearctic and Neotropical bioregions and the neo-volcanic belt mountain complex (Suárez-Mota and Téllez-Valdés 2014). The juxtaposition of these two biogeographic regions and mountain complexes results in a unique combination of wildlife from each region.

Despite Mexico's quail diversity, information on the basic life history, ecology, population status, and distribution of most Mexican quail species remains unknown (Carroll and Eitniear 2004). The Montezuma quail (*Cyrtonyx montezumae montezumae*) is one of the least studied species of pine-oak vegetation zones (Carroll and Eitniear 2000). Its cryptic coloration and reluctance to flush complicate field detection, and the species appears sensitive to most common tracking methods, such as radio-telemetry (Hernández et al. 2009). Thus, data on most aspects of its life history and ecology are limited (Stromberg 2000).

Montezuma quail are mostly restricted to the pine-oak vegetation zone; they reach their highest densities in open pine and oak woodland with an understory of low shrubs and perennial bunchgrasses (Leopold and McCabe 1957). Their primary distribution is in Mexico with a northern extension into the southern United States. Thus, their natural history and ecology can be best studied in this first country (Leopold and McCabe 1957). Our study objective was to collect basic nesting ecology information of Montezuma quail in central Mexico.

STUDY AREA

Our study covered an area of 3,156 km^2 in oak and pine-oak woodlands and grasslands in 8 northwestern counties (Acambay, Aculco, Almoloya de Juarez, Atlacomulco, Polotitlán, San Felipe del Progreso, Temascalcingo and Timilpán) of the state of México, and represents 1.4% of the total area for the state of México (INEGI 2000; Figure 1). Climate is temperate sub-humid with a mean annual precipitation of 1,000 mm (range 700–1500 mm), primarily occurring during summer (INEGI 2000). Local vegetation communities were composed primarily of woodlands (pine, oak, pine-oak, fir, fir-pine, pine-fir, and oak-pine) mixed with shrubs and native and nonnative grasslands (Espinosa-García and Sarukhán 1997). Pine-oak woodlands are common across the mountains at elevations of 2,800–2,950 m above sea level (Martinez and Matuda 1979). The tree stratum consists predominantly of 3 pine species (*Pinus occarpa, P. douglasina,* and *P. teocote*), 3 oak species (*Quercus crasifolia, Q. lauriana,* and *Q. conglomerata*), and 2 alder species (*Alnus jerullensis* and *A. firmifolia*). The shrub layer includes madroño (*Arbutus slandulosa*) and "escoba" (*Baccharis conferta*) with a herbaceous layer of muhly bunchgrasses (*Muhlenbergia* spp.; Rzedowski 1983, Rzedowski and Rzedowski 1985).

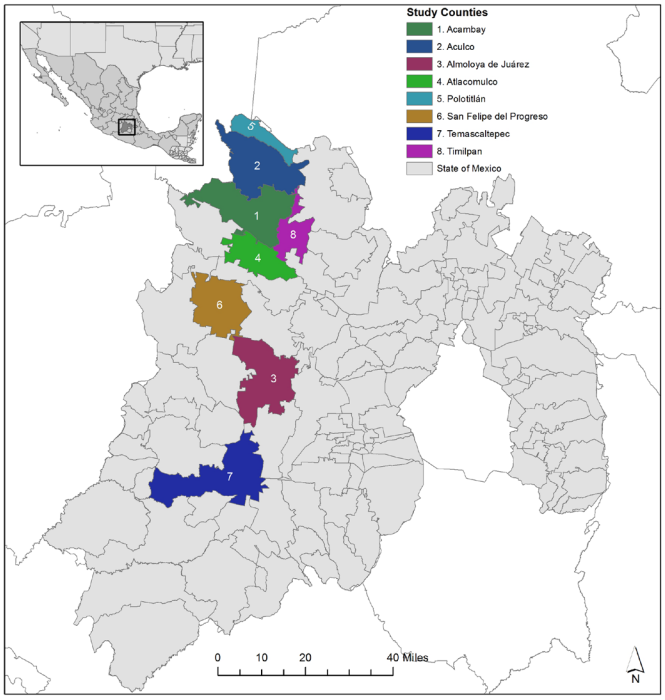

Fig. 1. Location of counties in the state of México, Mexico that were surveyed for Montezuma quail (*Cyrtonyx montezumae montezumae*) in 2003.

METHODS

We established 66 40-m wide transects of variable length (3–5 km) at 17 study sites. Study sites were selected because some of them contained the highest densities of Montezuma quail in the state of México (Tapia et al. 2002).

We conducted searches for quail along transects beginning at sunrise, continuing through mid-day, and resuming near sundown (0600–1200, 1600–1800), from May–September 2003. Search teams consisted of 4 observers and 2–3 bird dogs with >5 years' experience searching for Montezuma quail. The observers were spaced 10 m apart and walked 5–8 m behind the bird dogs (Bishop and Hungerford 1965, Brown 1978). Bird dogs have proven useful in studies estimating Montezuma quail densities in this region of the state (Tapia et al. 2002). When a bird dog located quail, observers slowly approached the pointing dog to locate the birds. We searched for nests within a 50-m radius of each quail point and conducted subsequent nest searches in locations with frequent quail sightings. We geo-referenced all nests found using a Global Positioning System device (Garmin® GPS 12XL™; Garmin, Olathe, KS, USA). We recorded vegetation community (i.e., oak woodland, pine-oak woodland, or grassland), nesting substrate, date found, and elevation (meters above sea level) for each nest. In addition, we measured nest height and depth and the diameter and orientation (the 4 cardinal directions) of the nest entrance. If eggs were found, we recorded clutch size and egg mass, texture, color, and shape. We calculated relative abundance as the number of quail observed per km.

RESULTS

We walked 254 km, observed 324 quail, and located 6 nests. We observed quail at 14 of 17 study sites and mean (± standard deviation) abundance was 1.1 ± 0.9 quail/km (range: 0.0–3.1; Table 1). We found nests at 4 of 17 study sites (Table 2). Mean abundance of nests was 0.02 ± 0.06 nests/km (range: 0.0–0.2). We found nests during July and August. Nests were located at elevations ranging from 2,568–2,692 m above sea level. Four nests were found in grassland-oak woodland, and the remaining 2 were found in grassland. The grass *Muhlenbergia* spp. was the most common nesting substrate. All nests were shaped like a lab flask, with a small oval entrance increasing in space to form an internal conical chamber with its base larger than the entrance (Figure 2). Mean nest height and depth were 122.2 ± 7.7 mm and 195 ± 61.8 mm, respectively. The nest entrance of 5 of 6 nests had a southern orientation. The mean smallest and largest diameter of the nest entrance were 136.0 ± 37.7 mm and 154.3 ± 46.5 mm, respectively (Figure 2). Clutch size (n = 4) ranged from 2–16 eggs and mean egg mass was 9.9 ± 0.1 g. All eggs were smooth in texture, white in color, and oval shaped with an elongated apical point. Mean egg length and width were 32.2 ± 0.2 mm and 24.6 ± 0.2 mm, respectively (n = 13).

Although no eggs were found at Nest CC, we observed a female leaving the nest. When Nest SnF3 was located, we found a female incubating the eggs. We subsequently visited the nest site from afar once a week. Hatching occurred 21 days after the nest was found. We determined a clutch size of 16 eggs based on the number of eggshells in the nest. We were fortunate to be able to observe the emergence of the hatchlings. Chicks pecked out small holes in the eggshells, began producing vocalizations immediately upon emerging, and promptly left the nest. Nests Yeb1 and Yeb2 were located within 1.5 m of each other. We found only 2 eggs in Nest Yeb1. We speculate that egg laying was not yet complete at the time of discovery. We found an egg on bare ground on July 23 at Tito's Ranch study site (San Felipe del Progreso County). We searched for a nest within a 50-m radius without success.

Table 1. Number of Montezuma quail (*Cyrtonyx montezumae montezumae*) and nests observed on transects in the state of México, Mexico, 2003.

			Observations		Relative abundance	
County, site		Accumulated transect length (km)	No. of quail	No. of nests	Quail/km	Nests/km
Acambay						
	Arroyo Zarco	20	18	0	0.9	0.0
	Peña Ñadó	6	0	0	0.0	0.0
Aculco						
	Cerro del Comal	18	30	1	1.7	0.1
	El 120	20	12	0	0.6	0.0
	La Cofradía	40	69	0	1.7	0.0
	San Francisquito	16	35	3	2.2	0.2
Almoloya de Juárez						
	Ocoyotepec	12	15	0	1.3	0.0
	San Lorenzo Toxico	16	12	0	0.8	0.0
	Yebucivi	12	37	2	3.1	0.2
Atlacomulco						
	Diximoxi	6	5	0	0.8	0.0
Polotitlán						
	Casas Viejas	6	0	0	0.0	0.0
San Felipe del Progreso						
	Rio Hoyo Buenavista	20	11	0	0.6	0.0
	San José del Rincón	16	20	0	1.3	0.0
	Tito´s Ranch	24	53	0	2.2	0.0
Temascalcingo						
	Puente Andaró	6	0	0	0.0	0.0
	Santa María Canchesdá	10	4	0	0.4	0.0
Timilpan						
	Buenavista	6	3	0	0.5	0.0
Total		254	324	6	1.28	0.02

Table 2. Characteristics of Montezuma quail (*Cyrtonyx montezumae montezumae*) nests in the state of México, Mexico, 2003.

County, Site	Nest ID	Date found	Vegetation community	Elevation (m a.s.l.)	Nesting substrate (mm)		Nest entrance			Clutch size
							Diameter (mm)			
					Height	Depth	Smallest	Largest	Orientation	
Aculco										
Cerro del Comal	CC	31 Aug 2003	Grassland-oak woodland	2692	121	162	90	105	SW	0
San Francisquito	SnF1	20 Jul 2003	Grassland-oak woodland	2589	121	280	90	101	SE	11
	SnF2	30 Jul 2003	Grassland-oak woodland	2568	111	143	162	184	SW	12
	SnF3	31 Aug 2003	Grassland-oak woodland	2570	135	134	140	140	E	16
Yebucivi	Yeb1	05 Jul 2003	Grassland	2650	121	261	156	180	SW	2
	Yeb2	05 Jul 2003	Grassland	2650	124	190	178	216	SW	0

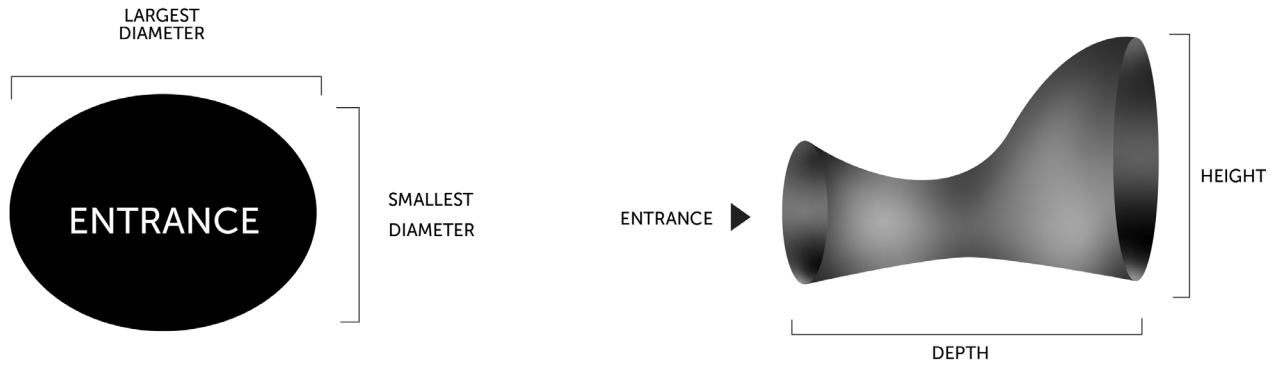

Fig. 2. Dimensions of Montezuma quail (*Cyrtonyx montezumae montezumae*) nests measured in the state of México, Mexico in 2003.

DISCUSSION

Our study adds basic descriptive information to a limited database of Montezuma quail nesting ecology. Data related to nest characteristics of Montezuma quail in central Mexico were not previously available. Thus, comparisons to other studies are limited.

We observed the first evidence of Montezuma quail forming pairs at the beginning of June. This timing differs slightly from pair formation documented during March–April in Arizona, USA (Wallmo 1954, Bishop 1964). However, the breeding phenology of Montezuma quail is closely tied to precipitation (Leopold and McCabe 1957). Thus, this slight difference in breeding phenology between studies could be due to variation in timing of precipitation. The nesting season (Jun–Aug) in our study corresponds to prior studies (Falvey 1936, Leopold and McCabe 1957).

The grass *Muhlenbergia* spp. was the most commonly used nesting substrate, probably due to its availability at our study sites. Nests were located within a narrow elevational range (2,568–2,692 m), and this grass is dominant at these elevations in our study area. Our general description of nests appears to be similar to prior research, but no other studies provide dimensions of Montezuma quail nests for comparisons.

The physical characteristics (mass, texture, color, and shape) of eggs for *C. montezumae montezumae* were similar to those reported for *C. montezumae mearnsi* in northwestern Chihuahua, Mexico (Bent 1932) and southeastern Arizona (Leopold and McCabe 1957). We observed that eggs had a smooth shell and were white. Bent (1932) noted that Montezuma quail eggs were smooth and somewhat glossy, ranging in color from pure white to creamy white. He described egg shape as short ovate or ovate pyriform.

Leopold and McCabe (1957) noted that Montezuma quail abundance in the pine-oak zone of Mexico was inversely related to the local abundance of livestock. Grazing removes important escape and nesting cover for Montezuma quail (Brown 1982). Our findings provide general support for the sensitivity of this species to grazing. All 6 nests that we found

were located in grassland and grassland-oak habitat in areas with little grazing. Because overgrazing is an occurrence widespread throughout the state of México (Herrera et al. 1998), grazing is likely to be limiting the distribution and abundance of Montezuma quail in this state.

MANAGEMENT IMPLICATIONS

Nest characteristics of Montezuma quail in central Mexico were previously not available. This information helps us understand in general the breeding biology and ecological function of this species (Mainwaring et al. 2014), but in particular its nesting habitat requirements. High-quality habitat for Montezuma quail depends on appropriate proportions of pine and oak woodland interspersed with low shrubs and perennial bunchgrasses (Hernández et al. 2019). We suggest cover provided by *Muhlenbergia* spp. is important for breeding habitat and nesting substrate. Current habitat for the species is at risk of deterioration and loss due to grazing, agriculture, and mismanagement of fire. In addition to conventional management practices (e.g., population and habitat monitoring, improvement, and protection), remote sensing imagery and spatial analysis within geographic information systems technology are critical to model potential habitat distribution, suitability, and management requirements. We suggest this study should be continued to 1) better understand the role of Montezuma quail nesting characteristics in this type of environment and the evolution of nesting morphology and its function (Mainwaring et al. 2014, Medina 2019, Perez et al. 2020) and 2) generate information on the species' persistence under current challenges from climate change.

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AGE, SEX, AND FAMILY COMPOSITION OF MONTEZUMA QUAIL COVEYS IN ARIZONA, NEW MEXICO, AND TEXAS

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ABSTRACT

The Montezuma quail (*Cyrtonyx montezumae*) is a popular game bird in Arizona and New Mexico, USA, but hunting seasons remain closed in Texas, USA. Estimates of age structure parameters and sex ratios in game birds are essential information for predicting population trajectories and developing sustainable harvest and conservation strategies. Montezuma quail form coveys during the winter as a behavioral strategy for improved survival. In this regard, we harvested 1–4 individuals from 112 Montezuma quail coveys in Arizona, New Mexico, and West Texas from 2009 through 2020 to estimate sex and age composition (juvenile vs. adults) of coveys. We also estimated size for all coveys from which we harvested birds. Mean covey size (± standard error) was 9.7 ± 0.7 individuals (range = 6–12), 9.1 ± 0.5 (range = 2–20), and 5.7 ± 0.7 (range = 2–12) for Arizona, New Mexico, and Texas, respectively although covey size decreased through the winter. The proportion of females among harvested birds was 0.33 ± 0.11, 0.40 ± 0.04, and 0.36 ± 0.33 for Arizona, New Mexico, and Texas, respectively. The proportion of juveniles among harvested birds was 0.83 ± 0.09, 0.71 ± 0.04, and 0.52 ± 0.10 for Arizona, New Mexico, and Texas, respectively. Coveys seem to contain more than one family group (paired birds with current progeny). We estimated that at least 6.2 ± 3.0% and 15.4 ± 10.0% of coveys were mixed families for New Mexico and Texas, respectively, as we harvested more than 2 adult males from the same covey. We did not collect same-sex adults from the same covey in Arizona. Our estimates set apart West Texas in lower average covey size and proportion of juveniles from Arizona and New Mexico at the northern edge of the species' distribution and may reflect a different population dynamic in the region. However, our estimates must be taken with caution as behavioral response differences between sexes and age categories may differ and may not accurately reflect the actual sex, age, and family composition of Montezuma quail coveys. In addition, results may be confounded by variability in environmental factors over our extended sampling period.

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Key words: age structure, *Cyrtonyx montezumae*, covey, Montezuma quail, sex ratio

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LANDSCAPE-SCALE EFFECTS OF HABITAT AND WEATHER ON INCREASING AND DECREASING SCALED QUAIL POPULATIONS

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ABSTRACT

Scaled quail (*Callipepla squamata*) have declined over the last half century; however, there is spatial variation within their geographic distribution. Interior populations have increased and peripheral populations have generally decreased. Declines have been attributed to habitat loss and degradation. Scaled quail populations also show interannual fluctuations related to precipitation. Our objective was to determine the relative impact of habitat and weather (i.e., precipitation and temperature) on scaled quail population dynamics. Our hypothesis was that habitat metrics would be more important for decreasing populations whereas weather metrics would be more important for increasing populations. We used publicly available datasets for scaled quail abundance measures (Breeding Bird Survey, Christmas Bird Count), weather (PRISM), and land cover (National Land Cover Data) collected over 3 5-year time periods (1990–1994, 1999–2003, 2009–2013). Data were collected at 2 scales: a route scale (5-km route buffer) and region scale (25-km circular buffer). We developed 25 *a priori* models that fit into 4 "model classes" (habitat amount, habitat fragmentation, matrix quality, weather). Model selection followed a 2-stage approach, where models were initially evaluated within each individual model class, then top models from each class were evaluated in combination to determine a global model. We used mixed-effects models with a negative binomial response distribution, treating route as a random effect. Weather variables were the primary explanatory factor for increasing populations at both scales. Similarly following our hypothesis, habitat variables were generally the most important for decreasing populations, but only at the route scale; weather variables dominated at the region scale. Both abundance datasets provided similar results and explanatory power ($R2 \approx 0.10$ for route scale; $R2 \approx 0.27$ for region scale), for both increasing and decreasing populations. Comparisons of land cover variables showed increasing populations to have higher amounts of habitat ($p = 0.0028$), higher mean patch area of habitat ($p = 0.0446$), and lower urban cover ($p = 0.0287$). Our hypothesis that weather variables account for more variation of increasing scaled quail populations was generally supported, likely because of increased amounts of habitat in these areas. However, given the low overall explanatory power of our models, it is likely that other factors such as habitat quality may be more important to scaled quail. Increasing temperature and reduced precipitation associated with climate change are likely to exacerbate scaled quail declines both directly and through continued habitat degradation, even within areas with increasing populations.

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Key words: *Callipepla squamata,* habitat, landscape-scale, scaled quail, weather

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MASKED BOBWHITE RECOVERY: THE NEED FOR A MULTIFACETED APPROACH

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ABSTRACT

Masked bobwhite (*Colinus virginianus ridgwayi*) is a critically endangered quail historically found in the Sonoran grasslands of southern Arizona, USA and Sonora, Mexico. Native populations of masked bobwhite may already be extinct in the wild, but captive populations exist in the United States at G. M. Sutton Avian Research Center (Oklahoma, USA), Buenos Aires National Wildlife Refuge (Arizona, USA), and various zoos. The 47,000-hectare Buenos Aires National Wildlife Refuge, located in south-central Arizona, was established primarily for reintroduction of this bird. Recovery efforts within the refuge boundary in the 1980s and 1990s were initially successful but suffered debilitating setbacks that ultimately resulted in failure. Substantial releases were suspended in 2005. Improved habitat restoration efforts and promising conditioning and release techniques led to the belief that reintroductions could again be attempted and successful. In 2016–2017 plans were developed to increase captive propagation and reinitiate release efforts. Releases began in 2018. Over-winter survival of birds released in 2018–2019 was encouraging, and reproduction of wild birds was documented in 2019. An existing base of wild birds established from these releases could help masked bobwhite populations recover in the state. Habitat restoration, better methods of rearing, release, and conditioning, and improved production from captive facilities also inspire hope that a full recovery of the species in Arizona is possible.

Citation: Johnson, L. A., M. J. Butler, J. G. Goodwin, Jr., R. Chester, G. M. Harris, S. E. Sesnie, and D. H. Wolfe. 2022. Masked bobwhite recovery: the need for a multifaceted approach. National Quail Symposium Proceedings 9:167. https://doi.org/10.7290/nqsp09YuyH

Key words: Buenos Aires National Wildlife Refuge, call-box, *Colinus virginianus ridgwayi,* conditioning, covey augmentation, endangered species, foster parent, habitat restoration, masked bobwhite, over-winter survival, quail releases

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HABITAT OF THE LONG-TAILED WOOD-PARTRIDGE IN CENTRAL MEXICO

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ABSTRACT

The long-tailed wood-partridge (*Dendrortyx macroura*; hereafter, wood-partridge) is a forest quail endemic to the temperate forests of the Trans-Mexican Volcanic Belt of central Mexico and is considered threatened according to the Secretariat of the Environment of Mexico. We studied 34 sites within the Natural Resources Protection Area River Basins of the Valle de Bravo, Malacatepec, Tilostoc and Temascaltepec in central Mexico to evaluate wood-partridge habitat during September–December 2019. We evaluated attributes of tree, shrub, and herbaceous vegetation, canopy cover, humidity, slope, and altitude. We also identified vegetation used for nesting, food, and shelter. The scant information published for other geographical areas indicates habitat consists of pine (*Pinus* spp.), pine-oak (*Quercus* spp.), and cloud forest. We found that the preferred habitat in the Trans-Mexican Volcanic Belt was forest dominated by *Alnus firmifolia, Pinus patula, Pinus pseudostrobus, Pinus teocote,* and *Quercus castanea*. Wood-partridge preferred sites with an average of 90% canopy coverage, 100% shrub cover, high percent humidity, slopes >30%, and altitudes that ranged 2,700–3,000 meters above sea level. Additionally, we located an inactive nest in an area with 100% shrub cover and 80% tree cover in forest dominated by *Pinus patula*, relative humidity of 55%, and a temperature of 19° C. This is the first investigation of this bird within this important biogeographic transition zone between the Nearctic region and the Neotropics. We report the basic characteristics of the habitat used by this species along with the first description of a nest in an area with high rates of deforestation, overgrazing, and forest fires. The "gallinita de monte" represents an important element of the biocultural heritage for the Mazahua and Otomí peoples, who are Indigenous inhabitants of this area. We recommend additional research on wood-partridge to determine the extent of poaching and collection of eggs for food; determine effects of forest management; determine its basic ecology including survival, reproduction, and population density; verify habitat relationship; and corroborate information that describes the traditional knowledge of the species by the native Mazahua and Otomí peoples. We suggest it is most important to learn more about and disseminate traditional knowledge of the species and to preserve its biocultural value and heritage, particularly for Indigenous communities.

Citation: García-Solórzano, D., C. Lopez Sanchez, E. Lopez-Gonzalez, and C. González-Rebeles Islas. 2022. Habitat of the long-tailed wood-partridge in central Mexico. National Quail Symposium Proceedings 9:168. https://doi.org/10.7290/nqsp09ECIb

Key words: central Mexico, *Dendrortyx macroura*, gallinita de monte, habitat, long-tailed wood-quail, nesting, Odontophoridae, Trans-Mexican Volcanic Belt

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VARIABILITY AND GENETIC STRUCTURE OF THE MONTEZUMA QUAIL IN THE NORTHERN LIMIT OF ITS DISTRIBUTION

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ABSTRACT

A species' geographic distribution of genetic variability is influenced by different factors including size of geographic distribution, dispersal capability, mating system, and migration. For instance, a low migration rate among populations may cause a decrease in genetic variation. Such is the case of the Montezuma quail (*Cyrtonyx montezumae*), a popular game bird with a limited flight capacity that prevents long-distance dispersal. In the northern limit of the species' distribution in Arizona, New Mexico, and Texas in the United States, the species inhabits oak forests that are separated from one another by deserts. Consequently, Montezuma quail populations are distributed in patches or islands. Knowledge of the species' genetic structure is likely to help inform habitat management decisions. The objective of this study was to determine patterns of genetic variation in populations of the Montezuma quail using 9 microsatellite DNA loci. We genotyped 119 individuals harvested from 4 populations: Arizona (AZ), western New Mexico (WNM), eastern New Mexico (ENM), and west Texas (WTX). Montezuma quail populations had low observed heterozygosity ($H_o = 0.22 \pm 0.04$) and a low number of alleles per locus ($A = 2.41 \pm 0.27$) compared to other quail species. A global population genetic differentiation index (R_{ST}) of 0.045 suggests a weak genetic structure. Max(R_{ST}) occurred among pairwise comparisons AZ-WTX, AZ-ENM, and WNM-WTX. A Bayesian allocation analysis indicates that individuals were separated into 3 groups ($K = 3$), placing the populations of Arizona and Texas in distinct groups apart from the 2 populations of New Mexico, which are in the same group. Despite this differentiation, the Bayesian allocation analysis suggests admixture among populations, which may be an indicator of migration between them, especially between the populations in New Mexico and Arizona. An isolation-by-distance analysis indicates that there is a strong correlation ($R^2 = 0.84$) and suggestive evidence ($P = 0.08$) of non-independence between geographical and genetic distances, though Montezuma quail populations in the southwestern United States may not be isolated. Climate change projections indicate an increase in aridity conditions in this region, especially in temperate ecosystems where the species occurs. In this scenario, corridors between the populations may disappear, thus causing their complete isolation.

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Key words: *Cyrtonyx montezumae*, dispersion, DNA microsatellites, genetic structure, isolation by distance, Montezuma quail

COMPOSITION OF MONTEZUMA QUAIL'S DIET IN ARIZONA, NEW MEXICO, AND TEXAS

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ABSTRACT

The Montezuma quail (*Cyrtonyx montezumae*) is a popular game bird and an indicator species of oak-pine savannas in the northern part of its range. In Arizona and New Mexico, USA, robust populations allow for a hunting season from mid-November through mid-February. However, there is no open hunting season for this quail in Texas, USA. Data on the Montezuma quail's diet can provide new information and improve management of the species. Our objective was to analyze the diet composition of the Montezuma quail in Arizona, New Mexico, and Texas. Specimens were collected by hunters in Arizona and New Mexico during 2016–2020 seasons and by researchers during 2018–2020 winter and spring seasons in Texas. We estimated the diet composition by macrohistological analysis of the collected quail crops. We found a high variety of food items: 178 items or morphospecies in crops (n = 175), from which 110 and 66 items were of plant and animal origin, respectively, and 2 unidentified items. We found an average (± standard error) of 5.89 ± 0.42 items/crop (range = 0–22) in Arizona (n = 107) samples, 4.15 ± 0.99 items/crop (range = 1–13) in New Mexico (n = 13), and 4.38 ± 0.40 items/crop (range = 1–12) in Texas (n = 55). Winter diet of Montezuma quail in Arizona was mainly represented by bulbs of *Oxalis* spp. (35.22% of dry weight), bulbs and rhizomes of *Cyperus* spp. (30.92%), acorns (*Quercus* spp.; 7.17%), and tepari beans (*Phaseolus acutifolius*; 6.50%). Winter diet in New Mexico consisted mainly of bulbs of *Cyperus* spp. (64.13%), beans of *Macroptilium* spp. (15.82%), and *Panicum hallii* grains (10.11%). In Texas, winter diet consisted mostly of rhizomes and bulbs of *Cyperus* spp. (28.17%), *Rhynchosia senna* beans (22.49%), *P. hallii* grains (19.54%), *Allium* wild onions (8.58%), and *Cylindropuntia imbricata* seeds (4.16%). The Montezuma quail's spring diet in Texas consisted mainly of rhizomes and bulbs of *Cyperus* spp. (61.64%) and bulbs of *Oxalis* spp. (19.46%). The Montezuma quail diet changes in composition and proportion according to the site and season, but bulbs and rhizomes of *Cyperus* spp. are the predominant food items in all 3 states. This work provides novel information about the winter and spring diet of Montezuma quail in Texas. Information about Montezuma quail diet at several temporal and geographic scales will prove to be highly relevant to implement better management and conservation strategies in the northern edge of the species' range.

Citation: Paredes-Acuña, A. G., A. Macías-Duarte, R. A. Castillo-Gámez, A. B. Montoya, and J. H. Weaver. 2022. Composition of Montezuma quail's diet in Arizona, New Mexico, and Texas. National Quail Symposium Proceedings 9:171. https://doi.org/10.7290/nqsp09W71Y

Key words: Arizona, *Cyrtonyx montezumae*, Montezuma quail, New Mexico, spring diet, Texas, winter diet

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WINTER DIET OF MONTEZUMA QUAIL IN ARIZONA AND NEW MEXICO

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ABSTRACT

Investigating the diet composition of Montezuma quail (*Cyrtonyx montezumae*) is fundamental for unveiling how food resources limit the species' population size and may provide relevant tools for their harvest and habitat management. The objective of this research was to determine the composition and geographic variation of the winter diet of the Montezuma quail in Arizona and New Mexico, USA, from quail crops harvested during the hunting seasons of 2008–2017. In addition, we used beta regression analyses to determine the effect of environmental factors and ecological variables (annual mean precipitation, annual mean temperature, landscape diversity, diet diversity, time of hunt, longitude, latitude, and elevation) on Montezuma quail diet composition. We found that acorns (*Quercus* spp.) and sedge rhizomes (*Cyperus fendlerianus*) are the most frequent food items of Montezuma quail in Arizona and New Mexico, respectively, followed by tepary beans (*Phaseolus acutifolius*), woodsorrel tubers (*Oxalis* spp.) and insects in both states. Individual crop wet mass is positively associated with time of day during winter. Geographic variation in Montezuma quail diet composition in Arizona and New Mexico was associated with mean annual precipitation for acorns and with geographic variation in mean annual temperature for rhizomes and tubers of sedge (*Cyperus* spp.). Geographic variation of other food items was not associated with those environmental factors. These functional relationships between the species' diet and environmental factors suggest that Montezuma quail preference towards these two principal food items is subject to climatic control. Therefore, warmer and drier environments in the southwestern United States and northern Mexico may affect the species' distribution through changes in food availability.

Citation: López-Bujanda, O. E., A. Macías-Duarte, R. A. Castillo-Gámez, and A. B. Montoya. 2022. Winter diet of Montezuma quail in Arizona and New Mexico. National Quail Symposium Proceedings 9:172. https://doi.org/10.7290/nqsp09Z2Ye

Key words: Arizona, *Cyrtonyx montezumae*, foraging, Montezuma quail, New Mexico, winter diet

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CHARACTERISTICS OF HUNTER-HARVESTED MONTEZUMA QUAIL WINGS AND IMPLICATIONS FOR MOLT PHENOLOGY

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ABSTRACT

We obtained 1,899 hunter-harvested Montezuma quail (*Cyrtonyx montezumae*) wings from southeastern Arizona, USA, from the 2008–2009 hunting season. We determined age and sex based on plumage characteristics for 98.2% (1,864) of the original sample. One-way analysis of variance (ANOVA) of wing-chord length found differences ($P < 0.001$) based on sex, but not age, with mean (± standard error) male wing chord (113.76 ± 0.15 mm) longer than mean female wing chord (111.03 ± 0.13 mm). Mean male and female wing-chord lengths from our study population were 6.8% and 7.7% shorter, respectively, than previously reported in the literature. We additionally calculated a complete prebasic molt cycle of 177 days based on previously reported preformative molt patterns. The primary benefits of our results are: 1) a more accurate sex-based wing-chord length based on a large sample size, 2) a method to back-calculate molt onset dates for hunter harvested after hatch year Montezuma quail, and 3) a potential means to model the influence of precipitation on population dynamics of Montezuma quail.

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Key words: Arizona, *Cyrtonyx montezumae,* molt phenology, Montezuma quail, wing chord

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Montezuma quail (*Cyrtonyx montezumae*) are found from the southwestern United States southeast to Oaxaca, Mexico along the Sierra Madre Occidental Mountains (Leopold and McCabe 1957, Johnsgard 1973, Stromberg et al. 2020). Reliable population monitoring methods (e.g., whistle counts, covey call count, and roadside counts) for Montezuma quail are limited due to the species' cryptic coloration, its secretive nature (Brown 1979, Harveson 2009, Chavarria et al. 2017, Sanders et al. 2017, Stromberg et al. 2020), and steep topography (Heffelfinger and Olding 2000). A lack of reliable population data both from indices and few field studies have resulted in much of our current knowledge about Montezuma quail being derived from anecdotal evidence or casual field observations (Brown 1979, Chavarria et al. 2017, Stromberg et al. 2020).

The Arizona Game and Fish Department (AZGFD) installed wing barrels to monitor Montezuma quail harvest trends beginning in the 1960s and continuing to the present (Zornes 2009). The hunter-harvested wing dataset represents one of the longest continuous monitoring efforts for Montezuma quail in the United States and has the potential to significantly improve our understanding of Montezuma quail life history and population dynamics. Hunter-harvested wings provide wildlife managers with a valuable, cost-effective tool to estimate population dynamics and annual reproduction indices for multiple game species, such as greater sage-grouse (*Centrocercus urophasianus*; Hoffman 1981, Hagen et al. 2018), sooty grouse (*Dendragopus obscurus*; Hoffman 1981, Zwickel 1982), American woodcock (*Scolopax minor*; Myatt and Krementz 2010), northern bobwhite (*Colinus virginianus*; Haugen 1957, Campbell et al. 1973, Wells and Sexson 1982), and California quail (*Callipepla californica*; Crawford and Oates 1986).

The Montezuma quail is the only North American quail species with sexually dimorphic wing plumage (Leopold and McCabe 1957, Harveson et al. 2007). Accordingly, hunter-harvested wings from this species allow managers and researchers greater insight into population trends based on age and sex, compared to other North American quail (e.g., northern bobwhite, mountain quail [*Oreortyx pictus*], scaled quail [*Callipepla squamata*], California quail, and Gambel's quail [*C. gambelii*]), for which wing surveys and studies are restricted to age-based analyses.

Our study goal was to provide a more robust analysis of Montezuma quail wing morphometrics and molt phenology. Specifically, our study objectives were to: 1) provide updated wing chord estimates based on a large sample size and 2) use molt characteristics (e.g., primary molt) of hunter-harvested Montezuma quail wings across age (e.g., after hatch year [AHY] and hatch year [HY]) and sex (male or female) to better understand molt phenology.

STUDY AREA

Wings for our study were harvested in Pima and Santa Cruz counties, Arizona, USA (Arizona Game Management Units 36, 37, and 38) within the Madrean Archipelago ecoregion (Ruhlman et al. 2012). Elevation of the Madrean Archipelago ecoregion ranges from 600–3,000 m above mean sea level with a mean annual precipitation ranging from 218–1,118 mm from lower to higher elevations (Lowe 1964). Precipitation is biseasonal with rainfall from frontal precipitation in winter and monsoonal storms in summer (Crimmins et al. 2011). Desert and semiarid grassland vegetation communities dominated low elevations, with Emory oak (*Quercus emoryii*) and juniper (*Juniperus* spp.) woodland vegetation communities dominant in mid-elevations, and ponderosa pine (*Pinus ponderosa*), Engelmann spruce (*Picea engelmannii*), and Douglas-fir (*Pseudotsuga menziesii*) found at higher elevations (Ruhlman et al. 2012).

METHODS

We obtained 1,899 hunter-harvested Montezuma quail wings from the AZGFD from the 2008–2009 hunting season (23 Nov 2008 to 11 Feb 2009). Hunter-provided wings were in their original submission packet, including date and location of harvest, use of dogs, and number of hunters in each submitting party (Heffelfinger and Olding 2000). We uniquely numbered all wings, recording harvest date and location in a database. We recorded age (e.g., HY or AHY) based on the presence or absence of buff-edged primary coverts, sex based on plumage coloration (Pyle 2008), flattened wing-chord length (mm), and feather molt (p1–p10) for each wing (Pyle 2008, Lyons et al. 2012). We used a 1-way analysis of variance (ANOVA) to test for differences between age and sex classification of mean wing-chord length.

Montezuma quail replace primary feathers sequentially from innermost (p1) to outermost (p10), with HY birds retaining p9 and p10 during their preformative molt (Pyle 2008, Stromberg et al. 2020). We recorded primary-feather molt for each wing and assumed the observed primary-feather molted was lost on the date of reported harvest (Randel et al. 2019).

To estimate preformative molt completion date for hunter-harvested wings, we subtracted the days post-hatching for each primary shed (e.g., p5 = 56, p6 = 77, p7 = 98, p8 = 119) from 135 (Leopold and McCabe 1957), adding the resulting number of days to the date of harvest. No corresponding estimates for prebasic molt duration or primary replacement time were found. To calculate the number of days required to complete the prebasic molt, we added 21 days each for replacement time of p9 and p10, based on preformative primary molt shedding times reported by Leopold and McCabe (1957), resulting in an estimated prebasic primary feather molt cycle of 177 days. We estimated prebasic molt onset by subtracting the assumed primary replacement time (days) of the preformative molt cycle from the date of harvest.

RESULTS

We examined Montezuma quail wings harvested over a 12-week period beginning 23 November 2008. We assigned

age and sex to 1,864 of 1,899 wings with 52.9% aged as AHY and the remaining 47.1% aged as HY. Males were more prevalent than females in our sample and represented 59.4% of all wings. We found a significant effect of sex on mean (± standard error [SE]) wing-chord length with male wing-chord length (113.8 ± 0.15 mm) greater than female wing-chord length (111.1 ± 0.13 mm, $F_{(3, 1626)} = 62.04$, $P < 0.001$). We did not find a significant difference in wing-chord length across age classes ($F_{(1, 1647)} = 0.83$, $P = 0.48$).

We detected completed preformative (HY) and prebasic (AHY) molts in all study weeks, with weekly percentages generally increasing for both. We additionally identified shed primary feathers in all weeks for preformative and prebasic molts. Shedding of p5 was restricted to the preformative molt with 17 December 2008 the last harvest date recorded for this primary. We recorded shedding of p6, p7, and p8 in both preformative and prebasic molts. Shedding of p9 and p10 is indicative of AHY individuals and restricted to the prebasic molt; the latest date we recorded for each was 3 February 2009 and 28 January 2009, respectively.

We estimated that the onset of the prebasic molt cycle for our study population ranged from 16 June to 23 October 2008. Our mean prebasic molt onset date was 13 August with no difference in mean prebasic molt onset based on sex (Figure 1).

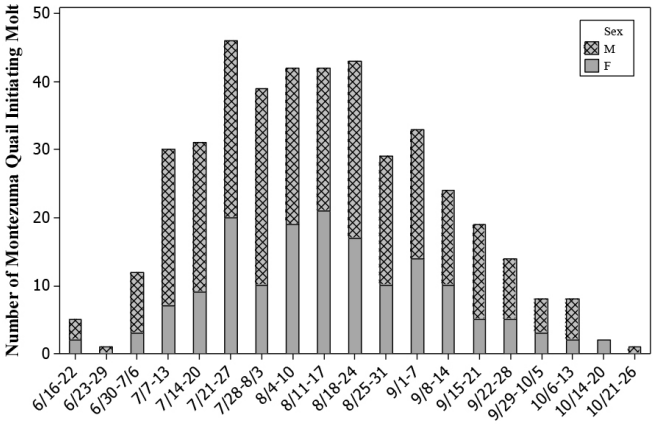

Fig. 1. Estimated onset of prebasic molt of male (cross-hatched) and female Montezuma quail based on hunter-harvested wings from the 2008–2009 Arizona, USA hunting season.

DISCUSSION

Our mean male wing-chord length (113.8 ± 4.0 mm) was 5.2% and 7.7% shorter than previously reported by Johnsgard (1973) and Stromberg et al. (2020), respectively. Our mean female wing-chord length (111.1 ± 3.5 mm) was 7.4% and 6.8% shorter than previously reported by Johnsgard (1973) and Stromberg et al. (2020), respectively. Eitniear and Becherer (2016) reported a mean wing-chord length of 129 mm, 12.7% larger than our pooled mean wing-chord length of 112.6 ± 0.1 mm. Our smaller mean wing-chord length for both male and female Montezuma quail is likely attributable to the larger sample size in our study than those previously reporting Montezuma quail wing-chord lengths. An alternate possible explanation for the decreased wing-chord length of our samples is climate-driven changes in morphology; investigating this explanation is beyond the scope of our single-season study. Decreases in fat-free mass and wing-chord length have been correlated to migratory species in western Pennsylvania, USA (Van Burskirk et al. 2010), common nightingale (*Luscinia megarhynochos*) in Europe (Remacha et al. 2020), and tree swallow (*Tachycineta bicolor*; Paquette et al. 2014). Further research of long-term wing datasets would be required to determine whether such a pattern is present in Montezuma quail and whether alternate hypotheses could be developed to explain the potential decrease in wing-chord length.

In our study of hunter-harvested Montezuma quail wings, we found evidence of primary feather molt (p5–p10) from November 2008 to February 2009. Molt phenology of Montezuma quail is currently assumed complete by November annually (Pyle 2008, Stromberg et al. 2020). Our findings are inconsistent with Stromberg et al. (2000) and Pyle (2008) but do coincide with the findings of Swarth (1909), who estimated prebasic molt initiation to be October or November. By using the harvest date, primary feather shed, and assumed replacement time, we suggest both preformative and prebasic molt may not be completed until late April of the subsequent year.

The preformative molt cycle for North American quail species has been extensively studied, specifically as a method for aging HY individuals (Stoddard 1931, Leopold 1939, Wallmo 1954, Johnsgard 1973, Calkins et al. 2020). By comparison the prebasic molt cycle of North American quail has lacked as intensive study, and as such molt and replacement timing of p9 and p10 is understudied or underreported for most North American quail species. We estimated that the complete prebasic molt timing for Montezuma quail was 177 days, with the onset of molt occurring as early as mid-June and as late as the third week in October. Our estimate of 177 days should be used as an approximation, and future research related to replacement and regeneration times of p9 and p10 in Montezuma quail should be conducted under control conditions to refine prebasic molt phenology for this species. Our use of 1,864 Montezuma quail wings to evaluate the effect of age and sex on wing morphometrics and molt phenology is, to our knowledge, the largest sample size obtained for this species.

Montezuma quail are 1 of 4 sexually dimorphic North American quail species; the others are northern bobwhite, California quail, and Gambel's quail. While these 4 quail species can readily be sexed when a live or whole specimen is present, Montezuma quail are the only species where sex can be assigned based on wing plumage characteristics alone. The ability to identify sex based on wing plumage alone presents unique research opportunities for Montezuma quail. In addition to assessment of the effect of age and sex on molt phenology, hunter-harvested wings can be used to derive more meaningful population demographic and reproduction estimates based on environmental variables such as timing and intensity of monsoon.

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EXAMINATION OF AN ANECDOTAL "OCTOBER DISAPPEARANCE" OF NORTHERN BOBWHITE IN THE ROLLING PLAINS OF TEXAS THROUGH DEMOGRAPHIC DATA

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ABSTRACT

Landowners and wildlife managers in the Rolling Plains ecological region of Texas, USA often report encountering northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) in summer but observe what they perceive as a decrease in quail by early to mid-fall. As most bobwhite research in the Rolling Plains is focused on either breeding season or overwinter survival and movement, researchers rarely record demographic data during this late summer and early fall period. We examined weekly survival probabilities of bobwhite (n = 244) across 7 sites in the western Rolling Plains Ecoregion from August to late November in 2016, 2017, 2019, and 2020. Bobwhites were captured and equipped with very high frequency (VHF) transmitters and tracked 1–5 times/week. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to evaluate a suite of candidate models comparing survival among and between years and survival between individual weeks to determine whether an unreported population decrease occurred during the study years. Our comparison of weekly survival probabilities considered survival to be different if 95% confidence intervals did not overlap. Our best supported model held survival constant among years and allowed survival to vary week by week. All other models received little support ($\Delta AIC_c > 14.0$). Examination of weekly survival probabilities failed to support a demographically driven hypothesis for decreased bobwhite observations from August to November. Though there was an observed decrease of weekly survival in the fourth week of September, it was not different than 16 of the 17 other weeks. We conclude that, for the years we measured, there was no support for a mass die-off hypothesis. Factors outside survival (e.g., a change in bobwhite behavior) may be driving the difference in detectability between late summer and late fall in the Rolling Plains of Texas.

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Key words: *Colinus virginianus*, northern bobwhite, Rolling Plains, survival, Texas

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The northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) has suffered range-wide population declines and region-specific extirpations during the last century (Pardieck et al. 2020). As one of the most popular hunted and economically significant game species, the bobwhite has rightly been the focus of great conservation and research effort to counter this decline (Burger et al. 1999, Rollins 2007, Johnson et al. 2012, Brennan et al. 2014). For a nonmigratory, ground-dwelling species, the bobwhite has an expansive range, extending across the midwestern and southeastern regions of the United States and the Caribbean, and into Mexico (Brennan et al. 2014). Despite the substantial body of bobwhite research, this large geographic range with differing climate, vegetation, stakeholder experiences, and management philosophies presents managers and researchers with challenges in managing at the population and metapopulation level while addressing region-specific issues. These region-specific philosophies and issues include differing opinions on "cultural management" (e.g., supplemental feeding, predator management), climate-driven population changes including drought, and perceived "die-offs" and their possible causes (e.g., drought, disease, parasites, predators).

As in other regions, habitat is paramount for bobwhites in the Rolling Plains ecological region of Texas, USA, with populations often fluctuating due to habitat quality, habitat accessibility, and availability of sufficient food and nesting resources (Rollins 2007). In the Rolling Plains, quail habitat is primarily influenced by 2 factors: rainfall and rangeland management (Jackson 1962, Rollins 2007). In addition to the long-term decline, Rollins (2007) analyzed Texas Parks and Wildlife Department data and noted bobwhite harvest was high (668,167 birds) in 1982, compared to a much lower harvest (87,570 birds) in 1996. This difference is in keeping with the trend observed by Jackson (1962), who stated bobwhites exhibit a "boom and bust" growth cycle that is correlated directly to annual precipitation averages (Koerth and Guthery 1991, Rollins 1999*a*, Hernández et al. 2005, Tri et al. 2013). In contrast, some observers have reported rapid bobwhite disappearance even during wet years, which they hypothesize is controlled by some factor unrelated to rainfall (Henry et al. 2020).

Landowners and hunters have reported observing bobwhites in summer, but very few during the start of hunting season (Brym et al. 2018). While numerous studies have indicated bobwhite population fluctuations are influenced by factors such as habitat loss, predation, land management, and drought (Koerth and Guthery 1991, Rollins 1999*b*, Brennan et al. 2005, Hernández et al. 2005, Hernández and Peterson 2007, Tri et al. 2013), stakeholders have suggested alternative explanations, including viral pathogens, parasites, decreases in fur buying resulting in an increase in mesomammals, and an increase in raptors (Rollins 1999*a*, Silvy et al. 2000, Urban et al. 2013, Brym et al. 2018). These alternative explanations remain unevaluated, and survival during the late summer to early fall periods has largely not been quantified for this continuous time period. Most published bobwhite survival data focus on the breeding season and winter survival, and this emphasis has left late summer and early fall understudied as a distinct portion of the bobwhite life cycle. The current uncertainty concerning the cause of a possible late summer and early fall disappearance of bobwhites could lead to missteps in how we allocate limited research and management resources (Johnson et al. 2014).

While this perceived incidence of declining bobwhite populations in the Rolling Plains may seem isolated and relatively small compared to the overall bobwhite population decline, landowners situated in a boom-bust cycle are sensitive to any perceived decline. Many stakeholders including landowners, managers, hunters, and natural resources management agencies could benefit from data and supplemental evidence to quantify this anecdotally observed time-specific decrease in bobwhite sightings. Scientists have long sought to explain the overall bobwhite population decline, and if this "October disappearance" were demographically driven, identifying it could inform bobwhite restoration decisions. Landowners also have a vested interest in understanding how a localized population fluctuation could be appropriately managed to inform harvest decisions (Jackson 1962, Brennan et al. 2005, Rollins 2007).

Our goal was to provide stakeholders with data that could explain this localized disappearance and further region-wide research to investigate bobwhite population declines. Using survival data across 4 of 5 consecutive years, we examined weekly survival of bobwhite from 1 August through 30 November. We hypothesized that if this disappearance were demographically driven, weekly survival rates would vary between when stakeholders observed an abundance of bobwhites and when their absence was first noted.

STUDY AREA

Our study area consisted of 7 ranches enrolled in The Quail – Tech Alliance's Anchor Ranch program across 7 counties in the western Rolling Plains of Texas (32°59'37"N, 101°8'41"W). These sites formed a latitudinal gradient across a large swath of the north-to-south extent of the western Rolling Plains. The counties were Collingsworth, Dawson, Dickens, Kent, King, Motley, and Nolan (Figure 1). Total precipitation ranged from 48.34 cm to 80.21 cm across study years in the northernmost study site (Collingsworth County), and the average temperature ranged from 16.5° C to 17.3° C (NOAA National Centers for Environmental Information 2021). In the southern study sites (Dawson, Dickens, Nolan counties) total precipitation ranged from 72.29 cm in the wettest year of the study (2016), to 39.80 cm in the driest year (2017). Average temperatures for these sites ranged from 16.2° C to 18.3° C across study years (NOAA National Centers for Environmental Information 2021).

The landscape varied from tight clays to large areas of sand and sandy loam. Vegetation included little bluestem (*Schizahyrium scoparium*), tobosagrass (*Hilaria mutica*), sand dropseed (*Sporobolus cryptandrus*), threeawns (*Aristida*

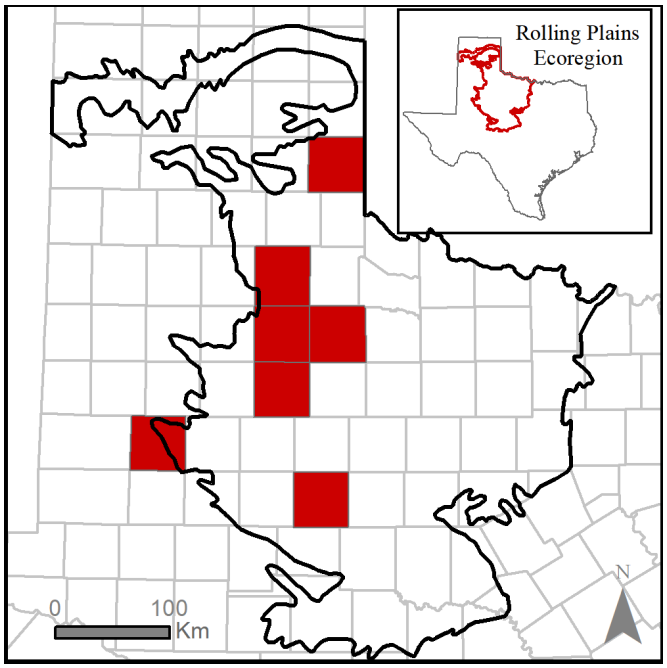

Fig. 1. Counties sampled for northern bobwhite (*Colinus virginianus*; n = 242) late-summer survival study in the Rolling Plains Ecoregion of Texas, USA, 2016, 2017, 2019, 2020.

spp.), annual broomweed (*Amphiachyris dracunculoides*), western ragweed (*Ambrosia psilostachya*), lotebush (*Ziziphus obtusifolia*), yucca (*Yucca glauca*), honey mesquite (*Prosopis glandulosa*), and sand shin oak (*Quercus havardii*).

METHODS

We captured bobwhites between 1 August–1 November in 2016, 2017, 2019, and 2020 with walk-in Stoddard style traps baited with sorghum (*Sorghum bicolor*; Stoddard 1931). Traps were covered with vegetation acquired nearby to provide thermal cover and concealment from predators. Each bobwhite was banded with a numbered Monel butt-end band (National Band and Tag, Newport, KY, USA) and weighed to the nearest gram with a digital scale (Ohaus Corp., Parsippany, NJ, USA). Bobwhites weighing ≥125 g were outfitted with a 6 g pendant-style transmitter with necklace harness (American Wildlife Enterprises, Monticello, FL, USA). Radio-marked bobwhites were tracked ≥1 time/week during 2016 and 2017 and ≥3 times/week in 2019 and 2020 using the homing telemetry method (White and Garrott 1990). During each telemetry session fate (i.e., alive, dead, unknown) was recorded for each bobwhite.

We organized our telemetry data into a weekly survival format covering 1 August–30 November and analyzed it in Program MARK using a model with staggered entry (White and Burnham 1999). To test our hypothesis of decreased weekly survival, we developed 3 sets of candidate models, each of which contained models that allowed survival to vary week to week and others that held weekly survival constant paired with functions that considered survival to be different on a year, ranch, or ranch and year basis using Program MARK. We developed these model suites to assess whether individual sites or years (as a surrogate for difference in rainfall and vegetation, disease outbreak, or increase in parasites or predators) were different than the other years or ranches (Table 1). We censored the first 7 days of each bobwhite's data as a conditioning period to minimize any transmitter-

Table 1. Three suites of models, each ranking 4 *a priori* candidate models used to assess weekly survival rates for northern bobwhite (*Colinus virginianus*) in the Rolling Plains Ecoregion of Texas, USA, 2016, 2017, 2019, 2020. Each suite was used to evaluate the possibility of a localized (Ranch) or time specific (Year) difference in survival (e.g., decrease in survival due to disease, parasite, increased predator abundance, or other unknown factor) or their interaction (Ranchyear). No direct comparisons or inferences were made between models in separate suites.

Suite	Model[a]	AIC_c[b]	ΔAIC_c	w_i	£	K
Ranch	S(t)	945.228	0.00	0.99	1	21
	S(.)	959.612	14.38	<0.01	<0.01	1
	S(g)	959.880	14.65	<0.01	<0.01	7
	S(ranch * t)	1,009.65	64.43	0.000	0	115
Year	S(t)	945.228	0.00	0.99	1	21
	S(.)	959.612	14.38	<0.01	0.00	1
	S(g)	961.764	16.54	0.000	0.00	4
	S(year * t)	963.496	18.27	0.000	0.00	71
Ranchyear	S(t)	982.286	0.00	1.00	1	21
	S(.)	999.774	17.49	0.00	<0.01	1
	S(g)	1,002.250	19.96	0.00	<0.01	10
	S(ranchyear * t)	1,098.150	115.86	0.00	0	158

[a] Ranch = samples grouped by study site, Year = samples grouped by year, Ranchyear= samples completely separated by year and ranch. S(t) = survival allowed to vary over time, S(.) = survival held constant, S(g) = survival different between groups, but constant across time, S(g * t) = survival allowed to vary across group (Ranch, Year, or Ranchyear) and across time.

[b] Abbreviations in column headers: AIC_c = Akaike's Information Criterion adjusted for small sample sizes, ΔAIC_c = differences in AIC_c, w_i = model weights, £ = likelihood, K = number of parameters.

induced survival effects (Burger et al. 1995, Buckley et al. 2015, McLaughlin et al. 2019). Quail hunting season in Texas opens the last weekend of October and closes the last day of February (Texas Parks and Wildlife Department 2022). To our knowledge, none of our tagged bobwhites was harvested during the weeks sampled.

We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c), ΔAIC_c values, and Akaike weights (W_i) to evaluate our models. We classified any model with ΔAIC_c <2 as competitive (Burnham and Anderson 2004). Using the Weekly Survival Rate (WSR) and the associated standard error (SE) and 95% confidence intervals (CIs), we evaluated the change in bobwhite survival over the study period. We considered WSR different if 95% CIs did not overlap.

All in-field methods, animal capture, marking, and handling protocols were approved by Texas Tech Institutional Care and Use Protocol #19007-01.

RESULTS

During 2016, 2017, 2019, and 2020 we placed radio-transmitters on 244 bobwhites on 7 sites across the western Rolling Plains of Texas. Bobwhites ≥125 g represented 92% of total captured birds (Table 2). We estimated weekly survival probabilities of all 244 bobwhites. The model that held survival constant between years while allowing survival to differ between weeks received most of the weight (Table 1). The differences in survival between weeks were not significant except for 1 week in September and another week in November, which were statistically different than each other (but not with any other weeks). Excluding weeks that no bobwhites perished, weekly survival estimates ranged 0.89–0.99 (Figure 2).

DISCUSSION

The goal of our project was to evaluate the role of survival in a perceived "October disappearance" of bobwhite in the Rolling Plains of Texas. Our major findings were that, across 4 different years on 7 different sites in the Rolling Plains of Texas, weekly survival rates were not different; the exception was the fourth week in September, which was different than a week in November. All other 95% CIs overlapped with the CI of the week with the lowest survival estimate. We rejected our hypothesis that any reported disappearance was demographically driven. Our data did not indicate a mass die-off or any rate of mortalities different than normal attrition for bobwhites for the years and sites studied during late summer or early fall (Teinert et al. 2014, Palmer and Sisson 2017, McLaughlin et al. 2019, Wann et al. 2020). We observed no detectible difference between most weeks, nor did we experience any substantial number of unexplained missing bobwhites. These findings illustrate the importance of using demographic data to assess population changes.

It is possible observers perceive a reduction in bobwhite abundance when a reduction has not occurred. Observers develop their perception of bobwhite abundance from a variety of sources, including hearing calling birds and sightings of adults and broods. However, observers can overestimate the abundance of wildlife, especially when using cues such as calls (Brewster et al. 2017). If anecdotal observations of fewer bobwhites during this time period were valid, and since there was no documented population decline, then the most likely explanation is some behavioral response that changes bobwhite detectability or distribution. On several occasions we observed movements from capture sites in August and September to other locations. For example, in 2016 ≥8 birds captured in August made permanent movements out of the study area that were ≥500 m (straight-line distance). Possible behavioral explanations include the "fall shuffle" as well as a change in behavior predicated on the fall raptor migration. Throughout the summer adult bobwhites shepherd their broods across the landscape in search of forage. It is possible there is an abundance of forbs and arthropods near the

Table 2. Northern bobwhite (*Colinus virginianus*; *n* = 244) radio-collared by county and year to measure late-summer survival in the Rolling Plains Ecoregion of Texas, USA, 2016, 2017, 2019, 2020.

County	2016	2017	2019	2020
Collingsworth			38 (97%)[a]	
Dawson	21 (97%)	20 (88%)		
Dickens	25 (82%)	12 (100%)		34 (100%)
Kent	11 (95%)			
King	14 (91%)			
Motley				56 (100%)
Nolan	13 (80%)			
Total	84	32	38	90

[a] Percentages in parentheses denote percentage of total captured bobwhites >125 g and thus radio-collared.

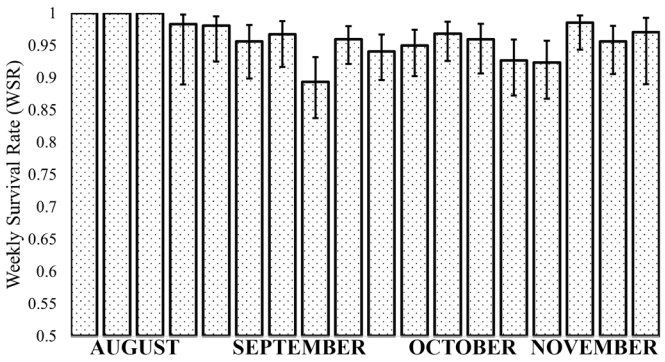

Fig. 2. Weekly survival rates for northern bobwhite (*Colinus virginianus*; *n* = 242), 1 August–30 November in the Rolling Plains Ecoregion of Texas, USA, 2016, 2017, 2019, 2020; y-axis truncated to detail differences in 95% confidence intervals.

roadside (Lee and Power 2013, Rotholz and Mandelik 2013), making broods more conspicuous than during other times of the year. During the early fall, brood groups separate to form coveys (Agee 1957), and it is possible this change in behavior reduces their detection probability between late summer and mid-fall. Additionally, raptor migration occurs in early fall for much of the Rolling Plains of Texas (Allan and Sime 1943). Predator avoidance may also change behavior and may cause bobwhites to select cover, making them less observable. While Turner et al. (2014) did not detect a difference in the amounts of woody cover in the home ranges of South Texas bobwhites before and during raptor migration, they acknowledged the resolution of their woody cover estimates may have been at too coarse a level to detect change.

Disease- and parasite-driven mortality events have been observed in other Galliformes. In 2003, West Nile virus was identified as a contributing cause of a 25% reduction in late summer survival in greater sage-grouse (*Centrocercus urophasianus*) across 4 sites (Naugle et al. 2004, Moynahan et al. 2006). Moynahan et al. (2006) documented a mortality rate 16 times greater than the background mortality rate during late July and mid-August, which the authors attributed to West Nile virus. West Nile virus has been observed in bobwhites in the Rolling Plains of Texas (Urban et al. 2013), but it has not yet been demographically linked to a bobwhite decline. We hypothesize that if a disease-driven "die-off" were occurring between nesting season and hunting season in bobwhites, the evidence would present similarly to Naugle et al. (2004). During 2 of the 4 years of our study we observed a small nonsignificant decrease in weekly survival estimates in either late September or early October that may have been consistent with raptor migration, but not precipitous enough to indicate an acute, mass die-off from either raptors or other causes (e.g., disease event).

We acknowledge sample sizes were unequal between years and ranches; however, our best candidate model pooled these groups. Models including ranch or year had >14 ΔAIC_c, and the beta values for approximately 17% of weeks crossed zero, so we did not consider these models informative and did not report them. We also acknowledge a difference in the length between location attempts in 2016, 2017 and 2019, 2020. Due to project logistics during the first 2 years, we located the birds ≥1 time/week while during subsequent years we located the birds ≥3 times/week. As this difference may have led to scavenged carcasses being incorrectly categorized as mammal depredations, we did not assess cause-specific mortality for this study. While we monitored 7 ranches across the western Rolling Plains for 4 years, there could have been a localized decline on a study site that we did not monitor. We concede parasites or disease may create the possibility of subacute debilitation that, while not detectable over short temporal scales, could be cumulative over time. However, other demographic factors such as reduced nest success and chick survival, which were documented in the areas, are the most likely factors contributing to population declines (Young 2019, Mote 2021).

Our results did not support a decline beyond normal attrition observed in other seasons (Teinert et al. 2014, Palmer and Sisson 2017, McLaughlin et al. 2019, Wann et al. 2020). While little published data exist for the specific time of our study—this temporal range is often divided into breeding and nonbreeding partitions—our mean weekly survival rate (0.96) and derived annual survival rate (0.13) is comparable to rates from studies during different time periods. Wann et al. (2020) worked with the fairly stable and high-density bobwhite populations found on properties managed for bobwhites in the southeastern United States and reported weekly survival probabilities for winter and summer (~0.95) and derived annual survival probabilities (0.11) similar to our study. During winter 2007–2008, Teinert et al. (2014) reported overwinter weekly survival similar to our data, with bobwhites in a single week experiencing a decrease from ~0.95 WSR to ~0.70. The authors attributed this decrease to inclement weather. Bobwhite densities in the Rolling Plains of Texas were relatively high during that year and the following year (Texas Parks and Wildlife Department 2021). While our goal was to merely identify the existence of a decline through demographic data and not its ultimate cause, the absence of an observed decline allows us to infer that no acute mortality event from a factor such as increased depredation or disease occurred during our study. With no steep decline in weekly survival in most weeks of fall, it is possible fall raptor migration may have had a greater effect on bobwhite behavior than it did population demographics. Certainly, migrating raptors use bobwhites as prey; however, our data do not support a raptor-driven population decline during the season and years that we studied. The single week we observed survival rates <90% occurred when migrating raptors move through the Rolling Plains of Texas; however, the impact was neither severe nor long enough to cause a substantial decline, as our data indicate. Finally, the suspected occurrence of an acute mortality event has been used to form hypotheses concerning the influence of disease processes on bobwhite populations in the Rolling Plains of Texas (Urban et al. 2013, Brym et al. 2018). However, our data do not support the occurrence of an acute mortality event during late summer–fall (Figure 2).

MANAGEMENT IMPLICATIONS

Our data provide evidential weight against mass mortality being responsible for decreased bobwhite observations between August and fall, and highlight the importance of using objective, quantifiable analyses to test hypotheses. The juxtaposition of anecdotal observations and a portion of the bobwhite life cycle that is often lost in the division between breeding and nonbreeding seasons have created a situation where managers may incorrectly attribute a perceived reduction in bobwhite abundance to an unknown cause. We encourage researchers to continue monitoring radio-collared bobwhites beyond the typical winter and summer seasons to further our knowledge of bobwhite survival and behavior in seasons not typically measured.

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ANALYSIS OF PREDATOR AVOIDANCE BEHAVIOR IN CALIFORNIA VALLEY QUAIL

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ABSTRACT

Quail populations have been in decline across the United States, primarily due to habitat loss and climate. For remedy, landowners and game managers have attempted to restore populations by releasing captive-reared quail. These releases were largely unsuccessful, presumably due to high predation losses. Recently, there has been an increased interest in quail translocations, which tend to have lower mortality rates than captive-reared bird releases. Translocations are expensive and unpredictable, and require many person-hours; releasing captive-reared quail would be more efficient if the practice were successful. We compared predator avoidance behavior between captive-reared and wild-translocated California quail (*Callipepla californica*) in an aviary using simulated predator attacks (raptorial and mammalian). We recorded predator detection time, antipredator response time, and antipredator response type. Antipredator response type (run, flush, or freeze) frequencies were different, where captive-reared quail ran more frequently than wild-translocated quail when encountering a simulated predator. Predator detection time between captive-reared and wild-translocated quail was not different. However, antipredator response time was quicker for captive-reared quail than wild-translocated quail when subjected to simulated raptorial and mammalian attacks. The differences in antipredator response time and response type may be due to the lack of predator interaction experience of captive-reared birds and offer insight into observed differences in postrelease mortality between captive-reared and wild-trapped quail.

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Key words: California quail, *Callipepla californica,* captive-reared, detection, habitat management, predator avoidance behavior, response, translocation

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HISTOPATHOLOGICAL ANALYSIS OF QUAILS IN THE TRANS-PECOS ECOREGION OF TEXAS

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ABSTRACT

Quail populations in Texas, USA, have declined over the past few decades due primarily to habitat loss. The role that parasites may play in such declines has been a recent topic of concern. To help address this question, we collected 12 scaled quail (*Callipepla squamata*), 8 Gambel's quail (*Callipepla gambelii*), and 3 Montezuma quail (*Cyrtonyx montezumae*) from across the Trans-Pecos ecoregion of Texas via hunter harvest, funnel traps, and night netting. Quail samples were necropsied to determine the abundance of eyeworms (*Oxyspirura petrowi*). Histopathological analyses were conducted on quail eyeballs and periocular tissues to gain information on parasite-related tissue damage and document other pathogenic factors. We calculated mean abundances of *Oxyspirura petrowi* for sampled scaled ($\bar{x}$ = 5.5, standard deviation [SD] = 2.5, $\tilde{x}$ = 3, n = 12), Gambel's ($\bar{x}$ = 6.4, SD = 4.2, $\tilde{x}$ = 1.5, n = 8), and Montezuma quail ($\bar{x}$ = 13, SD = 1.5, $\tilde{x}$ = 13, n = 3). Host tissues exhibited immune responses (i.e., lymphocytic conjunctivitis and plasmacytic adenitis) to *O. petrowi.* The observed immune responses indicated relatively mild irritation within the ocular tissues. It has been speculated that such irritation to ocular tissues could negatively impact quail vision. This potential impact is worth noting because quails rely on keen vision to detect predators. Future research should focus on measuring the effects of *O. petrowi* infections on quail survival.

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Key words: *Callipepla gambelii, Callipepla squamata, Cyrtonyx montezumae,* Gambel's quail, histopathology, Montezuma quail, *Oxyspirura petrowi*, parasite, scaled quail, Texas

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Quail (family Odontophoridae) populations in Texas, USA, have experienced declines over the past several decades, primarily due to habitat loss and fragmentation (Brennan 2007, Hernández et al. 2012). Recently, it has been hypothesized that parasites, specifically the helminth *Oxyspirura petrowi,* may also influence declines (Dunham et al. 2014). *Oxyspirura petrowi* infect the periocular tissues of their definitive hosts (Bruno et al. 2015, Shea et al. 2020). The species is an indirect life cycle endoparasite transmitted to quail when they consume the intermediate host, insects (Kalyanasundaram et al. 2019). Most of the previous research efforts focused on effects that parasites may have on northern bobwhite (*Colinus virginianus*) in the Rolling Plains ecoregion of Texas and southern Texas (Olsen 2014, Bruno et al. 2015, Dunham et al. 2016*b*). Studies conducted in the Rolling Plains ecoregion documented pathological effects of *O. petrowi* on the ocular and periocular tissues of northern bobwhite (Bruno et al. 2015, Dunham et al. 2016*b*). Bruno et al. (2015) found signs of corneal scarring, keratitis, and conjunctivitis caused by *O. petrowi.* Furthermore, Dunham et al. (2016*b*) documented inflammation, fibrosis, and adenitis caused by *O. petrowi.*

While parasites of quail (primarily northern bobwhite) have been studied extensively in other parts of Texas, little research has been conducted on parasites infecting quails in Texas' Trans-Pecos ecoregion. Four species of quail inhabit the Trans-Pecos: scaled quail (*Callipepla squamata*), Gambel's quail (*Callipepla gambelii*), Montezuma quail (*Cyrtonyx montezumae*), and northern bobwhite, though northern bobwhite are less common (Harveson 2007). Landgrebe et al. (2007) and Fedynich et al. (2019) surveyed portions of the Trans-Pecos ecoregion for quail endoparasites. However, both studies focused only on scaled quail and did not survey Gambel's or Montezuma quail. Due to differences in host life histories and habits, it is necessary to collect parasite data on all 3 species of quails (Harveson 2007). Additionally, only one of these studies (Bedford 2015) conducted histopathological analyses to determine whether parasites damaged the tissues that they infected. Histopathology, the study of changes in tissues caused by disease, is necessary to determine various pathogens' effects on their hosts (Stedman 1920, Cameron and Allen 2004). Staining cross-sections of tissues prior to viewing them under microscope, allows researchers to inspect tissue components at a cellular level (Cameron and Allen 2004, Gurcan et al. 2009). Past histopathological studies identified immune responses in the ocular tissues of quail due to *O. petrowi* infections (Bedford 2015, Bruno et al. 2015). Additionally, Bedford (2015) concluded that *O. petrowi* may be damaging their host tissues. Our objectives were 1) to determine whether scaled quail, Gambel's quail, and Montezuma quail were eliciting any immune responses to *O. petrowi,* 2) to determine whether there was a relationship between the level of elicited immune responses and parasite abundance, and 3) to determine whether *O. petrowi* were damaging the tissues that they infected in these quails.

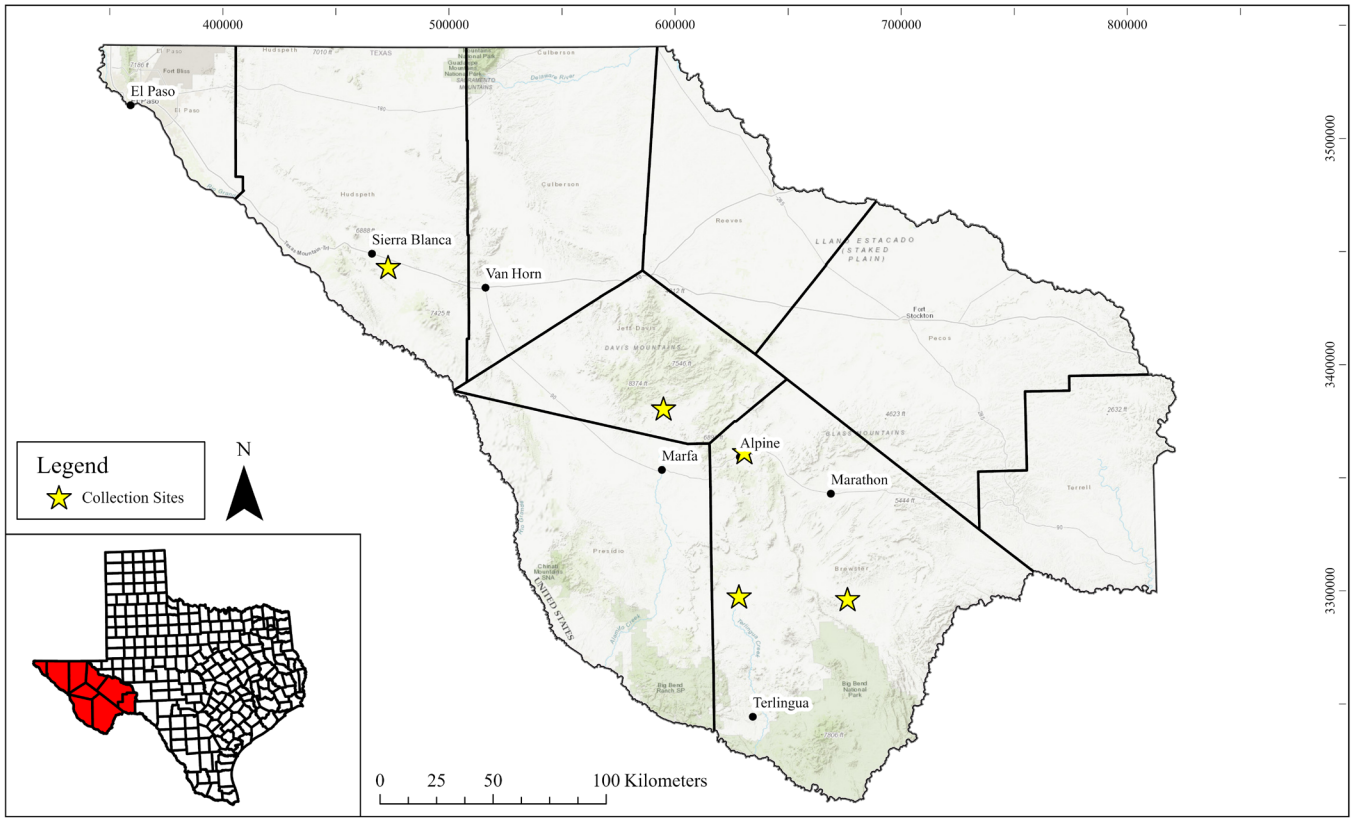

Fig. 1. Collection sites of desert quails that were used to determine the histopathological effects of *Oxyspirura petrowi*, April 2019–July 2020, in the Trans-Pecos ecoregion, Texas, USA.

STUDY AREA

The Trans-Pecos ecoregion of Texas is the westernmost region of the state. It is west of the Pecos River and extends to the Texas-New Mexico state boundary line (Chapman and Bolen 2017). The temperature in the Trans-Pecos averages around 17.3° C (NOAA National Centers for Environmental Information 2019). The region receives as little as 20 cm of rainfall in the west and up to 50 cm in the east (Chapman and Bolen 2017). The elevation ranges from 762 m to 2,667 m (Harveson 2007). Soils are generally basic, consisting of deep sands and gravel mulch (Powell 1998). Chihuahuan Desert scrub, desert grassland, and pine (*Pinus* spp.)–oak (*Quercus* spp.)–juniper (*Juniperus* spp.) woodland vegetation types make up a large portion of the Trans-Pecos (Powell 1998). The flora of the region is diverse, consisting of 2,188 plant species, including creosote bush (*Larrea tridentata*), Mexican pinyon pine (*Pinus cembroides*), teddy-bear cholla (*Cylindropuntia bigelovii*), and buffalograss (*Bouteloua dactyloides;* Powell 1998, 2000).

METHODS

Sample Collection

We collected quail for histopathological analysis from 3 ranches in Brewster County and one in Hudspeth County (Figure 1). We collected quail opportunistically over 2 years via hunter harvest, walk-in funnel traps, and night netting. We collected quail outside of the hunting season under Texas Parks and Wildlife Department (TPWD) scientific permit number SPR-1118-296. Additionally, all research protocols were approved by the Sul Ross State University (SRSU) Institutional Animal Care and Use Committee (SRSU-IACUC 18-0006).

We used standard funnel traps (Stoddard 1931) to trap scaled quail at one collection site near Alpine, Texas, where hunting was not allowed. We placed 3 traps along ranch roads 3 hours before sunset, baited with milo (*Sorghum bicolor*), and checked at sunset. We euthanized quail captured in funnel-traps by cervical dislocation.

We conducted night netting with spotlights, dipnets, and bird dogs to collect scaled quail from a site where firearms were not allowed (Labisky 1968, Greene 2013). We used bird dogs to locate quail during the late afternoon before the night of captures. At night, bird dogs were used to get a general location of the quail, spotlights were used to determine the exact location of quail, and then dipnets were used to capture the quail. We euthanized quail trapped via spotlight and dip netting by cervical dislocation upon collection. We placed all quail into individual zipper bags post-harvest. We recorded collection site and date in the field. We assigned each quail an identification number associated with the collection site and date. We then transported collected quail to the laboratory in a small plastic cooler. We immediately necropsied all quail upon arrival at the laboratory.

Sample Preparation

First, we determined age and sex of the quail. We aged scaled and Gambel's quail from 1 week to 12 weeks using primary feather replacement (Cain and Beasom 1983, Hernández and Guthery 2012). After 12 weeks, scaled and Gambel's quail were classified as a juvenile (J) or adult (A) by inspection of the primary covert feathers (Leopold 1939; Cain and Beasom 1983). We aged Montezuma quail by inspection of the greater primary coverts (Leopold 1939). We sexed all scaled, Gambel's, and Montezuma quail by examination of the gonads.

Eyeworm Extractions

We examined quail for *Oxyspirura petrowi* using a methodology as described by Dunham et al. (2016*a*). We conducted examinations at this stage of the study without the aid of microscope because *O. petrowi* are macroscopic parasites. We lifted each eyelid using forceps to visually inspect for *O. petrowi.* Then, we removed eyelids with surgical scissors. The nictitating membrane was then lifted using a probe to examine for *O. petrowi.* After the initial examination, we removed the upper mandible, and made incisions along the nasal cavities using surgical scissors. Next, the eyeballs and periocular tissues, namely the Harderian gland, naso-lacrimal duct, and conjunctiva, were removed, placed into a petri dish, and examined for *O. petrowi* using curved forceps. At each step of the examination, any *O. petrowi* observed were extracted. Once extracted, we counted *O. petrowi* and preserved them in 10% neutral buffered formalin. We placed eyeballs and periocular tissues in 10% neutral buffered formalin for histopathological analysis.

HISTOPATHOLOGICAL ANALYSES

We submitted fixed eyeballs and periocular tissues to the Texas A&M Veterinary Medicine Diagnostic Laboratory (TVMDL) in College Station, Texas, where Dr. Erin Edwards, a board-certified anatomic pathologist, conducted histopathological analyses. Formalin-fixed tissues were embedded in paraffin, sectioned at a thickness of 4 μm, and stained with modified hematoxylin and eosin using a Tissue-Tek Prisma Plus Automated Slide Stainer (Sakura Finetek USA, Inc., Torrance, CA, USA). Glass slides were digitally scanned with a Hamamatsu NanoZoomer S360 (Hamamatsu Photonics, Hamamatsu City, Shizuoka, Japan) and examined by Dr. Edwards. Immune responses identified within tissues were classified on an ordinal scale as either Minimal, Mild, Moderate, or Severe.

Statistical Analyses

We used Spearman's correlation to determine whether there was a correlation between *O. petrowi* abundances and level of immune response. We used Spearman's correlation because the immune response variable was recorded as an ordinal variable (Laerd Statistics 2015). Spearman's correlation tested the strength and direction of the relationship between *O. petrowi* and immune response (Laerd Statistics 2015).

RESULTS

We examined 12 scaled quail, 8 Gambel's quail, and 3 Montezuma quail for *O. petrowi.* Ten scaled quail, 5 Gambel's quail, and all 3 Montezuma quail were infected with *O. petrowi* (Table 1). We calculated mean abundances of *O. petrowi* for sampled scaled ($\bar{x}$ = 5.5, standard deviation [SD] = 2.5, $\tilde{x}$ = 3, n = 12), Gambel's ($\bar{x}$ = 6.4, SD = 4.2, $\tilde{x}$ = 1.5, n = 8), and Montezuma quail ($\tilde{x}$ = 13, SD = 1.5, $\tilde{x}$ = 13, n = 3).

From histopathological analyses, quail eyes were diagnosed with plasmacytic adenitis and lymphocytic conjunctivitis within the periocular tissues. All individuals experienced multifocal levels of coalescing, chronic, plasmacytic adenitis within the Harderian gland attributed to *O. petrowi* infections (Table 2). Ten samples (4 scaled quail, 4 Gambel's quail, and 2 Montezuma quail) were also diagnosed with chronic lymphocytic conjunctivitis (Table 3). The Spearman's correlation concluded that there was no correlation between *O. petrowi* abundances and plasmacytic adenitis ($r_s(23) = -0.200$, $p = 0.360$). From the Spearman's correlation, we observed no correlation between *O. petrowi* abundances and lymphocytic conjunctivitis ($r_s(10) = 0.116$, $p = 0.597$).

Table 1. Abundances of *Oxyspirura petrowi* in 3 species of quail collected for histopathological analyses, April 2019–July 2020, in the Trans-Pecos ecoregion, Texas, USA.

Individual	Collection date	Quail species	Cohort[a]	*O. petrowi* abundance
1	Apr 2019	Scaled	AM	4
2	Apr 2019	Scaled	AF	2
3	Apr 2019	Scaled	JM	7
4	Apr 2019	Scaled	AF	8
5	Apr 2019	Scaled	JM	0
6	Apr 2019	Scaled	JF	3
7	Apr 2019	Scaled	AM	4
8	May 2019	Scaled	JF	3
9	Mar 2020	Scaled	AF	2
10	Mar 2020	Scaled	JM	32
11	Mar 2020	Scaled	JM	1
12	Apr 2019	Scaled	AM	0
13	May 2019	Gambel's	AM	35
14	May 2019	Gambel's	JM	9
15	May 2019	Gambel's	JM	0
16	Apr 2020	Gambel's	JM	0
17	Apr 2020	Gambel's	JF	2
18	Jun 2020	Gambel's	JF	4
19	Jun 2020	Gambel's	JM	0
20	Jun 2020	Gambel's	JM	1
21	May 2020	Montezuma	AM	15
22	Jul 2020	Montezuma	AF	11
23	Jul 2020	Montezuma	JM	13

[a] A = adult, J = juvenile, M = male, and F = female.

DISCUSSION

Lymphocytic conjunctivitis and plasmacytic adenitis were common diagnoses among our samples. Lymphocytic conjunctivitis is a condition described as an inflammation of the conjunctiva, a thin clear tissue that lies over the white part of the eye and the eyelid, with lymphocytes (Sallinger 2010). Lymphocytes are a type of white blood cell that helps the body determine the appropriate immune response to foreign bodies (Stedman 1920). The other common diagnosis, plasmacytic adenitis, is a condition described as the inflammation of a gland with plasma cells (Stedman 1920, McMillan and Engelbert 1963). In this case, inflammation occurred in the Harderian gland (Peters 2004). Plasma cells are a type of white blood cell that produces antibodies which attack foreign bodies (Stedman 1920). The conjunctiva and Harderian gland are organs that *O. petrowi* infect and therefore it is likely the immune responses were associated with *O. petrowi* infection (Bruno et al. 2015, E. Edwards, TVMDL, personal communication).

One purpose of these histopathological analyses was to determine whether desert quail elicit an immune response to parasite infection. From these analyses, we concluded that all infected samples exhibited some degree of immune response to *O. petrowi.* However, there was no correlation between the level of immune response and *O. petrowi* infection. This may be due, in part, to the small sample size used for the analysis (Israel 1992). As is the case with most studies of wild populations, we were unable to control for potentially influential variables.

For instance, each sampled quail experienced a unique suite of stressors and available resources prior to collection. Stress and nutrient deficiency in avian species can result in decreased immunocompetence, the capacity of an individual to elicit an immune response (Latshaw 1991, Svensson et al. 1998). Immunosuppressed individuals are more prone to parasitic infections (Evering and Weiss 2006). Individual #10 was infected with 35 *O. petrowi* and was diagnosed with minimal plasmacytic adenitis (Table 2). A lower level of immune response and a higher level of parasitic infection could mean that the individual had a dampened immune system before infection. Conversely, Individual #5 did not have any *O. petrowi* present but was diagnosed with severe plasmacytic adenitis (Table 2). The plasma cells, present in greater numbers in the Harderian gland, may be remnants from a previous infection.

It is possible that the immune responses observed during histopathological analyses were residual effects from previous parasitic infections. The duration of an infection may influence the level of immune response exhibited. This may also explain why immune responses were not observed in parasitized individuals. If the hosts were infected recently, it is possible that the body had not exhibited an immune response yet. A study conducted on pen-raised quail in a controlled environment is necessary to isolate the variable of interest.

These histopathological analyses were also used to determine whether *O. petrowi* were damaging tissues. Similar to previous studies, our sample size was small,

Table 2. *Oxyspirura petrowi* abundances and plasmacytic adenitis severity in quails collected, April 2019–July 2020, in the Trans-Pecos ecoregion, Texas, USA.

Individual	Collection date	Quail Species	Cohort[a]	*O. petrowi* abundance	Plasmacytic adenitis[b]
1	Apr 2019	Scaled	AM	4	Mild
2	Apr 2019	Scaled	AF	2	Mild
3	Apr 2019	Scaled	JM	7	Moderate
4	Apr 2019	Scaled	AF	8	Mild
5	Apr 2019	Scaled	JM	0	Severe
6	Apr 2019	Scaled	JF	3	Mild
7	Apr 2019	Scaled	AM	4	Moderate
8	May 2019	Scaled	JF	3	Moderate
9	Mar 2020	Scaled	AF	2	Moderate
10	Mar 2020	Scaled	JM	32	Moderate
11	Mar 2020	Scaled	JM	1	Moderate
12	Apr 2019	Scaled	AM	0	Moderate
13	May 2019	Gambel's	AM	35	Minimal
14	May 2019	Gambel's	JM	9	Moderate
15	May 2019	Gambel's	JM	0	Mild
16	Apr 2020	Gambel's	JM	0	Mild
17	Apr 2020	Gambel's	JF	2	Mild
18	Jun 2020	Gambel's	JF	4	Minimal
19	Jun 2020	Gambel's	JM	0	Mild
20	Jun 2020	Gambel's	JM	1	Mild
21	May 2020	Montezuma	AM	15	Mild
22	Jul 2020	Montezuma	AF	11	Mild
23	Jul 2020	Montezuma	JM	13	Mild

[a] A = adult, J = juvenile, M = male, and F = female.
[b] Categories are based on Texas A&M Veterinary Medicine Diagnostic Laboratory methodology.

Table 3. *Oxyspirura petrowi* abundances and lymphocytic conjunctivitis severity in quails collected, April 2019–July 2020, in the Trans-Pecos ecoregion, Texas, USA.

Individual	Collection date	Quail species	Cohort[a]	*O. petrowi* abundance	Lymphocytic conjunctivitis[b]
2	Apr 2019	Scaled	AF	2	Minimal
4	Apr 2019	Scaled	AF	8	Mild
5	Apr 2019	Scaled	JM	0	Mild
7	Apr 2019	Scaled	AM	4	Minimal
14	May 2019	Gambel's	JM	9	Moderate
15	May 2019	Gambel's	JM	0	Minimal
17	Apr 2020	Gambel's	JF	2	Mild
18	Jun 2020	Gambel's	JF	4	Mild
22	Jul 2020	Montezuma	AF	11	Mild
23	Jul 2020	Montezuma	JM	13	Minimal

[a] A = adult, J = juvenile, M = male, and F = female.
[b] Categories are based on Texas A&M Veterinary Medicine Diagnostic Laboratory methodology.

and inferences should be made cautiously (Bedford 2015, Bruno et al. 2015, Dunham et al. 2016b). Histopathological analyses in northern bobwhite collected from the Rolling Plains ecoregion found signs of keratitis, conjunctivitis, and adenitis caused by *O. petrowi* (Bruno et al. 2015, Dunham et al. 2016b). Inflammatory responses were noted in scaled quail collected in Texas' Rolling Plains ecoregion (Fedynich et al. 2019). Similarly, we documented lymphocytic conjunctivitis and plasmacytic adenitis in a large portion of our samples. Northern bobwhite in the Rolling Plains were also diagnosed with corneal scarring, corneal ulcerative erosions, and lesions within the Harderian gland (Bruno et al. 2015, Dunham et al. 2016b). Bedford (2015) concluded that *O. petrowi* could cause pathological damage to host tissues. In contrast, we found no evidence to suggest that *O. petrowi* damaged host tissues that they infected. The observed immune responses, lymphocytic conjunctivitis, and plasmacytic adenitis do not indicate severe tissue damage but rather a tissue irritation (E. Edwards, TVMDL, personal communication). Additionally, there were no signs of lesions, ulceration, or necrotic tissue commonly found when tissue damage occurs (E. Edwards, TVMDL, personal communication). Instead, our results indicate that only tissue irritation was occurring due to parasitic infection.

MANAGEMENT IMPLICATIONS

We confirmed the presence of quail endoparasites in scaled, Gambel's, and Montezuma quail in the Trans-Pecos ecoregion of Texas and suggest that quail biologists and managers should discuss potential management strategies. The immune responses in quail detected from the histopathological analyses were indicative of tissue irritation and not damage. Moreover, we were unable to relate these immune responses directly to parasitic infection. A study conducted in a controlled, artificial environment would be useful for answering this question. However, without knowing how *O. petrowi* affects quail survival, it will be difficult to determine what, if any, science-based management actions should be taken.

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EXPLORING A PLANT-DIVERSITY HYPOTHESIS TO EXPLAIN HELMINTH PREVALENCE IN NORTHERN BOBWHITE IN TEXAS

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ABSTRACT

Helminths, in particular eyeworms (*Oxyspirura petrowi*), may be a factor influencing northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) populations in Texas, USA. Mean eyeworm prevalence in Texas appears to be greater in the Rolling Plains (55.1%) than the Rio Grande Plains (16.4%), a pattern generally attributed to possible differences in the occurrence of insects, the intermediate hosts of eyeworms. We explored an alternative hypothesis centered on plant diversity. Many plants possess phytochemicals with anthelmintic properties. Because wild animals suffering from parasitic infestations are capable of self-medicating via diet selection, organisms foraging in diverse communities may be expected to possess lower parasite levels. We predicted that plant diversity would be greater and bobwhite diet more diverse in the Rio Grande Plains than the Rolling Plains, which in turn would potentially expose bobwhites to more plants with anthelmintic properties and therefore result in lower parasite prevalence. We conducted a literature review of plant diversity, anthelmintic plants, and bobwhite diet in Texas to explore this hypothesis. Our results indicated that 1) plant diversity was higher (24–96%), 2) the number of anthelmintic plants greater (33%), and 3) bobwhite diet more diverse (120%) in the Rio Grande Plains compared to the Rolling Plains. We documented a mean (± standard error) eyeworm prevalence of 16.4 ± 7.27% in the Rio Grande Plains (n = 4 sites) and 55.05 ± 2.93% in the Rolling Plains (n = 20 sites). The mean cecal-worm prevalence was documented at 74.8 ± 18.21% in the Rio Grande Plains (n = 5 sites) and 79.79 ± 2.12% in the Rolling Plains (n = 19 sites). Regarding plant diversity, the Rio Grande Plains contained more potential anthelmintic plants (n = 96 species) than the Rolling Plains (n = 72 species). In cross-referencing these plants with the bobwhite diet, we found that 23 plants with possible anthelmintic properties had been documented in the bobwhite diet in the Rio Grande Plains, whereas only 17 such plants were documented in the bobwhite diet in the Rolling Plains. Our study provides circumstantial evidence for the plant-diversity hypothesis and warrants experimental testing.

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Key words: anthelmintic plants, cecal worms, *Colinus virginianus,* eyeworms, northern bobwhite, nutritional wisdom, plant diversity, self-medication

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EXPLORING THE RELATIONSHIPS BETWEEN SOUTH TEXAS NORTHERN BOBWHITE POPULATIONS AND CECAL WORMS VIA SYSTEM DYNAMICS

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ABSTRACT

Community ecology historically focused on plants and free-living organisms; however, problems such as defining habitat boundaries and obtaining adequate sample sizes arise when evaluating such communities. The unique nature of host-helminth systems allows parasite community ecologists to avoid these problems when testing ecological hypotheses. Unlike free-living communities that have artificially constructed boundaries, parasite communities have well-defined unambiguous boundaries within host individuals. Due to the inherently complex and dynamic nature of ecological systems, traditional experimental methods often require expensive, long-term trials beyond investigators' time and resource budgets. Conversely, a system dynamics approach facilitates learning about such systems via simulation of ecosystem processes integrated with historical data (both quantitative and qualitative). Relatively few studies focus on parasites in South Texas, USA, although research on avian host-parasite systems has shown that parasites can potentially regulate host populations. The northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) is a game species of ecological, economic, cultural, and recreational importance in Texas that has been experiencing a long-term, widespread decline. To holistically examine the bobwhite-helminth system in South Texas, we created a system dynamics model capturing the feedback relationships between a South Texas bobwhite population, a grasshopper (family Acrididae) population, and the corresponding cecal worm (*Aulonocephalus pennula*) populations on a hypothetical 1,000-acre ranch in South Texas. The model structure, constructed in Vensim® PLE 7.2 software (Ventana Systems, Inc.), integrates the hypothesized biotic and abiotic drivers (precipitation, parasite load, insect abundance, and quail density) unique to the host-helminth system over 7 years (2012–2019). Our specific objectives were to 1) develop a working baseline model to replicate the synergistic population dynamics among bobwhite, grasshopper, and cecal worm populations and then 2) test hypotheses about each population's boom-and-bust cycles resulting from environmental stressors (e.g., drought). Applications of the model can provide landowners and natural resource managers with a better understanding of the complex dynamics occurring among bobwhite, grasshopper, and cecal worm populations in South Texas.

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Key words: *Aulonocephalus pennula*, cecal worm, *Colinus virginianus*, helminths, northern bobwhite, simulation model, Vensim

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APPLYING MULTISTATE MARK-RECAPTURE MODELS WITH STATE UNCERTAINTY TO ESTIMATE SURVIVAL AND REPRODUCTION OF QUAIL

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ABSTRACT

Obtaining unbiased estimates of vital rates and understanding how vital rates change in response to environmental stimuli are a continual pursuit of ecologists. Multistate mark-recapture (MSMR) models provide a flexible framework for evaluating dependent vital rates in a comprehensive analysis. For example, a bird must remain alive during breeding season to initiate a nest (i.e., transition from a nonbreeding to a breeding state); thus, the probability that a bird initiates a nest is dependent on the probability that it is still alive. Traditional MSMR models allow only for the estimation of survival, detection, and state transition parameters and depend on the assumption that observers can correctly classify the true state of the animal without error. If the potential for state misclassification exists, incorporating parameters to estimate state uncertainty will reduce biases in the biological parameters of interest. I applied an MSMR model with state uncertainty (MSMR-SU) to estimate short-term survival, dispersal, and reproduction in translocated scaled quail (*Callipepla squamata*) reintroduced to a large landscape in West Texas, USA. I tested for the effects of release treatment, source population, age, release location, and year on demographic parameters (e.g., survival, dispersal, nest initiation, renesting rate, and nest success). I demonstrated a novel method of estimating nest initiation and renesting rate for avian species using a MSMR-SU model. MSMR-SU models provide a flexible and rigorous approach for evaluating effects of variables on demographic parameters for quail and other species.

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Key words: *Callipepla squamata*, hidden Markov, multistate mark-recapture, reproduction, scaled quail, state uncertainty, survival, translocation

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DETECTION RATES OF NORTHERN BOBWHITE COVEYS USING A SMALL UNMANNED AERIAL SYSTEM-MOUNTED THERMAL CAMERA

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ABSTRACT

The northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) requires intensive monitoring to evaluate management efforts and determine harvest rates. However, traditional monitoring techniques (e.g., covey-call surveys) are labor-intensive and imprecise. Small unmanned aerial systems (sUASs) mounted with thermal cameras have demonstrated promise for monitoring multiple avian species and could provide a less intensive and more effective approach to monitoring bobwhite coveys, assuming coveys produce a recognizable heat signature. To assess sUAS monitoring, we evaluated the influence of bobwhite covey size (3, 6, and 12) and cover type (grass, shrub, and forest) on covey detectability by a sUAS equipped with a thermal camera. We hypothesized that forest would have the lowest covey detection due to trees obstructing detection of the thermal signature and that larger covey size would improve covey detection due to the formation of larger, more visibly distinct thermal signatures. We placed groups of known-size, pen-reared bobwhites in steel mesh cages (3, 6, and 12 individuals/cage) in 3 vegetation types (grass, shrub, and forest) among predetermined locations on a private farm in Clay County, Mississippi, USA (3 replicates, 27 total cages). At civil twilight on 5 March 2020, the sUAS flew a systematic route over the cage area at 30 m above ground level, capturing thermal infrared photographs every 5 seconds. To assess detection, we distributed 57 photographs to 31 volunteers and asked them to assign a binary value for detection (1, 0) regarding covey presence in each photograph. Overall true positive rate was 0.551 but improved with increasing covey size. By vegetation type, simulated coveys in grass had the lowest true positive rate by photograph (0.403), followed by forest (0.562) and shrub (0.605). Results indicate that sUASs and thermal camera technology could be a viable method for surveying intact bobwhite coveys, especially if detection of smaller groups and those in denser vegetation improves. As this technology advances, we recommend that future research focus on evaluating the efficacy of this novel methodology through assessing the influence of weather conditions, camera specifications, flight speed, and altitude, as well as assessing machine learning for processing photos.

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Key words: Black Belt Prairie, *Colinus virginianus*, far infrared, northern bobwhite, small unmanned aerial system, sUAS, thermal imagery

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RELATIONSHIPS BETWEEN METEOROLOGICAL AND OTHER VARIABLES AND BOBWHITE SPRING CALL COUNTS

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ABSTRACT

Accurate assessment of quail population trends is critical to the success of future conservation efforts. Financial considerations and time constraints often limit population trend estimates to indices, the most common of which are spring call counts and autumn covey counts. While all indices have limitations and caveats, spring call count data specifically possess variability that makes them ill-suited for detecting fine-scale trends. However, because spring call counts record calling males and are relatively easy to conduct, they are assumed to represent an index of breeding potential and produce the most data per unit cost. Here, we examine their variability, comparing the number of male northern bobwhites (*Colinus virginianus*; hereafter, bobwhite) calling and weather measurements recorded during >4,000 spring call counts conducted May–July 2014–2017. The number of male bobwhites recorded per call count decreased >2 hours after sunrise, as ambient temperatures increased, but increased with relative humidity. An increase in ambient noise was associated with recording fewer male bobwhites. There was no correlation with either wind speed <16 km/hour for 3 of 4 years, or with the Palmer Drought Severity Index. Comparing these results with other spring call counts in the literature highlights inconsistency in spring call count timing, and discrepancies between call count protocols and weather conditions that affect detection probability. We suggest incorporating these results into future call counts to more accurately assess bobwhite population trends.

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Key words: abundance, climate, *Colinus virginianus*, drought, meteorology, northern bobwhite, quail, spring call counts, Texas, variability

Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) population numbers display high annual variability (Sauer et al. 2020), and are difficult to predict (Anderson 2001, 2003; Engeman 2003, 2005). As a result, wildlife managers, researchers, and conservationists need a practical, accurate, and reliable method to assess annual bobwhite population trends. Historically, indices of bobwhite population abundance such as spring call counts (Bennitt 1943) have been used to assess bobwhite population trends because they are more practical and require fewer resources than other methods (Engeman 2003). However, many underlying assumptions and variable factors affect the reliability of spring call counts (Anderson 2001, 2003). Standardizing location, timing, and conditions of spring call counts can produce data more suited for comparison (Engeman 2003, 2005). Weather conditions also influence the probability of detecting bobwhites during spring call counts (Anderson 2001), but this influence is poorly understood. To date, few published studies have critically examined these relationships. Thus, the goal of this study was to examine the relationships between spring call count results and meteorological, temporal, and other variables.

Northern bobwhite spring call counts have been used to assess bobwhite population trends to advise management, research, and conservation (Stoddard 1931, Bennitt 1951, Ellis et al. 1972, Burger et al. 2006, Reyna et al. 2012). The calls recorded are emitted by male bobwhites only, primarily during nesting, mating, and brooding season (Stoddard 1931, Bennitt 1951, Rosene 1957, Kabat and Thompson 1963, Ellis et al. 1972). Spring call counts are assumed to have a linear, positive relationship with bobwhite population density (Gibbs 2000). However, many factors influence the probability of detecting a calling bird (Nichols et al. 2000, Farnsworth et al. 2002, Royle and Nichols 2003, Mackenzie et al. 2005).

To reduce variation, some aspects of a spring call count are standardized (Robbins et al. 1986). These include time of day, time of year, duration of call counts, and limitations

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of weather conditions under which call counts may be conducted. Additionally, spring call counts are typically recorded at predetermined points or along a predetermined route. The observer records all male bobwhites heard calling for a set amount of time, often 2–8 minutes (Rosene 1957, Kabat and Thompson 1963, Ellis et al. 1972, Curtis et al. 1989), before moving to the next point. Spring call counts are timed to coincide with the local breeding season, with daily start times ranging from 45 minutes before sunrise (Hansen and Guthery 2001) to 25–30 minutes after sunrise (Robel et al. 1969), and listening period durations of 1.5–3 hours (Bennitt 1951, Rosene 1957, Kabat and Thompson 1963).

Hansen and Guthery (2001) recommended bobwhite spring call counts be performed at or near the peak of calling activity. The date of peak spring calls varies spatially and temporally, but generally occurs from the last week in May through the second week in July (Burger et al. 2006). For example, spring calling peaked 20 June–20 July in Missouri, USA (36.5°N–40.5°N; Bennitt 1951), 15 June–17 July in Kansas, USA (36.56°N–39.07°N; Robel et al. 1969), mid-late May with secondary, smaller peaks mid-June–late July in Georgia, USA and northern Florida, USA (30.5°N–32.7°N; Terhune et al. 2006), and 19 June in Oklahoma, USA (36.0°N–36.2°N; Hansen and Guthery 2001).

While more difficult to control for, weather conditions can influence call detection probability (Anderson 2001). However, these influences are not always consistent (Table 1). Although temperature varies spatially and temporally (Tomecek et al. 2017), it is consistently negatively correlated with the number of cock calls recorded in all but one year of one study (Elder 1956; Table 1). Similarly, wind speed was negatively correlated with the number of male bobwhites recorded (Elder 1956, Robel et al. 1969, Hansen and Guthery 2001) except when the observer alternated between "upwind" and "downwind" to determine mean audibility distances (Bennitt 1951). Additionally, drought conditions may reduce nesting and brood rearing in bobwhites (Stanford 1972). As a result, the Palmer Drought Severity Index (PDSI; Palmer 1965) has been correlated with a decrease in male calling (Bridges et al. 2001, Reyna et al. 2012). Though there are valid criticisms of the PDSI (Alley 1984, Dai et al. 2004), it remains one of the most prominent drought indices used, particularly for the central United States (Dai et al. 2004).

Protocol from Burger et al. (2006) proscribes data collection when cloud cover exceeds 75%, presumably due to decreased calling activity. However, separate from light intensity (Robel et al. 1969, Hansen and Guthery 2001), the relationship between cloud cover and bobwhite calling activity is either not significant (Bennitt 1951, Elder 1956) or equivocal at best, with trends inconsistent from year to year (Hansen and Guthery 2001). In South Texas, USA, calling activity increased following summer rains, but conducting call counts during rain is not recommended, presumably due to noise considerations (Lehmann 1984).

Although spring call counts are the most common index of bobwhite relative abundance, few studies have analyzed the relationship between meteorological, temporal, and other variables and spring call counts. Of 4 previous studies (Table 1), only Robel et al. (1969) collected weather data at each call count location. Other studies recorded weather data hourly or at the start and end of each call count route, which may be the reason for some of the inconsistencies in determining

Table 1. Correlations between meteorological conditions and number of male bobwhite (*Colinus virginianus*) calls recorded during spring call counts by previous studies. + = positive correlation; - = negative correlation; 0 = no correlation.

Factor	Measured	Correlation(s)	Reference
Temperature	Hourly	-	(Bennitt 1951)
	Start and end	+/-[a]	(Elder 1956)
	Each stop	-	(Robel et al. 1969)
	Hourly	-	(Hansen and Guthery 2001)
Wind speed	Hourly	0	(Bennitt 1951)
	Start and end	-	(Elder 1956)
	Each stop	-	(Robel et al. 1969)
	Hourly	-	(Hansen and Guthery 2001)
Humidity (%)	Hourly	0	(Bennitt 1951)
	Start and end	-/+	(Elder 1956)
	Each stop	-[b]	(Robel et al. 1969)
	Hourly	+	(Hansen and Guthery 2001)
Barometer	Hourly	0	(Bennitt 1951)
Cloud cover	Hourly	0	(Bennitt 1951)
	Hourly	-/0[c]	(Hansen and Guthery 2001)
Light intensity	Each stop	0	(Robel et al. 1969)
	Hourly	-	(Hansen and Guthery 2001)

[a] 1954–1955
[b] Correlation recorded only outside of peak calling time
[c] 1998–1999

the relationship between the number of male bobwhites recorded and weather (Table 1). Thus, the objectives of this study were to 1) record the number of bobwhites calling along with meteorological, temporal, and other variables during >4,000 spring call counts to determine how the number of bobwhite calls recorded varies with the weather, time of day, and ambient noise; and 2) improve protocols for future spring call counts.

STUDY AREA

Northern bobwhite spring call counts were conducted in Clay and Montague counties (Figure 1) in the Central Great Plains Ecoregion of North Texas (Griffith et al. 2004). Vegetation was primarily mesquite-lotebush (*Prosopis* spp.-*Ziziphus obtusifolia*) to the west, and post oak (*Quercus stellata*) woods, forest, and grassland mosaic to the east with portions of post oak parks, mesquite brushland, cropland, and cottonwood-hackberry (*Populus deltoides*-*Celtis* spp.) forest (McMahan et al. 1984). In 2016, land use in the 2 counties was approximately 72.2% rangeland, 11.6% forest, 10.6% cropland, hay, and pasture, and 3.5% urban or otherwise developed (Jin et al. 2019). In addition to access granted from private ranches, the 2 counties also had approximately 3,700 km of publicly accessible roads (Texas Department of Transportation 2015) from which to collect data.

METHODS

Bobwhite calls and meteorological, temporal, and other variables were recorded at preestablished data collection points (DCPs) set approximately 1.6 km apart (Figure 1; Whitt and Reyna 2017). All data collection points for this study were located 33.42°N–34.15°N. Since calling begins earlier in southern U.S. latitudes (Rosene 1957, Terhune et al. 2006), we began spring call counts in mid-May, a week earlier than recommended by Burger et al. (2006). Counts were generally performed Tuesday–Friday and continued until all DCPs were visited. Data were collected 16 May–24 June 2014 and 19 May–30 June 2015 in Clay County, and 16 May–1 July 2016 and 16 May–6 July 2017 in Clay and Montague counties. More data collection time was required 2015–2017 due to multiple rain delays and flooding. Calls were recorded within the first 3 hours after sunrise. It was not feasible to visit all points within the 8-week study period by recording only 1 hour/day as recommended by Kabat and Thompson (1963) and Burger et al. (2006). The latter recommendation was based on results from Hansen and Guthery (2001), who noted that peak time of calling occurred 30–75 minutes after sunrise. However, they also noted that while extending the listening period to 3 hours resulted in undercounts for high-density sites, it had no significant effect on presence and absence detection in low-density sites. Bennitt (1951) also measured the highest activity in the first hour after sunrise, but calling activity decreased significantly only after hour 3.

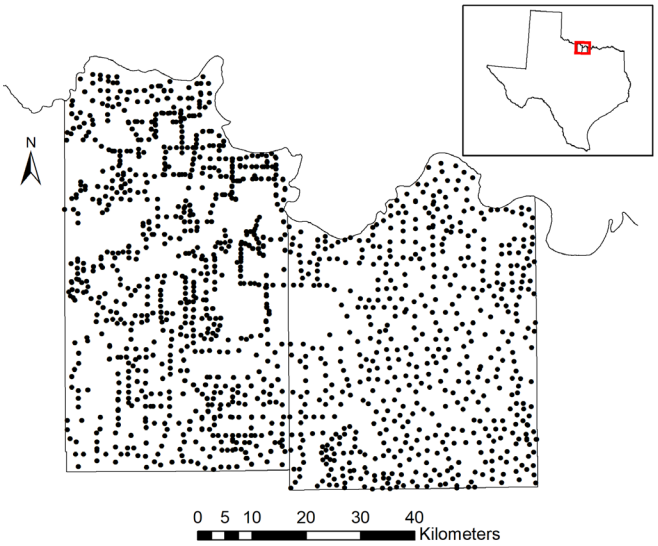

Fig. 1. Data collection points (black dots; 1,213 points) for spring call counts for northern bobwhite (*Colinus virginianus*) in (left) Clay County and (right) Montague County, Texas, USA, 2014–2017. Inset shows extent of main map.

Call counts were conducted by trained field technicians. Technicians lacking experience trained with experienced observers in the field for ≥1 day. Technicians were assigned a predetermined region each day and provided with a pen, clip board with data collection sheets, hand-held global positioning system (GPSMAP® 64st; Garmin Ltd., Olathe, KS, USA) with coordinates of each DCP preloaded, and pocket weather meter (Kestrel 3500, Nielsen-Kellerman, Boothwyn, PA, USA).

To reliably detect trends, point counts require an estimate of detection probability (Anderson 2003, Engeman 2003, Johnson 2008). Counts are often performed in conjunction with distance sampling theory to produce this estimate. However, assumptions of distance sampling are regularly violated. For example, not all occurrences at the point are detected (Alldredge et al. 2008, Applegate et al. 2011, Murray et al. 2011). During spring call counts, only males are recorded, so sex ratios remain unknown (Applegate et al. 2011). Even experienced observers have difficulty assigning a correct distance to observations (Alldredge et al. 2008, Murray et al. 2011), a violation that could be exacerbated with technicians unfamiliar with the study area (Wellendorf and Palmer 2005). Multiple observers can also be used to estimate detection probability (Rosenstock et al. 2002, Thomas et al. 2010). Data for unreconciled double observer counts (Riddle et al. 2010*a*) were collected either by technicians during their second day of training, or when the number of technicians exceeded the number of available vehicles.

Beginning at sunrise, technicians recorded approximate distance and direction of each male bobwhite heard during a 5-minute listening period before continuing to the next DCP. Technicians were instructed to avoid nearby obstructions and to move about 20 m from any vehicle before recording to reduce interference from the vehicle (Rosene 1957). Immediately

before or after the call count, local weather conditions were recorded at each DCP using the pocket weather meter, including temperature, dewpoint, relative humidity, wind speed, and barometric pressure. Cloud cover percentage was estimated visually (Wellendorf and Palmer 2005). Counts were discontinued when local wind speeds exceeded 16 km/hour (Hansen and Guthery 2001). Call counts were conducted regardless of cloud cover, but call counts were not conducted during rainfall.

To standardize counts for statistical analysis, calendar dates were converted to ordinal dates. Local sunrise times could vary by as much as 5 minutes between 2 DCPs 1.6 km apart. For purpose of analysis, "sunrise" was standardized to sunrise time at the Clay County Courthouse in Henrietta for Clay County DCPs and at the Montague County Courthouse in Montague for Montague County DCPs. Count times were converted to the number of minutes after sunrise that the 5-minute data collection period began.

Ambient sound can also affect point call counts (Simons et al. 2009). Accordingly, technicians were equipped with a hand-held sound meter (SD-200, 3M Co., Two Harbors, MN, USA), mounted on a 152-cm tripod adjusted to the technician's head height, beginning in May 2017. Sound levels were measured during the entire 5-minute call count. The sound meter could measure sound levels either A- or C-weighted, but minimum, maximum, and average sound levels were recorded in dB(A) on the data sheet since A-weighted is considered a better approximation of loudness levels for human hearing (Fletcher and Munson 1933).

For all months with >50 data points, monthly call count medians were compared with Palmer Drought Severity Index (PDSI; Palmer 1965) values for the Clay County region (NOAA National Centers for Environmental Information 2018). The PDSI uses temperature and precipitation data to estimate relative dryness, ranging from -4 (extreme drought) to +4 (extremely moist).

Statistical analyses were performed using SPSS (version 27.0.0.0, IBM, Endicott, NY, USA). Data were not normally distributed and best fitted an over-dispersed Poisson distribution. Transformation of count data is not recommended in most cases and can result in inconsistent coefficient estimates (O'Hara and Kotze 2010, St-Pierre et al. 2018). Correlations between the independent variables and the number of male bobwhites recorded per DCP were first examined using Spearman's rank correlation (Zar 1996). We used negative binomial regression with the log-link function to generate linear models (Hilbe 2011). Fit was compared using the Akaike Information Criterion (AIC). Model coefficient significance was evaluated using the t-statistic (within model) or Wald test (between models).The most important model components were used to generate regression models by year. Models were fitted using the least squares method. Model types (linear, quadratic, cubic) were chosen based on coefficient significance. Since data were not collected in Montague County 2014–2015, statistical comparisons between years were made using Clay County data only. We grouped call counts into 30-minute groups based on time since sunrise to aid in evaluating resource allocation decisions though this grouping was not biologically relevant. Groups were compared using Mann–Whitney *U* (2 groups) or Kruskal-Wallis (>2 groups) tests with Bonferroni correction (Cabin and Mitchell 2000). Decisions regarding negative binomial model fit were made at $\Delta AIC > 2.5$ for sample sizes >246 (Hilbe 2011). Statistical decisions were made at $\alpha = 0.05$.

Detection probability (p_d) analysis was performed using the unreconciled double observer method (Riddle et al. 2010*a*). Analysis was performed with Program PRESENCE, version 2.12.9 (U.S. Geological Survey, Patuxent, MD, USA), assuming variable site abundance and detection probability.

RESULTS

Of 4,497 spring call counts conducted at 1,213 DCPs in Clay (2014–2017) and Montague (2016–2017) counties, Texas, 4,438 were included in this study, with 59 censored for missing or illegible data. Median number of male bobwhites per DCP was 2 (minimum [min] = 0, interquartile range [IQR] = 2–4, maximum [max] = 16) with data from both counties combined. Median number of males recorded per DCP for Clay County was 2 (min = 0, IQR = 3–5, max = 16) and 0 (min = 0, IQR = 0–1, max = 14) for Montague County (Figure 2), across all years.

By year, median number of male bobwhites recorded per DCP in Clay County was 2 (min = 0, IQR = 0–4, max = 11) in 2014, 3 (min = 0, IQR = 1–5, max = 16) in 2015, 3 (min = 1, IQR = 0–5, max = 16) in 2016, and 3 (min = 0, IQR = 0–5, max = 15) in 2017 (Figure 3a).

Median number of male bobwhites recorded per DCP in Montague County was 0 (min = 0, IQR = 0–1, max = 11) in 2016, and 0 (min = 0, IQR = 0–1, max = 14) in 2017 (Figure 3b).

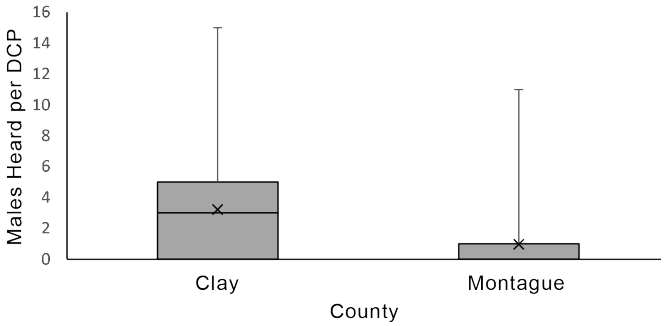

Fig. 2. Box-and-whiskers plot of male bobwhite (*Colinus virginianus*) calls recorded at data collection points during spring call counts in Clay and Montague counties, Texas, USA, 2014–2017. Crosses indicate means.

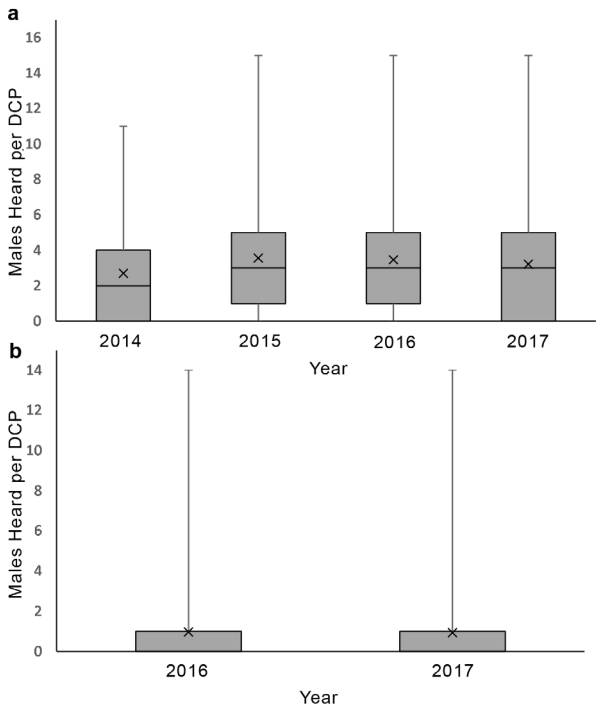

Fig. 3. Box-and-whiskers plots of male bobwhite (*Colinus virginianus*) calls recorded at data collection points during spring call counts in a) Clay County, Texas, USA, 2014–2017, and b) Montague County, Texas, 2016–2017. Crosses indicate means.

Spearman's Rank Correlations

Relative humidity (ρ =0.275, $p < 0.001$, $N = 3{,}767$) and temperature (ρ =-0.252, $P < 0.001$, $N = 3{,}821$) had the highest correlation with the number of males calling during spring call counts, with data from all years and DCPs combined (Table 2). There were smaller negative correlations with time since sunrise (ρ = -0.200, $P < 0.001$, $N = 4{,}211$), and dewpoint temperature (ρ = -0.119, $P < 0.001$ $N = 3{,}643$), and a small positive correlation with cloud cover (ρ = 0.174, $P < 0.001$ $N = 3{,}638$). Of the 4,438 datasheets analyzed, approximately 860 had ≥1 weather variable missing for various reasons (e.g., weather meter battery failure); thus, n values differ among analyzed factors.

Correlations between temperature, relative humidity, cloud cover, and time of day with number of male bobwhites recorded were consistent in direction (positive or negative) from year to year, but varied in magnitude (Table 2). Cloud cover was positively correlated with number of male bobwhites recorded 2015–2017. There was no correlation between barometric pressure and number of male bobwhites recorded per DCP in 2014 ($P = 0.133$), but there were positive correlations for 2015–2017 (ρ = 0.075, $P = 0.031$; ρ = 0.064, $P = 0.020$; ρ = 0.120, $P = 0.001$, respectively). There was no correlation with wind speed and number of male bobwhites recorded in 3 of 4 years, and a negative correlation (ρ = -0.079, $P = 0.024$) in 2015.

Table 2. Spearman's rank correlation coefficient (ρ) for number of male northern bobwhites (*Colinus virginianus*) heard by year vs. recorded temporal and meteorological variables in Clay and Montague counties, Texas, USA, May–July 2014–2017. Date = Julian date; Time = number of minutes after estimated sunrise; Temp = temperature (ºC); RH = relative humidity (%), DP = dewpoint temperature (ºC); Wind = wind speed (m/second); BP = barometric pressure (mbar); Cloud = cloud cover (%).

Year		Date	Time	Temp	RH	DP	Wind	BP	Cloud
2014[a]	ρ	0.031	-0.169	-0.259	0.204	-	-0.044	-0.157	-
	p	0.406	<0.001	0.001	0.028	-	0.431	0.133	-
	N	702	581	172	116	0	321	93	0
2015	ρ	-0.022	-0.299	-0.232	0.216	-0.112	-0.079	0.075	0.132
	p	0.549	<0.001	<0.001	<0.001	0.001	0.024	0.031	<0.001
	N	760	825	820	820	819	821	820	815
2016	ρ	-0.270	-0.275	-0.378	0.283	-0.231	-0.023	0.064	0.294
	p	<0.001	<0.001	<0.001	<0.001	<0.001	0.397	0.020	<0.001
	N	1337	1332	1330	1329	1328	1329	1325	1316
2017	ρ	0.079	-0.207	-0.131	0.258	-0.026	-0.041	0.120	0.107
	p	0.002	<0.001	<0.001	<0.001	0.307	0.110	<0.001	<0.001
	N	1553	1543	1499	1499	1496	1508	1459	1507
All years	ρ	-0.093	-0.200	-0.252	0.275	-0.119	-0.036	-0.111	0.174
	p	<0.001	<0.001	<0.001	<0.001	<0.001	0.25	<0.001	<0.001
	N	4352	4281	3821	3767	3643	3979	3697	3638

[a] Dewpoint and cloud cover not recorded in 2014

Regression Models

The distribution parameter for negative binomial regression was 1.51. Log relative humidity (B = 0.003, $P < 0.001$), time (in minutes) since sunrise (B = -0.005, $P < 0.001$), and log temperature (B = -0.071, $P < 0.001$) had the best single-factor fit with the number of males calling during spring call counts when data from all years were combined (Table 3). Other significant factors were ordinal date (B = -0.007, $P < 0.001$), wind speed in m/second (B = -0.061, $P = 0.004$), and barometric pressure in mbar (B = -0.022, $P < 0.001$). Independent variables producing the most relevant multifactor models were, in decreasing order of explanatory power, relative humidity, temperature, wind speed, time since sunrise, and barometric pressure. The 5-factor model did not improve upon the 4-factor model.

When call count data were separated by year, relationships between the numbers of male bobwhites recorded and log temperature, log relative humidity, log time since sunrise, log ordinal date, and log wind speed were not different in 3 of the 4 study years (Table 4). The 95% confidence interval [CI] for slope included zero for relative humidity in 2014, temperature in 2016, and time since sunrise in 2017. The 95% CIs for slope for ordinal date and wind speed included zero in years 2014–2016 and were negative in 2017.

There was no difference in the relationship between log relative humidity and number of male bobwhites recorded in 2014, 2016, and 2017, but the slope of increase in number of male bobwhites heard at higher relative humidity (Figure 4) was lower in 2015 (Wald $\chi^2 = 15.4$, $P < 0.001$). The number of male bobwhites heard declined more as temperature increased in 2014 than in the other 3 years (Figure 5), and less in 2015 (Wald $\chi^2 = 13.4, 26.7$, $P < 0.001$). All 4 years showed a decline in number of male bobwhites heard over 3 hours (Figure 6), but the curve for 2015 was steeper (Wald $\chi^2 = 41.5$, $P < 0.001$) than in 2014, 2016, and 2017.

Palmer Drought Severity Index

A nearly 5-year North Texas drought ended early in 2015 (Shaw 2015, National Weather Service Forecast Office 2018). There was a small correlation between number of male bobwhites recorded and PDSI for Clay County 2014–2017 ($\rho = 0.087$, $P < 0.001$), but this correlation was not present ($P =$

Table 3. Selected log link (y = a + b*log[x]) negative binomial regression models for number of male northern bobwhites (*Colinus virginianus*) heard by year vs. temporal and weather variables recorded May–July 2014–2017 in Clay and Montague counties, Texas, USA. All significant single-factor models are shown along with the best-fitting 2,-, 3-, 4-, and 5-factor models. A lower ΔAkaike Information Criterion (ΔAIC) indicates a better model fit. Distribution parameter = 1.51; CI = confidence interval; RH = relative humidity (%); Time = number of minutes after sunrise; Temp = temperature (ºC); Date = ordinal date; ; Wind = wind speed (m/second); Cloud = cloud cover (%); BP = barometric pressure (mbar).

Model	B	95% CI	*P*	K	AIC	ΔAIC
RH	0.033	0.005	<0.001	3	15371.668	80.057
Time	-0.005	0.001	<0.001	3	15396.806	105.195
Temp	-0.071	0.013	<0.001	3	15419.594	127.983
Date	-0.007	0.003	<0.001	3	15519.887	228.276
Wind	-0.061	0.04	0.004	3	15529.537	237.926
Cloud	0.005	0.001	<0.001	3	15530.118	238.507
BP	0.022	0.09	<0.001	3	15530.989	239.378
Intercept only	0.957	0.45	<0.001	2	15535.875	244.264
Temp	-0.041	0.015	<0.001	4	15340.832	49.221
RH	0.026	0.006	<0.001			
Temp	-0.027	0.006	<0.001	5	15326.669	35.058
RH	-0.042	0.014	<0.001			
Time	-0.085	0.04	<0.001			
RH	0.022	0.005	<0.001	6	15292.915	1.304
Temp	-0.029	0.007	<0.001			
Time	-0.024	0.011	<0.001			
Wind	-0.004	0.003	0.047			
RH	0.023	0.006	<0.001	7	15291.611	0
Temp	-0.019	0.019	0.035			
Time	-0.05	0.044	<0.001			
Wind	-0.003	0.001	0.025			
Date	-0.004	0.004	0.049			

Table 4. Selected log link (y = a + b*log[x]) negative binomial regression models for the number of male northern bobwhites (*Colinus virginianus*) heard during 2014–2017 vs. relative humidity (%), ambient temperature (°C), ordinal date, number of minutes after sunrise that the call counting period began, and wind speed (m/second). CI = confidence interval.

Year	B[a]	95% CI	Wald χ^2	DF	P
Relative humidity					
2014	0.018	±0.027	1.674	1	0.196
2015	0.024	±0.011	18.904	1	<0.001
2016	0.016	±0.012	7.128	1	0.008
2017	0.026	±0.010	23.608	1	<0.001
Temperature					
2014	-0.071	±0.061	5.085	1	0.024
2015	-0.052	±0.026	15.251	1	<0.001
2016	-0.013	±0.026	0.9	1	0.343
2017	-0.099	±0.031	40.579	1	<0.001
Ordinal date					
2014	0.001	-0.007	0.138	1	0.711
2015	0.005	-0.008	1.379	1	0.24
2016	0.006	-0.006	2.639	1	0.104
2017	-0.012	-0.006	14.605	1	<0.001
Minutes after sunrise					
2014	-0.003	-0.002	8.161	1	0.004
2015	-0.006	-0.002	32.423	1	<.001
2016	-0.005	-0.002	24.807	1	<.001
2017	-0.000005	-0.00002	0.198	1	0.656
Wind speed					
2014	-0.054	-0.11	0.907	1	0.341
2015	-0.084	-0.089	3.472	1	0.062
2016	-0.039	-0.093	0.698	1	0.404
2017	-0.091	-0.079	5.011	1	0.025

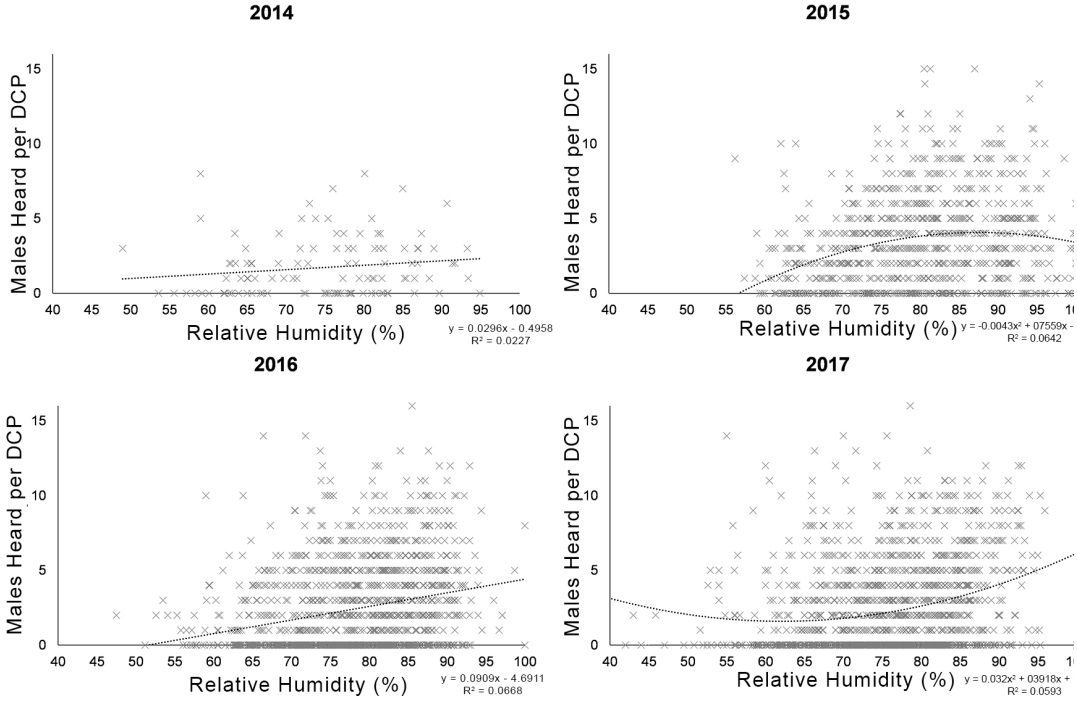

Fig. 4. Scatterplot (crosses) of number of male bobwhite (*Colinus virginianus*) calls recorded at each data collection point by relative humidity during spring call counts in Clay and Montague counties, Texas, USA, 2014–2017. Dashed line indicates line of best fit. All parameter coefficients were significant at $P < 0.001$.

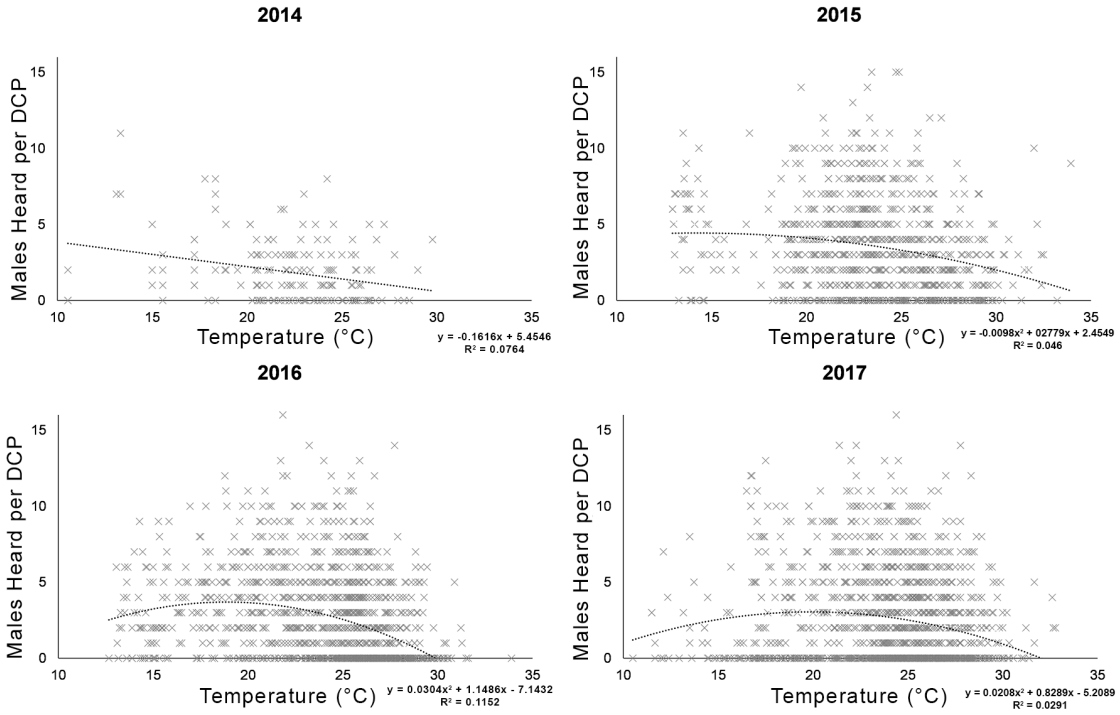

Fig. 5. Scatterplot (crosses) of number of male bobwhite (*Colinus virginianus*) calls recorded at each data collection point by ambient temperature during spring call counts in Clay and Montague counties, Texas, USA, 2014–2017. Dashed line indicates line of best fit. All parameter coefficients were significant at $P < 0.001$.

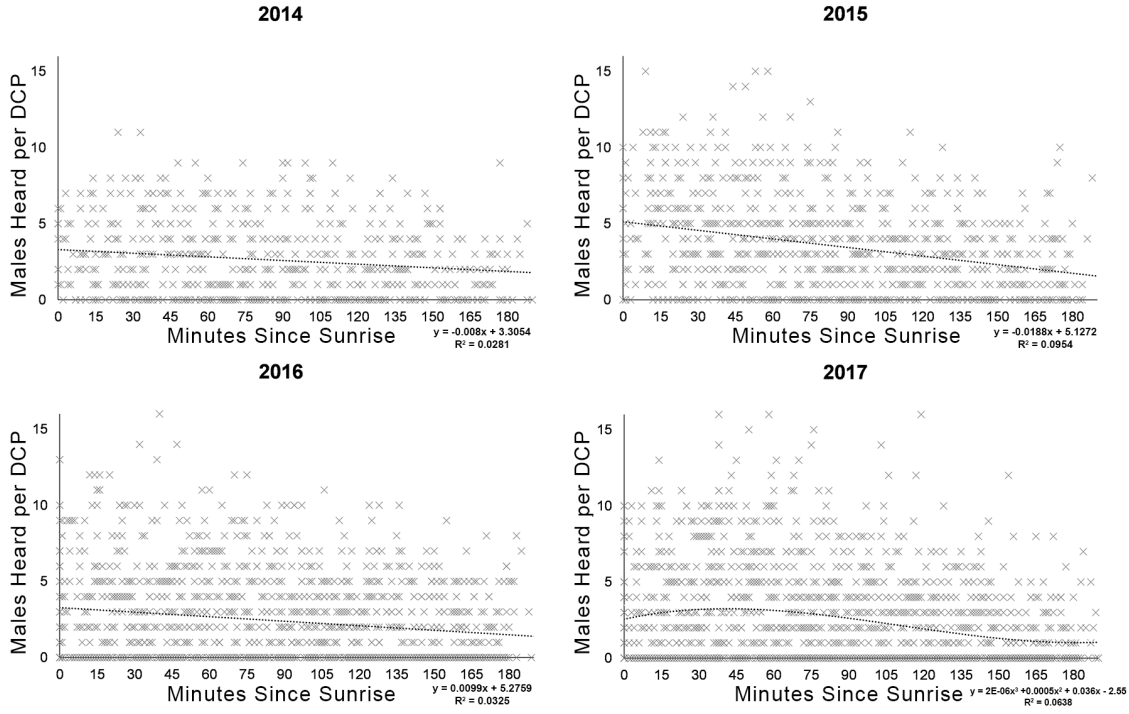

Fig. 6. Scatterplot (crosses) of number of male bobwhite (*Colinus virginianus*) calls recorded at each data collection point (DCP) by number of minutes after sunrise that the counting period began for spring call counts in Clay and Montague counties, Texas, USA, 2014–2017. Dashed line indicates line of best fit. All parameter coefficients were significant at $P < 0.001$.

0.13) when including call count data for Montague County (2016–2017). In Clay County, fewer male bobwhites per DCP were recorded in the drought year of 2014 (median = 2, min = 0, IQR = 1–3, max = 11) than in subsequent years (median = 3, min = 0, IQR = 1–5, max = 15).

Ambient Noise

Ambient sound levels were recorded 905 times at DCPs during 2017. Minimum levels ranged from 43–91.2 dB(A) minimum, 43–95.5 dB(A) mean, and 43–102 dB(A) maximum. There was a negative correlation between number of male bobwhites recorded and minimum (ρ = -0.165, $P < 0.001$, N = 905), mean (ρ = -0.098, P = 0.004, N = 886), and maximum (ρ = -0.11, P = 0.004, N = 756) ambient noise levels. However, there was no significant relationship between the number of male bobwhites recorded and log minimum (P = 0.223), log mean (P = 0.282), or log maximum (P = 0.457) sound levels, as the 95% CI for slope included zero.

Detection Probabilities

Using the unreconciled double observer method (Riddle et al. 2010*a*) on 558 sites, p_d was calculated to be 0.82.

DISCUSSION

We conducted a large-scale examination of relationships between meteorological, temporal, and other variables and the number of male bobwhites heard calling. Key findings were that the number of males recorded calling decreased ≥120 minutes after sunrise, decreased as temperature increased, and increased with relative humidity and cloud cover. There was no correlation between wind speed and the number of males recorded overall, or during individual years, except during 2017. However, larger numbers (>10) of males were recorded disproportionately when wind speed was too low to measure (χ^2 = 5.374, DF = 1, P = 0.020). We did not see a peak in calling activity. The number of males recorded did not increase or decrease during the study period (May–Jul) for 2014–2016, or when all years were pooled, but decreased slightly during 2017 (B = 0.018 ± 0.006, $P < 0.001$).

There is strong agreement among published studies that the number of bobwhites calling peaks by about 1 hour after sunrise, though day-to-day variations are common. The median number of male bobwhites recorded in this study did not decrease until ≥120 minutes (Figure 7). Based on our results, 90 minutes after sunrise is sufficient for fairly consistent results, and study length should not exceed 120 minutes after sunrise.

An assumption that temperature is a major factor in the relationships between weather variables and number of male bobwhites recorded would be reasonable. The timing of bobwhite reproduction in our study area may be an adaptation to avoid harsher conditions of mid- to late summer (Guthery et al. 1988). A link between drought and bobwhite population declines in semiarid regions has long been hypothesized (Henika 1947, Jackson 1951, Robinson and Baker 1955, Reyna and Burggren 2017, Reyna 2019). While bobwhite mortality during drought does not appear to increase significantly, bobwhite population numbers tend to decrease during drought years (Stoddard 1931, Robinson and Baker 1955, Jackson 1962, Reyna et al. 2012). Drought or high temperature reduces bobwhite calling activity and shortens the bobwhite breeding season (Guthery et al. 1988, 2000; Reyna et al. 2012). The decrease in reproductive effort may be due to interruption of reproductive hormone cycles caused by heat stress (Cain and Lien 1985, Guthery et al. 1988, Giuliano et al. 1998), thus reducing calling behavior.

It is unclear why relative humidity was more strongly correlated with the number of bobwhites recorded than temperature when the opposite is more common in the literature. This may reflect a greater relative importance of

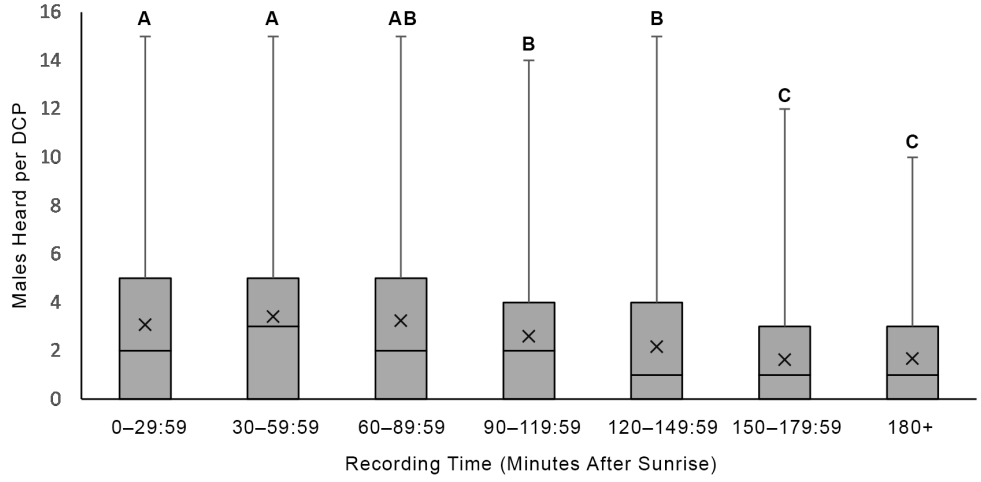

Fig. 7. Number of male bobwhites (*Colinus virginianus*) recorded at data collection points for each 30-minute period after sunrise during spring call counts in Clay and Montague counties, Texas, USA, 2014–2017. Crosses indicate means; letters indicate statistical grouping.

moisture to quail in semiarid rangeland (Guthery 1999), as all previous studies except Hansen and Guthery (2001) were conducted in more humid subtropical continental regions (Kottek et al. 2006). More calling activity and juvenile production have been observed in years with more moisture and less heat as compared to more hot and dry conditions (Bridges et al. 2001, Reyna et al. 2012). Alternatively, relative humidity may be functioning as a proxy for temperature in our analysis as air temperature and relative humidity are inversely related (Eagleman 1985).

Covariance between the multiple individual independent variables confounds more precise determination of how independent variables relate to the number of male bobwhite calls heard. Curiously, except for a brief statement linking light intensity and temperature to the time of day (Hansen and Guthery 2001), these relationships have not been previously addressed. Air temperature and wind speed tend to increase after sunrise. Morning cloud cover and relative humidity decrease as air temperature rises (Eagleman 1985). Air temperature tends to increase with ordinal date through May, June, and July in the bobwhite's range, due primarily to increased insolation (Eagleman 1985, Arguez et al. 2011). With the exception of dewpoint and barometric pressure, which are largely independent of temperature, correlations between weather variables and the number of male bobwhites recorded per DCP cannot be completely differentiated from an increase in temperature over the course of a morning.

Regression Models

Unsurprisingly, the independent variables with the highest correlation with the number of male bobwhites recorded had the best fit in negative binomial regression models. However, variables with low or marginally significant correlation (e.g., wind speed and ordinal date) produced improved models. One caveat when dealing with large (>1,000) sample sizes is overparameterization of regression models (Heckmann et al. 2014), which can produce a model that is highly accurate in describing the data that generated it but performs poorly elsewhere. Overparameterization is unlikely here, as our negative binomial regression model saw no improvement with >4 independent variables. However, caution should be given when using coefficients generated here, as they are unlikely to apply universally to spring bobwhite call counts, and their calculated values coefficients are less important than their direction (positive or negative) and their magnitude relative to each other.

We saw no major differences in the relationship between number of male bobwhites recorded and relative humidity, ambient temperature, or the number of minutes after sunrise. When comparing number of male bobwhites heard with log relative humidity, we noted that the negative coefficient for x^2 for 2015 stands out (Figure 4), but it may be an artifact of the lack of lower relative humidity readings that year. Spring and summer rains were unusually heavy in the study area during 2015 and <1% of call counts had relative humidity measurements <60%, with none <55%.

Ambient Noise

The most common source of measurable ambient noise in Clay County (other than technician movements) was vehicular traffic, most notably at DCPs near U.S. Highways 82 and 287. In Montague County, the most common source of ambient noise was natural gas compressor stations. The number of male bobwhites recorded did not appear to vary with recorded sound levels. High numbers of birds (≥10) were recorded only at DCPs with minimum ambient noise levels ≤43 dB(A), but this result was not significant ($\chi^2 = 2.10$, DF = 1, $P = 0.15$). The volume of bobwhite calls has been estimated at approximately 100 dB (Rusk et al. 2009) and the audibility radius from <500 m (Bennitt 1951) to 900 m (Rusk et al. 2009), depending on wind, atmospheric conditions, and terrain. Ambient sound capable of masking faint bobwhite calls was clearly audible at ≤43 dB(A), the lower limit for our sound meters. It seems intuitively clear that ambient noise may interfere with detecting the faintest bobwhites, most likely when the noise level is greater than the detected sound level of the quail, but more data are needed to determine to what degree and at what sound intensity this occurs. For future studies involving ambient sound and bird calls, we recommend a more sensitive sound meter.

Detection Probabilities

Our calculated p_d of 0.82 was consistent with the 0.69–0.84 estimated by Murray et al. (2011) and the 0.80–0.90 given by Riddle et al. (2010b).

Challenges

There are numerous critiques of point call counts and spring call counts for bobwhites in particular. The most well-founded critiques are those regarding indices in general (Anderson 2001, 2003). There are also critiques specific to spring call counts, primarily discrepancies between count results and fall quail populations or hunter harvest (Rosene 1957, Norton et al. 1961, Reyna et al. 2012, Sisson and Terhune 2017, Kubečka et al. 2019).

One of the difficulties with spring call counts is that researchers are attempting to produce long-term regional population information by collecting data at microscales (Hernández 2020). This problem may be compounded by other microscale effects, such as weather, noise levels, and the dates on which the data are collected.

Another difficulty is that spring call counts, while conducted at a time of biological significance, are valued primarily for their ability to predict populations during a time of economic significance, the hunting season. This predictive value ranges from near zero (Labisky and Preno 1971), to useful but not necessarily reliable (Rosene 1957, Norton et al. 1961, Schwartz 1974), to very high (Curtis et al. 1989). Correlation between spring call counts and fall harvest is often lower in semiarid regions than humid subtropical regions. In the Great Plains, it is stronger during non-drought years (Bennitt 1943, Reyna et al. 2012, Sisson and Terhune 2017).

Bennit (1951) found a correlation between whistle counts and the percentage of adult male birds in the hunter's bag, but there does not seem to be a clear correlation between spring call counts and fall age ratios (Kabat and Thompson 1963, Schwartz 1974). Spring call counts represent, at best, an index of breeding potential. Spring call counts cannot indicate how successful the breeding season—and by extension, the fall hunting season—will be.

There is also a spatial component to the difficulty of using spring call counts to predict fall hunting success. Though bobwhites do not migrate, winter habitat is different from breeding season habitat. Bobwhites disperse into different habitat between spring call counts and autumn (Murphy and Baskett 1952, Urban 1972, Townsend et al. 2003), with the greatest movements in more fragmented landscapes (Fies et al. 2002). This behavior suggests why index values constructed closer to harvest time, or on larger scales, are considered more accurate predictors of the fall population abundance (Kozicky et al. 1956, Rosene 1957, Kubečka et al. 2019). It is difficult to describe variation in call counts in terms of any single factor or group of factors. While even the most influential of weather conditions here produced a Spearman's rank correlation coefficient of <0.3, it is sufficient that protocols for spring call counts should include recording weather conditions at both the time and location of each point count. These correlations can be highly variable, but could also be region-specific.

Sisson and Terhune (2017) recommended that breeding season counts be conducted at the peak of calling activity. This may be logistically unfeasible for large-scale surveys and is complicated by the variability in peak bobwhite calling activity from year to year, ranging from May (Terhune et al. 2006) to late July (Robel et al. 1969). Even in a single location, breeding season peak timing can vary by as much as 2 months in consecutive years (Hansen and Guthery 2001). Additionally, one of the predicted effects of climate change is that breeding season will begin earlier in the year (Crick and Sparks 1999, Marra et al. 2005), requiring a corresponding change in the timing of call counts. Our data do not suggest a peak time for call counts in our study area. We recommend that replicate call counts be spaced out over the breeding season to increase the likelihood of listening during the breeding season peak. For North Texas, this study suggests beginning before 15 May.

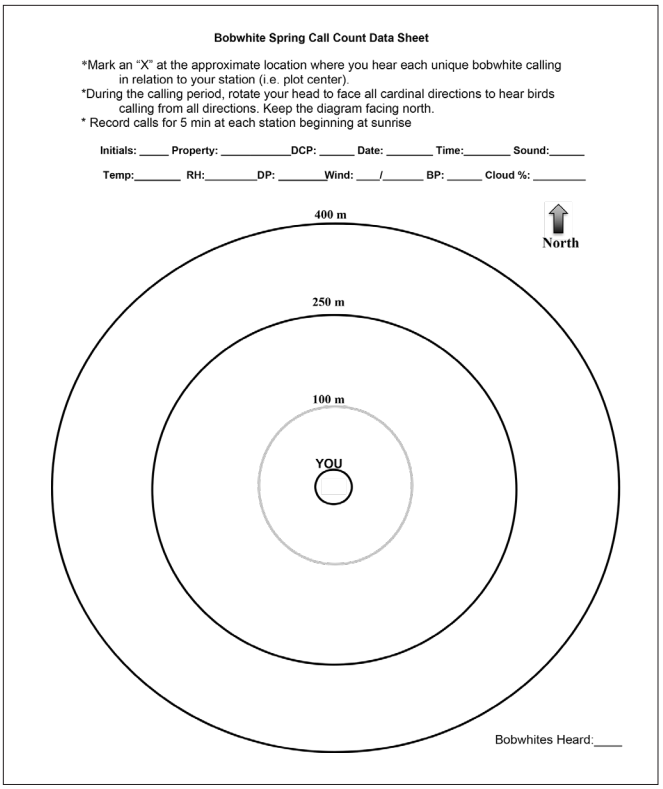

Fig. 8. Example data sheet for recording bobwhite spring call counts. Initials = technician initials; property = ranch name (if applicable); DCP = Data Collection Point number (if applicable); Date = calendar date; Time = clock time; Temp = ambient temperature in ºC; RH = relative humidity (%); DP = dewpoint temperature (ºC); Wind = wind speed in km/hour and direction; BP = barometric pressure (mbar); Cloud = cloud cover (%).

MANAGEMENT IMPLICATIONS

The results of this study suggest a few key considerations when conducting spring call counts for northern bobwhites. First, we recommend using a data sheet with blanks for each variable (Figure 8) to facilitate consistency in data collection. Recording meteorological, temporal, and sound variables can help clarify variation in annual spring call counts recorded. Second, we recommend conducting call counts <120 minutes after sunrise. Because it was proscribed by our protocol, we have limited data on call counts at wind speeds >16 km/hour. However, we see little evidence either from our data or in the literature, that call counts should be prohibited above certain cloud cover percentages or at wind speeds <16 km/hour. We recommend such restrictions be removed from spring call count protocols, at least for those on semiarid rangeland.

Quail management, research, and conservation require an accurate assessment of population numbers to aid decision making and to evaluate the results of those decisions. With climate change predicted to have major impacts on the bobwhite's range (Wilsey et al. 2019, Strauss et al. 2021), there is an increasing need to assess and monitor bobwhite populations. Population censuses often involve tradeoffs between accuracy and the amount of resources required (Rusk et al. 2007, Kubečka et al. 2019). Researchers have addressed this limitation by either resorting to the use of indices (e.g., morning covey-call surveys. Spring call counts are a relatively low-cost census method for bobwhites and can be useful in assessing long-term trends as long as deficiencies inherent in point counts are mitigated. Incorporating recommendations from this study into spring call count protocols could help managers more accurately assess bobwhite population numbers.

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THE EFFICACY OF VIDEO CAMERAS TO ACCOUNT FOR NORTHERN BOBWHITES FLUSHED, BUT UNDETECTED, DURING AERIAL SURVEYS

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ABSTRACT

Over the past 20 years, conventional distance sampling from a helicopter platform has been used to estimate northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) density over large areas of rangeland vegetation. However, it has been speculated that aerial surveys can complicate the ability to meet the distance sampling assumption of detecting 100% of the target objects on the transect line due to the restricted observer view from the helicopter. We attempted to use video cameras to determine whether missed detections occurred and whether digital methods could improve the precision of bobwhite density estimates. Our objectives were to 1) determine whether video cameras are a viable option to detect if coveys are flushing behind the helicopter and missed by observers, 2) determine whether coveys are flushing underneath the helicopter and missed by observers, and 3) explore the use of video cameras in a mark-recapture distance sampling framework. We recorded video while traversing line-transects with a helicopter during 4 distance-sampling surveys across 2 ranches in South Texas, USA. For objective 1, we reviewed footage from cameras with a backward-facing view and detected only 1 pair of bobwhites (0.001% of 889 coveys detected) that flushed on video footage recorded during the surveys but were unnoticed by observers. These results indicated that when coveys flushed, they rarely flushed behind the helicopter, and the helicopter flew at what seemed to be the proper speed and altitude to detect late flushes. For objective 2, we reviewed footage from a helicopter-mounted camera that was recorded within a swath underneath the helicopter's center. We recorded 22 flushes within the swath, none of which was missed by the observers in the helicopter; as a result, we could not complete an MRDS analysis in Program Distance. This study improved confidence in fulfilling the assumptions of distance sampling and resulting density estimates but was limited to flushing birds only.

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Key words: aerial survey, *Colinus virginianus*, detection, distance sampling, northern bobwhite, video

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Monitoring and manipulative studies of animal populations depend on reliable density estimates to detect changes over time. Distance sampling techniques are often used in research because they account for objects undetected by the observer and provide density estimates with measures of variability. Line-transect distance sampling uses the observed perpendicular distances from the detections (x) to the transect (0) to estimate detection probability (Laake et al. 2008). Three fundamental assumptions determine the reliability of density estimates and associated variance measurements obtained through conventional distance sampling (CDS; Buckland et al. 2001): 1) objects directly on the line or point are directed with 100% certainty, or a probability of 1, where $g(0) = 1$; 2) objects are detected at their initial location and do not move in response to the observer; and 3) distances are measured accurately. Failure to satisfy the first assumption leads to difficulties when estimating detection probabilities and biases density estimates low if $g(0) < 1$ (Buckland et al. 2001, Bächler and Liechti 2007). The estimated $g(0)$ must be evaluated by addressing perception bias (when observers fail to detect animals at 0 distance even though animals are present) and availability bias (when animals are unavailable for detection; Marsh and Sinclair 1989).

Several studies have evaluated the use of line-transect distance sampling with northern bobwhites (*Colinus virginianus*; hereafter, bobwhite). These studies tested the feasibility of satisfying the 3 key assumptions (Guthery 1988, Rusk et al. 2007, Schnupp 2009) and obtaining the minimum number of detections from various platforms (e.g., helicopter, vehicle, walking). In tests of the first assumption, Rusk (2006) found that he was able to detect 70% of radio-marked coveys at 0 distance during fly-over trials and Schnupp (2009) found that he was able to detect whether radio-marked coveys were present in 94% of the 92 trials he flew. This discrepancy (70% vs. 94%) led us to further investigate the ability of observers to detect 100% of the objects at 0 distance. Additionally, adverse weather, dense brush, or an inexperienced observer may alter the results expected under ideal conditions. Using video cameras instead of radio-marked coveys may provide a less labor-intensive way to determine detection probability.

A proposed solution to the potential visibility biases in aerial surveys is the inclusion of high-resolution cameras mounted on aerial platforms (Buckland et al. 2015). Digital surveys using cameras to collect detection data with photographs or video (or both) have helped improve detection and reduce disturbance (i.e., response to observers) of water birds over large tracts of open water (Burt et al. 2009, Hexter 2009). Current methods include using a series of video cameras to survey large strips and estimating density via plot sampling (i.e., where observers can make a complete count in the swath). In applying this technique to bobwhites, an altitude higher than 10 m would be necessary to count birds within a reasonable swath width (50 m); however, previous research has suggested the low altitude (10 m) of a helicopter is necessary to elicit a covey flush in the case of quail (Shupe et al. 1987). Prior research has not tested the feasibility of counting bobwhites using cameras without observers in a strip transect.

When observers are unsure or unable to satisfy the first assumption of distance sampling, Buckland et al. (2001) recommend mark-recapture distance sampling (MRDS; Laake and Borchers 2004; Borchers et al. 2006), which allows relaxation of this assumption. In addition to the assumptions of CDS, the MRDS method requires some level of independence between observers, and the resulting analysis must be able to identify duplicate detections that qualify as "marks" by one observer and "recaptures" by another (Burt et al. 2014). The introduction of laser rangefinders in bobwhite surveys has allowed researchers to better meet the second and third assumptions of distance sampling, which involve detection location and measurement of distance (Schnupp et al. 2013). However, a helicopter must hover to measure perpendicular distances with rangefinders accurately. Hovering removes any independence between the groups of observers necessary in the independent-observer configuration for MRDS. Full independence requires constant movement by the helicopter and, as a result, for observers to visually estimate distances, which can introduce measurement error (Schnupp 2009). An alternative setup for MRDS surveys is a trial-observer configuration with point independence (Laake 1999, Laake and Borchers 2004). Here, the detection of one observer sets up trials on the line or point only for the other observer (Laake 1999). By implementing this approach with a camera mounted underneath the helicopter, the camera could act as the observer setting up trials on the lines for the observers in the helicopter (Laake and Borchers 2004). Prior research has not tested the feasibility of counting bobwhites using cameras without observers in a strip transect. However, there is potential to combine digital surveys with trial-observer MRDS by using the camera to set up trials for detection at $g(0)$ (E. Rexstad and L. Thomas, Centre for Research into Ecological and Environmental Modelling, University of St. Andrews, personal communications). This method would relax the assumption of 100% detection at $g(0)$ and still allow observers to measure exact distances and estimate covey size. Using a video camera may also help address availability and perception bias at $g(0)$ given that the camera's resolution is sufficient to detect unflushed birds.

We used data collected during the initial phase of a long-term study on cattle grazing and bobwhite populations to assess whether video cameras can be used to: 1) evaluate missed detections behind the helicopter, 2) evaluate missed detections on the line, and 3) serve as a trial observer in an MRDS framework. For the first objective, we hypothesized that the altitude and speed of the survey we used were sufficient to elicit a covey flush upon approach, indicating bobwhite coveys would not flush behind the helicopter. For the second objective, we hypothesized that the camera would pick up all flushing bobwhites on the line (0 m) during surveys. If observers missed any of these coveys, we would be able to incorporate those detections into an MRDS analysis that would alleviate the constraints of satisfying the first assumption of CDS.

STUDY AREA

We conducted our study on 2 East Foundation ranches: the San Antonio Viejo Ranch and the Ranchito Ranch in Jim Hogg County, Texas, USA (Figure 1). We conducted video surveys during annual surveys on a 7,689-ha pasture on the San Antonio Viejo Ranch and 2,111 ha of the Ranchito Ranch. These ranches lie within the South Texas Plains ecoregion (Gould et al. 1960). The 30-year average annual precipitation in the area was 53.6 cm (PRISM Climate Group 2018). Based on the 30-year records, average temperatures were 12–13° C in January and 27–30° C in July (PRISM Climate Group 2018). Elevation in Jim Hogg County ranged from 60 m to 240 m. These areas were dominated by sandy soils. Woody plant communities in the study areas were dominated by honey mesquite **(***Prosopis glandulosa*), huisache (*Acacia farnesiana*), brasil (*Condalia hookeri*), granjeno (*Celtis pallida*), and prickly pear (*Opuntia* spp.). Seacoast bluestem (*Schizachyrium scoparium* var. *littorale*), purple threeawn (*Aristida purpurea*), Lehman lovegrass (*Eragrostis lehmanniana*), spotted beebalm (*Monarda fruticulosa*), and woolly croton (*Croton capitatus*) dominated the herbaceous plant community.

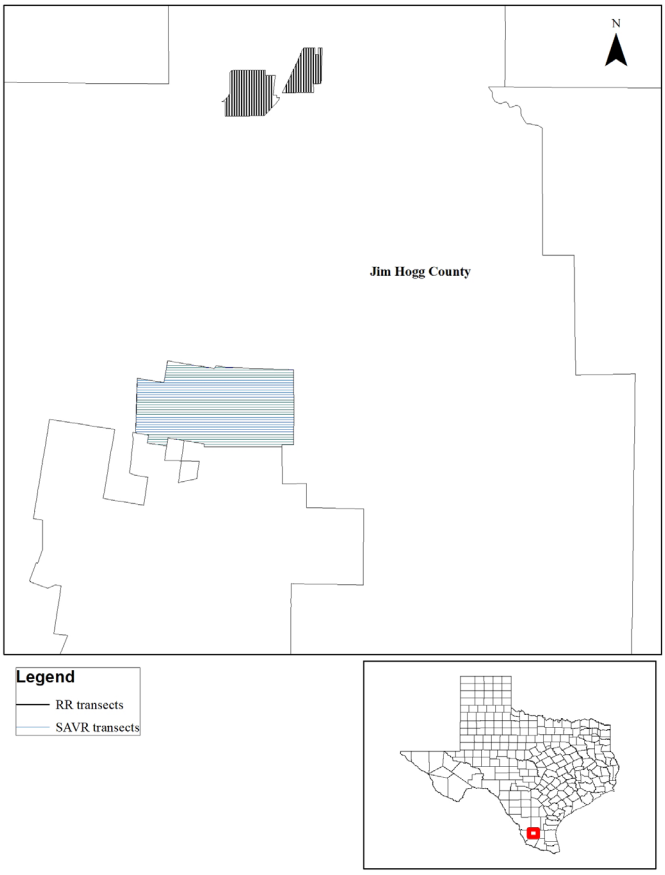

Fig. 1. Map of the flight transects and survey boundaries on the Ranchito Ranch (RR) and San Antonio Viejo Ranch (SAVR) in Jim Hogg County, Texas, USA used in 2015, 2016, and 2021.

METHODS

Aerial Surveys

We video-recorded 2 surveys in December 2015, 1 survey in December 2016, and 1 survey in March 2021. Surveys in December were conducted on the San Antonio Viejo Ranch, and the survey in March was conducted on Ranchito Ranch. Transects were spaced 200 m apart on both study sites (Figure 1). The surveys in 2015 were replicate surveys that occurred within 10 days of each other (hereafter, survey 1 and survey 2). For all surveys, 3 observers and the pilot traversed transects in a Robinson R-44 helicopter (Rio Grande Helicopters, Laredo, TX) at a height of approximately10 m and a velocity of 37 km/hour (as recommended by Rusk et al. 2007, Schnupp 2009, Schnupp et al. 2013) in sequential order with a random start point. Altitude may have varied between 7 m and 15 m based on brush cover and terrain; however, the pilot aimed to fly at 10 m when able. We followed the search and survey protocol developed by Schnupp et al. (2013), where the front-seat observer scanned the area directly in front of the helicopter to the doorframe of the back seat, and the 2 back-seat observers scanned the area from the doorframe to the tail rotor. The pilot also made detections when able but was not considered an observer.

When a covey was detected, the pilot moved the helicopter into a hover position that was perpendicular to the transect line; the back-seat observers took a reading of range, azimuth, and inclination with a laser rangefinder (Trimble Laser Ace 1000, Trimble Navigation Ltd., Sunnyvale, CA, USA) at the initial point of detection. The laser rangefinder was linked to a Juno hand-held unit (Trimble Juno 5 series handheld, Trimble Navigation Ltd.) via Bluetooth, which records and stores the following information: observer positions and names, date, time of detection, survey region, transect number, transect length, covey location (x, y), covey size, and the range, azimuth, and inclination of each detection via the CKWRI Wildlife Survey Database application (Schnupp Consulting, LLC, Kingsville, TX). At data import, each covey location was stored at the helicopter's position at the time of detection. CyberTracker uses the information collected by the laser rangefinder (range, azimuth, and inclination) to calculate the location of the covey. Perpendicular distance is then calculated from the flight path to the moved covey location.

Camera Methods

Rear-mounted cameras.—In 2015, we installed 2 Model Hero3+® (GoPro, San Mateo, CA) cameras angled at the tail rotor on either side of the helicopter doorframes to observe whether coveys were flushing after the helicopter passed (Figure 2A). We attached the cameras using 2 pilot-approved GoPro roll bar mounts. We recorded footage at a resolution of 720 pixels and 60 frames/second to review footage at 0.5 speed. We faced cameras backward to investigate visibility bias in our survey methods. If coveys waited to flush after

a helicopter passed, we wanted to know whether observers could still detect these late flushes. We also wanted to test whether the GoPros could detect bobwhites that did not flush and were not detected by observers. Following the survey, we matched count data from observers inside the helicopter against video footage by converting the video start and end time into real-time (GoPros are not enabled with a time stamp on-screen). We indicated positive detections in the video when the helicopter increased altitude and turned 90° into a hover. Any coveys in the footage that were passed by the helicopter, not detected (no hover or pause in the video), and not matched with a detected time stamp were considered a missed detection.

Tow ball-mounted cameras.—In 2016 and 2021, we used a FlightCam 360 (Flight Flix LLC, Maple Grove, MN, USA) camera with an 8-hour streaming capability on a single battery instead of the GoPro. We mounted the camera, facing down (0°), to the tow ball of the helicopter (Figure 2B) with a pilot-approved clamp with vibration control (VibeX Ball Mount; Flight Flix LLC). We recorded footage at a resolution of 960 pixels to increase battery life and 60 frames/second for review at ≤0.5 speed. Because the FlightCam was enabled with an onscreen time stamp, we could match exact covey detection times from inside the helicopter to the video footage. We used the previously described methods to determine whether observers detected or missed a covey during post-survey reviews.

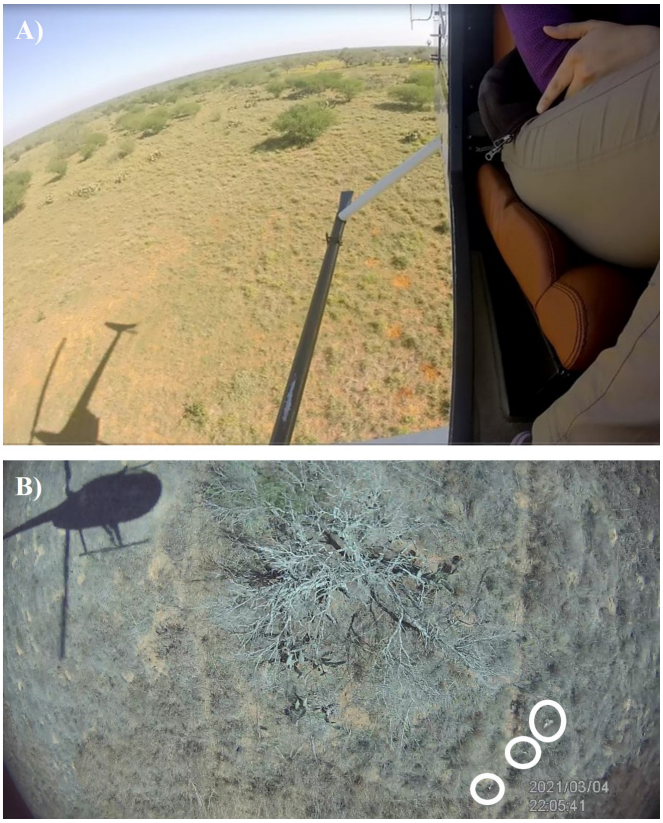

Fig. 2. Camera view from A) rear-facing mount in 2015 and B) tow-ball (downward facing) mount in 2016 and 2021. A covey flush is shown in the bottom right (white circles). Cameras were mounted to an R-44 helicopter during distance sampling surveys for northern bobwhites (*Colinus virginianus*) conducted on the Ranchito Ranch and San Antonio Viejo Ranch in Jim Hogg County, Texas, USA.

These surveys served as a trial run for using a digital observer in trial-observer MRDS with point independence using Program Distance, version 7.3 (Thomas et al. 2010). For observers to be able to use this mark-recapture method, the camera must be able to determine the covey size and perpendicular distance or distance bin (coveys within the camera's swath width) for any detections marked by the camera at 0 distance but not recaptured by the observers in the footage. To measure distances within the swath, the camera is set at a known angle (0°), and an object with a known length and height is recorded at the survey altitude to set a scale for the video. We calculated swath width using the following formula,

$$Width = \frac{\text{Altitude}}{\cos(\propto)} \times 2\tan\frac{AOV}{2},$$

where AOV corresponds to the camera angle of view. In Program Distance, we analyzed the data by 1) using the swath as a distance bin from 0 to x distance on either side of the centerline, and 2) determining the centerline of the video (0 distance) and measuring the distance to covey by equating the number of pixels in the video to a meter using an object of known distance present in the video. While we conducted MRDS sampling, there were no differences between camera detections and observer detections, and therefore we could not run an MRDS analysis for the trial-observer point independence in Program Distance.

RESULTS

Rear-mounted Cameras

From the 2015 footage, we reviewed 12 hours and 36 minutes of footage at 0.5 speed from both the left- and right-side cameras from survey 1 and 8 hours and 8 minutes of footage from survey 2. We observed 484 coveys over 380.3 km of transect for survey 1 and 405 coveys over 380.3 km of transect for survey 2. We identified one pair of bobwhites (<1% of total detections) on camera missed by observers; this pair flushed 30 seconds after a separate detection was made. This pair may have been a part of the detection. We suspected the resolution of the GoPros was not sufficient to detect coveys that did not flush but could not document this empirically because either no unflushed coveys were recorded, or all coveys flushed.

Tow Ball-mounted Cameras

During the 2016 survey, the bolt that connected the camera to the tow-ball mount broke and the camera was secured to the helicopter using available materials. As a result, we could not properly adjust the camera angle. Due to the camera angle from this video, we could not calculate the

camera swath width. However, we analyzed the footage for any missed detections.

We reviewed 4 hours and 47 minutes of footage at 0.5 speed, approximately 50% of the total survey. The time stamp on this video made detection matching more reliable than the previous year. We observed 178 coveys over 192.8 km of the transect. There were no obvious flushes of large coveys missed by observers during the recorded survey. On 5 occasions (3% of 178 detections), we observed singles or pairs of birds flushing shortly after a covey was detected (<5 seconds); these birds were likely part of the detection made. On one occasion, we observed an undercount of the covey size recorded. We corrected the count using the video; however, it was rare to confirm counts as individuals disappeared when the video was paused, or part of the covey flushed out of frame. On 6 occasions, a single bird flushed outside of recorded covey detections (>60 seconds), but we could not make a positive identification on the bird species either because of the poor resolution or because it flew out of the frame too quickly.

In 2021, we reviewed 2 hours and 50 minutes of survey footage at 0.3–0.5 speed with the camera at 0° (pointed to the ground). We observed 85 coveys over 96.1 km of transect at a survey altitude of 10 m and an AOV of 120° at 10 m from the subject. Our swath width for this survey was 6.4 m. In matching the time stamp on the video to our survey footage, we did not observe any missed detections recorded by the camera. Like previous surveys, we recorded 4 occasions of a single bird flush outside of a covey detection where we could not identify the species. The resolution on this camera may not be able to detect any birds on the ground that did not flush; the camera did not record any known coveys on the ground to test this theory.

The camera and the observers detected 100% of detections within the swath width or 22 of the 85 total detections (26%). Of these 22 flushes, the perpendicular distance measured by observers using laser rangefinders was within the swath width of 6.4 m on 3 occasions (13% of duplicate occasions). This may indicate a different issue with the precision of our rangefinders. Throughout the survey, observers detected 15 coveys on the ground, 7 of which occurred within the camera swath: however, on-the-ground coveys could not be seen on the video. If we account for any variation in altitude during detections, larger swaths may have been recorded. If we recorded at 15-m altitude, our swath width would increase to 9.6 m, putting duplicate detections within the swath in 5 instances (22% of duplicate occasions). At a maximum, if the altitude were 20 m at the time of detection, our swath width would increase to 12.8 m, where duplicate detections within the swath occurred in 6 instances (27% of duplicate occasions).

DISCUSSION

Rear-mounted Cameras

The video footage data from these surveys supported the prediction that bobwhite coveys rarely flush behind the helicopter or that observers can detect these flushes. We observed birds flushing once the helicopter passed, but they flushed in the field of view of the back-seat observers and were detected. The results from the rear cameras reinforce the supposition that the helicopter survey speed and altitude are sufficient to flush coveys upon approach. The vantage points of the camera in 2015 allowed us to view the observer and, in some instances, a covey flush in the same frame. When both could be seen, we could confirm instances where observers were not recording distances from the initial point of covey flush. When observers incorrectly identified the initial flush point, we witnessed observers angling the rangefinder toward a different location than where the observed flush occurred. This can be corrected in future surveys by using trained observers, and evidence of an assumption violation enforces the need for observer training days where observers can practice detecting coveys with rangefinders with less pressure.

Given that pairs of bobwhites are typically rare in December, the single missed flush may be the result of 1) part of the larger detected covey flushing for the second time or 2) part of a larger detected covey that did not flush initially. If a rangefinder malfunctioned or did not register a reading on the first hit, the hover became prolonged while observers resolved technical difficulties. During an extended hover, coveys may have settled and partially flushed (i.e., only a fraction of the covey flushes) again once the survey was resumed. Observers in the helicopter communicated to avoid double counting a flushed covey; however, we could not determine this from the video alone. The only remedy is to note which coveys partially flush or flush twice in the helicopter and mark them with the time stamp on the electronic system.

Tow Ball-mounted Cameras

We were able to confirm that the observers missed no flushing birds within the swath width (area recorded by the camera); however, we could not detect unflushed birds with the camera alone. We succeeded with using the tow-ball cameras in a trial-observer configuration on the line, but the observers would have had to miss detections for the MRDS analysis to run. In this case, the Flight Flix camera with a tow ball mount allowed us to obtain the view necessary to survey directly below the helicopter. This camera also had a time stamp, which made matching the observations on the video to the data more efficient. In both 2016 and 2021, we observed occasions where singles and pairs of bobwhites flushed in proximity (time and distance) to other detections. These were likely part of a detected covey that did not flush together. As described earlier, we often observed delayed flushing in the helicopter and typically made the call to include these as part of the detected covey; however, we could not confirm these detections through the footage.

With our current camera, we could not estimate $g(0)$ and incorporate that known detection probability into the distance analysis. In natural color, the footage could not address availability bias at $g(0)$ in that we could not see unflushed coveys in the video. Therefore, we cannot compare our

findings to the $g(0)$ of 70% and 94% obtained by Rusk (2006) and Schnupp (2009) via radio-marked birds.

Additionally, had the cameras recorded a covey missed by the observer, we would have been unable to confidently 1) estimate covey size and 2) match the distances recorded by the camera to the observers. The angle of the camera and speed of the helicopter made it difficult to count covey size accurately; therefore, an average would need to be used. We could match only 3 of the distances measured by observers to the detections in the camera swath, which indicates some error in the rangefinder's ability to place points at the correct location. Since we did not miss any detections (flushed) that the camera recorded, the use of digital methods was extremely time-consuming to post-process compared to human observer-only methods.

Bröker et al. (2019) used an approach similar to the one that we detail to determine the density of narwhals (*Monodon monoceros)* in Greenland. The authors used human observers to make track-line (0 m) detections and oblique-facing cameras on either side of a fixed-wing aircraft to record images every 3 seconds from 0 m to 515 m on either side of the helicopter. They found that both the images and observers recorded a statistically similar number of sightings and produced similar density estimates; however, the measured distances and group sizes differed (Bröker et al. 2019). The results from both Bröker et al. (2019) and this study succeeded at providing researchers with confidence in their ability to make detections. Still, they fell short of supplementing or replacing observers entirely due to limitations in the cameras.

Future research could focus on the use of thermal or infrared cameras with unmanned aerial systems (UASs) to aid in covey size estimation and the detection of unflushed coveys under certain conditions, particularly at night when bobwhites are roosting (identifiable by a circular configuration). In natural color, the resolution at ground level was poor in the cameras used in this study, making it difficult for observers to positively identify missed detections as bobwhites unless the shape and covey formation were clear. Thermal cameras were found to increase detections of several kangaroo species by 30% compared to observers in western Australia (Lethbridge et al. 2019). Despite limitations in survey time and area, UASs with thermal cameras used at night may be able to operate at a higher altitude to survey a broader swath and obtain a complete count of roosting coveys in the camera swath. This would take care of both perception and availability bias, particularly in the open grasslands of South Texas, where brush cover was not high. Surveys incorporating UAS technology have been employed in surveys of nesting birds (Choi et al. 2020), marine mammals (Hodgson et al. 2019), and terrestrial mammals (Van Andel et al. 2015), but not for terrestrial birds such as bobwhites. Additionally, the most promising uses of UAS and digital methods are their ability to increase observer safety by reducing helicopter time and potentially increase the precision of distance estimates.

There should be a continued focus on using technology and MRDS to relax the assumptions of distance sampling with bobwhites. Our study shows that human observers can confidently detect objects that flush during distance sampling surveys both on the line and behind the helicopter but cannot give insight into the detection of unflushed coveys.

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ESTIMATING NORTHERN BOBWHITE DENSITY IN PRIVATELY OWNED FORESTS ACROSS THE SOUTHEASTERN UNITED STATES

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ABSTRACT

Rigorous density estimates can inform management, conservation planning, and policy decisions. Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) populations are declining throughout their range, including the southeastern United States. Numerous private land conservation initiatives are underway to restore bobwhite populations in these areas, but baseline estimates of density spanning privately owned forests are sparse. This information gap makes it difficult to evaluate the population-level effects of these conservation programs or develop expectations for timelines to reach population targets. We sought to understand baseline densities across privately owned pine forests in the southeastern United States in areas targeted for bobwhite conservation. We sampled 138 pine stands a total of 286 times across Alabama, Florida, Georgia, North Carolina, and South Carolina from 2018 to 2020 using autumn distance sampling point counts. We sampled 110 stands that were either planned or applied U.S. Department of Agriculture, Natural Resources Conservation Service (NRCS) management contracts, specifically Working Lands for Wildlife (WLFW) Northern Bobwhite partnerships or similar Environmental Quality Incentives Program contracts. The WLFW contracts were solely in focal counties identified in the National Bobwhite Conservation Initiative 2.0 plan and by cooperating state wildlife agencies. Contracts were on average 17.4 ha (SD = 27.0). We also sampled 28 areas with extensive (>200 ha) and intensive (e.g., at least every 3 years for the last ~10 years) habitat management for bobwhite. We used a hierarchical distance sampling model to estimate density. Density was lowest in North Carolina and South Carolina. Densities in Alabama were slightly greater, and greatest densities were in Georgia and Florida. However, the majority of observed densities were 2 coveys/40 ha or below, and all were below 4 coveys/40 ha. Large and intensively managed sites on average had 4 times greater density compared to smaller contracts. Specific densities will be reported in the future. Our sampling efforts fill an important information gap regarding densities throughout private lands in the southeastern United States. Our models indicate that bobwhite densities are generally low in pine forests of the Southeast even in counties identified as having the greatest conservation potential. The relatively greater densities at large and intensively managed sites illustrate the need for more intensive landscape-scale planning when implementing private land conservation. Pending research will compare densities at planned and applied NRCS contracts in the context of landscape-scale habitat amount.

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Key words: broad-scale monitoring, *Colinus virginianus,* density, northern bobwhite population assessment, southeastern United States

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EVALUATION OF A SOLAR-RECHARGED MICRO-GPS DATALOGGER FOR NORTHERN BOBWHITE IN THE ROLLING PLAINS OF TEXAS

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ABSTRACT

The use of Global Positioning Systems (GPS) transmitters on northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) could increase our understanding of fine-scale movements and habitat use for a declining game bird species. We evaluated solar-recharged micro-GPS dataloggers to determine the effectiveness of the units on free-ranging bobwhite and we conducted a controlled experiment to determine the accuracy of the dataloggers under a variety of canopy cover. We deployed the micro-GPS dataloggers on 25 bobwhites between August 2016 and April 2017 across 4 different ranches in the Rolling Plains of West Texas, USA. Accuracy (± standard error) for the 8 dataloggers across 3 trials for the stationary tests was 25.4 ± 3.8 m. Daily movement of bobwhite averaged 0.96 ± 0.09 km and morning movements averaged 0.49 ± 0.07 km. Average 95% and 50% minimum convex polygons for bobwhite area utilization were 15.2 ha and 3.6 ha, respectively. Our data indicate that solar-recharged micro-GPS dataloggers can be used to monitor bobwhites' short-term fine-scale movements in West Texas.

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Key words: *Colinus virginianus*, daily movement, dataloggers, MCP, micro-GPS, northern bobwhite

Researchers traditionally have used very high frequency (VHF) telemetry to monitor wildlife to collect various forms of data (e.g., survival and movement; Burger et al. 1991, 1995; Parry et al. 1997). However, concerns have been raised about potential bias, ranging from personnel experience to equipment failures (Springer 1979, Fuller et al. 2005). For example, a researcher's presence may affect the animal's natural movements and introduce biases in estimates of habitat utilization. Additionally, adverse terrain and researcher errors may negatively affect VHF telemetry precision and accuracy (White and Garrott 1990, Fuller et al. 2005). Researchers have deployed Global Positioning Systems (GPS) equipment to monitor animal movements (Steiner et al. 2000, Hulbert and French 2001, Phillips et al. 2003). Advances in GPS technology have decreased the size of these GPS devices (from 150 g to 0.05 g) so dramatically that GPS dataloggers can now be placed on moderately small birds (i.e., <150 g).

Use of GPS transmitters has made possible research on large- and fine-scale movements (Bouten et al. 2013, Fremgen et al. 2017), and foraging (Phillips et al. 2003, Fedy et al. 2012) for large (~10 kg) and small (~109 g) avian species (Guthrie et al. 2011, Schwemmer et al. 2017, Watts et al. 2017, Moskat et al. 2019). Micro-GPS dataloggers for avian species have aided in estimating habitat utilization (Moskat et al. 2019, Wann et al. 2019). However, the reliability of such dataloggers should be carefully examined for target species to determine accuracy and precision (Forin-Wiart et al. 2015).

Northern bobwhite (*Colinus virginianus*, hereafter, bobwhite) is a popular game species in decline across much of its range (Hernández et al. 2013). Previous research has utilized the homing technique via VHF technology and equipment to monitor survival, nesting, and movement (Burger et al. 1991,

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1995; Buckley et al. 2015, 2018). To date, a study conducted in 2015–2017 has yielded 2 peer-reviewed manuscripts on using GPS on bobwhite. Marquardt et al. (2017) reported using 3.6 g PinPoint (Lotek Wireless, Inc., Newmarket, Ontario, Canada) GPS units and documented problems with battery life and number of location fixes. However, these units could be practical for short-duration studies. Additionally, Cohen et al. (2020) reported on use of these devices in research on movement and habitat utilization for bobwhite in Texas, USA. They found that home ranges estimated using GPS location fixes were comparable to those created from VHF telemetry data and recommended additional work across the different habitat types which bobwhites use. Due to the short battery life of the previous GPS dataloggers, it is important to test new GPS technology for use on bobwhite.

Our objectives were to 1) assess the accuracy of solar-recharged micro-GPS dataloggers, 2) compare the accuracy of micro-GPS dataloggers and human telemetry data collection, and 3) assess the effectiveness and feasibility of using such GPS units on wild bobwhite for future research.

STUDY AREA

Our stationary trials occurred on the Texas Tech University Native Rangeland in Lubbock, Texas, USA (33°36.260'N, 101°53.986'W). The dominant vegetation for the property consisted of honey mesquite (*Prosopis glandulosa*), blue grama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*), purple threeawn (*Aristida purpurea*), silver bluestem (*Bothriochloa saccharoides*), Arizona cottontop (*Digitaria californica*), and sand dropseed (*Sporobolus cryptandrus*; Sorensen 2010). Our research was conducted across 5 different locations in the Rolling Plains of West Texas. Vegetation and soils on the 4 study sites for the field trials consisted of the following: mostly honey mesquite and tobosa grass (*Hilira mutica*) on clay loam soils in Dickens County (Esperanza Ranch; 33°24.936'N, 100°53.445'W); shinnery oak (*Quercus havardii*) complex in Kent County (Morrison Ranch; 33°20.167'N, 100°59.269'W); midgrass prairie with mesquite encroachment over loam soils in King County (Pitchfork Ranch; 33°37.132'N, 100°28.593'W); and midgrass-shortgrass community with sideoats grama (*Bouteloua curtipendula*) and plains bristlegrass (*Setaria vulpiseta*) with fine sandy loam soils in Lamesa County (Indian Canyon Ranch; 32°46.610'N, 101°48.696'W; USDA NRCS 2017).

METHODS

Micro-GPS Datalogger

We evaluated 8 PICA solar-recharged micro-GPS dataloggers manufactured by Ecotone Telemetry (Ecotone Ltd., Gdynia, Poland). The internal memory of the datalogger held ~65,000 location fixes and the 25.4-mm × 12.7-mm solar panel recharged a 4.15 volt battery. Each datalogger had a mass of 5.6 g without any augmentations. The overall dimensions of each GPS datalogger unit were 35 mm × 16 mm × 10 mm (length × width × height). We coated each datalogger with a single thin layer of brown low-gloss paint to match feather coloration of bobwhites. We attached a 2.0 g VHF radio transmitter (American Wildlife Enterprises, Monticello, FL, USA) to the upper left side of each datalogger with epoxy resin (Loctite, Rocky Hill, CT, USA; Figures 1, 2) to help locate deployed units. After all components were compiled, including the harness material, the units weighed ~8.4 g.

Each PICA datalogger had ultra high frequency (UHF) digital upload and download capabilities through a portable base station for remote data collection. The manufacturer-documented maximum download distance was ~200 m, depending on topography. The PICA datalogger could be programmed to acquire location fixes at intervals from continuous to 240 minutes between fixes for a duration up to

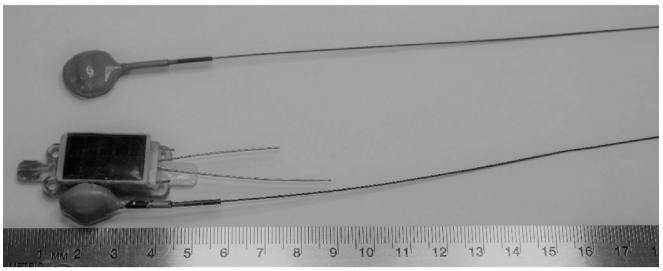

Fig. 1. Ecotone solar-recharged micro-GPS datalogger with a 2.0 g VHF transmitter (top unit) and how they were combined (bottom unit) for stationary and field trials in the Rolling Plains of West Texas, USA, 2016–2017.

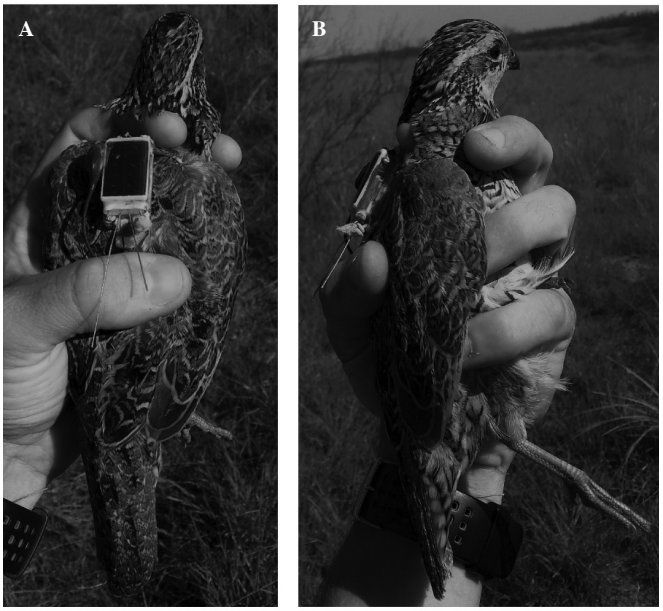

Fig. 2. Female northern bobwhite (*Colinus virginianus*) with a solar-recharged micro-GPS datalogger backpack attached, showing A) dorsal and B) profile views, in the Rolling Plains of West Texas, USA, fall 2016.

24 hours. The PICA dataloggers could record data as soon as they were deployed or could be delayed for 24 or 48 hours. Each unit was set on a 1 minute broadcast interval which would transmit the data to the base station when in range. We employed a 90 second search time for the GPS satellite acquisition. The manufacturer stated that each unit had a full charge at ~4.15 volts and when the charge was < ~3.5 volts the battery level would be too low to transmit data to the base station, but the unit could still acquire GPS location fixes.

Stationary Trial

We evaluated the datalogger accuracy, download distance, and battery life in native rangeland conditions at 0, 25, 50, 75, and 100% canopy cover. We estimated the percent vegetation cover with a densitometer placed at a height of ~10 cm. We attached 8 dataloggers to wooden stakes at ~45° angle at 10 cm above the ground to simulate backpack-style attachment to bobwhites. GPS accuracy and battery life were measured for 7 days under each cover type at 5, 10, and 60 minute GPS fix intervals. Each unit was active 13 hours/day during daylight hours. We measured the true location of the dataloggers with a Trimble GeoXT GeoExplorer GPSr unit (Trimble Inc., Sunnyvale, CA, USA) by averaging 100 fixes/trial. We measured the Euclidean distance between the estimated location of each GPS dataloggers and the true location to determine the accuracy of each datalogger by point-centroid in QGIS (version 2.18.6; Quantum GIS Development Team 2017; https://www.qgis.org, accessed on 15 Apr 2017). We calculated the download distance by using the known location of each datalogger, and beginning at 200 m from the units we closed the distance at a rate of 1 meter/minute until the base station wirelessly connected remotely to the unit. We used 200 m as the starting distance based on the manufacturer's suggested maximum download distance of the dataloggers. We used a hand-held Garmin eTrex 20x GPSr (Garmin Ltd., Olathe, KS, USA) unit to close in on the known location of the dataloggers. We began moving toward the dataloggers only when the Garmin units were at their most accurate (±2 m) based on the unit's internal error measurements. Each unit was scheduled to broadcast a signal for the base station to record data every 60 seconds.

Field Trial

We captured bobwhite using walk-in funnel type traps (Stoddard 1931) baited with milo during winter 2016–2017. We determined age and sex of the bobwhite by plumage and wing characteristics (Leopold 1939, Petrides and Nestler 1943, Rosene 1969). Each bobwhite was weighed to the nearest gram and received a No. 8 butt-end aluminum leg band. We placed dataloggers on bobwhites weighing ~170g to be within the recommended "5% rule" for wildlife research (Fair et al. 2010, Millspaugh et al. 2012). We attached each micro-GPS datalogger backpack-style with a 2.5 mm elastic shock cord around each wing and a 10 mm distance between the GPS unit and the back of the bird. We tested each wing individually and simultaneously to ensure ease of movement for flight. We downloaded location data and established survival (i.e., VHF signal change location or visual confirmation) of each bird weekly. We recovered each micro-GPS datalogger when the battery of the VHF or GPS unit was depleted or if predation occurred. We uploaded programming for each GPS datalogger before releasing the birds with either a 10 minute (morning movement) or 60 minute (daily movements) duty cycle per location. We chose to delay each duty cycle a full 24 hours after capture to minimize the effects of capture and to allow the bobwhite to acclimate to the backpack before data collection began. We measured daily and morning movement for bobwhite by calculated straight-line distance between each consecutive location fix using QGIS (Figure 3). We combined all daily and morning movements, respectively, to estimate the average movement for bobwhite. We split location times into daily (30 minutes before sunrise to 30 minutes after sunset) and morning (30 minutes before sunrise to 10:00 a.m.) categories. Daily movements data were collected as 1 location fix/hour (~10 locations) and morning movements were assigned as 1

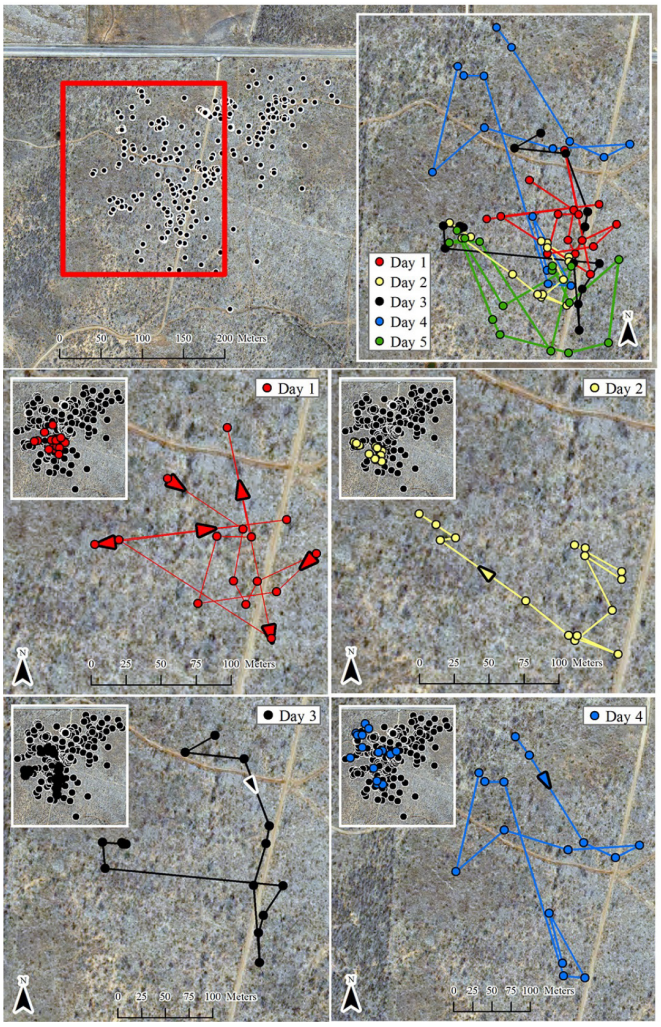

Fig. 3. Movement of northern bobwhite (*Colinus virginianus*) fitted with a solar-recharged micro-GPS datalogger monitored for 4 days on the Esperanza Ranch in the Rolling Plains of West Texas, USA, spring 2017.

fix/10 minutes until 10:00 (~25 locations). We calculated 50% and 95% minimum convex polygons (MCPs) for each bird in QGIS. We also examined the power consumption for each datalogger for the duration of its deployment. We attempted to remove all backpack GPS dataloggers by recapturing the bobwhite before the VHF transmitter expired at 82 days. We recaptured bobwhite by flushing the bird 3 times, then grabbing the bird by hand or using a hand-held fishing dip-net. All aspects of this research were in accordance with Texas Tech University Animal Care and Use Committee # 16008-02.

RESULTS

Stationary Trial

We used the same 4 dataloggers for the 5, 10, and 60 minute duty cycle error trials on the Texas Tech University native rangeland. We also ran a third control test on the Esperanza Ranch (5 minute interval). The overall accuracy for the 4 dataloggers across the 3 trials was 25.42 m ± 3.80 (mean ± standard error) from 9,921 locations. The 10 minute location acquisition period was the most accurate with 21.19 m (±1.79) while the 5 minute and 1 hour location fix had an average accuracy of 27.79 m (±2.43) and 27.28 m (±7.34), respectively. We noted that location accuracy and location fix rate decreased as vegetation cover increased (Table 1). The battery power dropped below 3.50 volts on day 4 for the units placed in the 50–100% vegetation cover types whereas units in the 0–25% vegetation cover type lasted a full 5 days. None of the units in the 5 minute location fix group lasted throughout the full 7 day trial. The recharge rate for the 10 minute and 60 minute location fix trial group was sufficient throughout the 7 day trial period (Figure 4). During the stationary trials, the average download distance was 67.95 m (±14.48) from the dataloggers with a range of 33–145 m.

Field Trial

We deployed solar-recharged micro-GPS dataloggers on 25 bobwhites between August 2016 and April 2017. We measured daily movement for 13 bobwhites on 4 ranches and morning movements for 4 bobwhites on 1 ranch. Eight bobwhites with dataloggers were censored due to either predation early in the deployment (<3 days) or improper duty cycle uploaded. We removed these bobwhites from any data analysis. Average time deployed was 18.5 days (range = 6–52 days). Daily movement of bobwhite averaged 960 m (±9) with 2,795 locations and morning movements averaged 490 m (±7) from 1,672 locations. Measured area of use for the daily movements was 15.17 ha (±1.60) and 3.58 ha (±0.36) for the 95% and 50% MCPs, respectively. The morning areas used by bobwhite were slightly larger for the 95% MCPs (17.76 ha ± 5.78) and consistent for the 50% MCPs (3.04 ha ± 0.90). On average, GPS dataloggers were ~4.67% (± 0.14) of a bobwhite's body weight. The average distance from birds that were flushed was 46.6 m (36.7 m for 3 birds with dataloggers on the Esperanza Ranch and 51.0 m for 4 birds on the Morrison Ranch). We were unable to recover 3 GPS dataloggers due to a malfunction with the VHF transmitters. Power consumption and recharge varied between each datalogger attached to bobwhites (Figure 5).

Table 1. Accuracy results (± standard error [SE]) for 4 solar-recharged micro-GPS dataloggers with a 5-minute, 10-minute, and 1-hour location fix schedule during a stationary trial in West Texas, USA, spring 2017.

Datalogger unit	Vegetation cover	Location schedule	Error rate (m) ± SE	Locations (n)
PIC01	0%	5-mins	31.19 ± 3.56	1,130
PIC04	25%	5-mins	28.53 ± 1.84	1,333
PIC10	50%	5-mins	28.30 ± 2.87	905
PIC07	75%	5-mins	28.60 ± 2.08	983
PIC08	100%	5-mins	22.37 ± 1.83	808
PIC01	0%	10-mins	09.22 ± 0.52	907
PIC04	25%	10-mins	13.12 ± 0.90	917
PIC10	50%	10-mins	17.49 ± 1.22	921
PIC07	75%	10-mins	32.01 ± 2.67	513
PIC08	100%	10-mins	34.14 ± 3.64	516
PIC01	0%	1-hour	29.84 ± 15.49	273
PIC04	25%	1-hour	11.99 ± 1.58	196
PIC10	50%	1-hour	13.67 ± 1.82	196
PIC07	75%	1-hour	46.57 ± 9.10	100
PIC08	100%	1-hour	34.36 ± 8.75	100

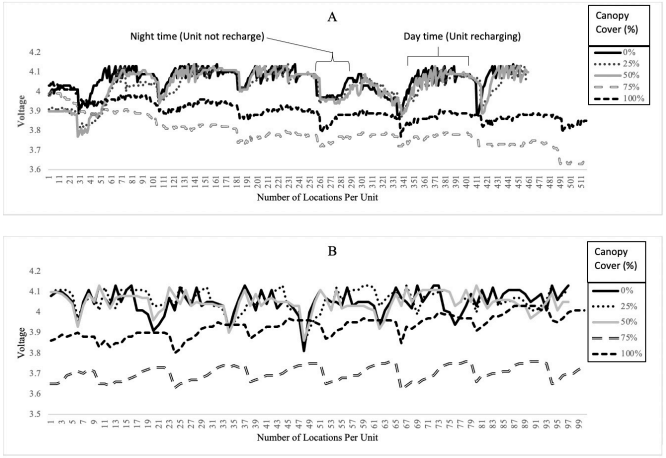

Fig. 4. Power consumption of 4 solar-recharged micro-GPS dataloggers with location fixes set for A) every 10 minutes and B) every 60 minutes over a 7-day trial period in 0–100% vegetation cover in the Rolling Plains of West Texas, USA, fall 2016.

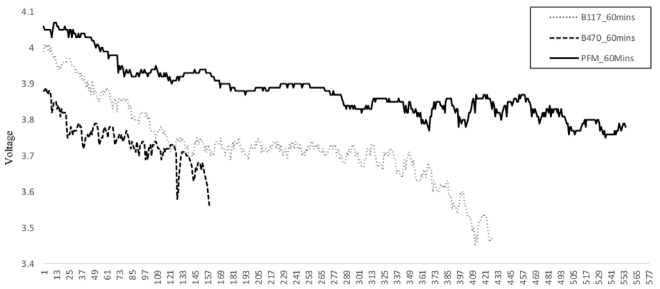

Fig. 5. Example of power consumption for solar-recharged micro-GPS dataloggers with location fixes set for every 60 minutes for northern bobwhite (*Colinus virginianus*) in the Rolling Plains of West Texas, USA, fall 2016.

DISCUSSION

Based on our results for accuracy and field tests, we believe these units have advantages and undoubted potential for monitoring bobwhite behavior, resource selection, and movements at the fine scale (i.e., roost and daily movement). Our stationary trials showed that PICA micro-GPS units exhibited a similar unit accuracy (27–31 m) to a previous research project (Marquardt et al. 2017) which used a different micro-GPS with shorter battery life. The units we selected were equipped with solar panels which we had hoped to increase the battery life of previous units. We found that as canopy cover increased during the stationary data collection the accuracy of the micro-GPS unit decreased and power consumption outpaced solar recharge, resulting in only ~1–2 days of data collection. We found that if bobwhite used areas with <50% canopy cover the solar panels on the units could maintain an adequate charge to continue data collection for 50+ days with a duty cycle of a location fix per 60 minutes for 13 hours/day. Previous research has shown that bobwhite in the Rolling Plains ecoregion of Texas tend to select areas with <50% canopy cover (Dabbert and Verble-Pearson 2017). Battery power consumption and deployment durations will depend on research needs such as an increased duty cycle (i.e., more locations per day), weather conditions (i.e., cloud cover), and bobwhite behavior (e.g., nesting). So if the research question revolves around nesting or is centered in a dense canopy, a reduced data collection cycle may be needed to increase battery power and ultimately longevity of the unit before it needs to be recovered.

Our data indicate that solar-recharged micro-GPS dataloggers can be used to monitor short-term movements for bobwhite in the Rolling Plains of West Texas. Previous research with VHF telemetry conducted on bobwhite found that mean daily movement of 149.31 m (±6.24) and an average distance reported for bobwhite of 960 m (± 9; Terhune et al. 2006). When we compared our data with Marquardt et al. (2017), their daily movement was higher (1,206–2,998 m) than our recorded movements. Yet our daily movement is slightly larger than movements reported by Cohen et al. (2020), which ranged from 704–785 m when they used micro-GPS units. These differences in daily movement could be due to the micro-GPS units used, location fix schedule, environmental conditions, or vegetation composition. Additionally, our home-range data showed a slightly smaller area (14.54 ha) than bobwhite home range (95% MCP) recorded in Southwest Georgia, USA (16.78 ha; Terhune et al. 2006). Yet bobwhite home range can vary based on resource availability, which could explain the difference we observed in our comparison with Terhune et al. (2006) regardless of differences in monitoring technology. Nevertheless, with micro-GPS units, we were able to utilize a large number of locations for multiple birds to estimate home ranges across multiple ranches at the same time, which could be costly or near impossible when using conventional VHF monitoring techniques.

A concern when using any monitoring technology on wildlife is that the units do not impede or harm the subject animals. When retrieving dataloggers from live bobwhite, we examined every bird for bruising under the wings or feather growth problems under each unit and did not observe any adverse effects caused by the solar-recharged GPS dataloggers. Yet a major concern we had with these units was the potential of the semi-reflective solar panel on each unit to draw the attention of raptors. Examining the effects of the micro-GPS units on bobwhite survival was outside the scope of the current project. Other researchers have found that upland game birds (i.e., greater sage-grouse [*Centrocercus urophasianus*]) fitted with dorsal solar GPS transmitters exhibited lower survival compared to VHF-tagged individuals (Caudill et al. 2014). It should be noted that Caudill et al. (2014) used suture dorsal-mounted backpack transmitters, which can have negative impacts on reproduction and survival (Paquette et al. 1997) and was different from our dorsal attachment method. We recommend that future research examine behavioral and survival impacts of solar-charged micro-GPS dataloggers on bobwhite across its range.

Even though the micro-GPS dataloggers can collect multiple locations without an observer present, currently there are limitations with the technology. The recharge capability of the solar units is limited by environmental conditions (i.e., sunny day vs. cloudy day). When solar-recharged GPS dataloggers are placed on wild free-roaming bobwhite, the duty cycle and environmental conditions must be considered to maintain sufficient voltage for the unit to function. When the duty cycle is set for intensive location fixes (e.g., 5 minutes), the recharging capabilities for the solar-recharged unit could be about 5 or 10 days with a 60 minute duty cycle with intermittent cloudy days (50% cloud coverage or more). If researchers can change the work duty schedule remotely before a cloudy day, it could reduce this potential negative impact on battery life. Another drawback for the GPS datalogger is the necessity for combining a VHF transmitter to relocate the datalogger or bird. With the current technological trade-off between small VHF unit and VHF battery power and detection distance, the best unit we could find was 2 g. These 2 extra grams could add too much weight to the units during certain times of the year when bobwhite

weigh less (i.e., winter months) and could cause units to exceed the <5% body weight threshold that is recommended for telemetry units attached to wildlife (Caccamise and Hedin 1985, Aldridge and Bringham 1988, Bridge et al. 2011). White (2021) observed that bobwhite equipped with a ~8.5 g solar GPS and VHF backpack had a significantly lower daily survival probability than bobwhite wearing traditional 6 g necklace-style VHF transmitters. However, the author was unable to establish a positive linear relationship between increasing bobwhite mass and daily survival probabilities and suggested that the maximum tolerable mass may be lower for backpack configurations (White 2021). Since we began our research, however, technological advances have decreased the weight of VHF (<1.0 g) and micro-GPS (4.5 g) transmitters considerably, which could make this consideration a moot point. It is also our intent to acknowledge that the rapid improvements and reduction in the size of GPS devices are ever-changing, which could provide researchers with more-suitable equipment for monitoring for their species of interest. We suggest that researchers and managers should pay close attention to the available literature and wildlife monitoring equipment manufacturers for the newest forms of technology for monitoring wildlife to provide the best available information for behavior, habitat use, and environmental impact on their species of interest.

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EVALUATING THE HARVEST RATE RECOMMENDATION FOR NORTHERN BOBWHITES IN SOUTH TEXAS

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ABSTRACT

The current harvest rate recommendation for northern bobwhites (*Colinus virginianus*; hereafter, bobwhite) in South Texas, USA is 20% of the autumn population, including crippling loss. This recommendation is based on population simulations of empirical data. We completed the first field evaluation of the 20% harvest recommendation by comparing prehunting and posthunting bobwhite density estimates on a hunted and nonhunted site in South Texas during the 2018–2019, 2019–2020, and 2020–2021 statewide bobwhite hunting seasons in Jim Hogg County, Texas. We conducted line-transect distance sampling surveys on 4 occasions per year (early November, mid-December, late January, early March) from a helicopter platform and prescribed the 20% annual bobwhite harvest from the November density estimate. According to our bobwhite density estimates, we found that bobwhite mortality (e.g., population decline) varied seasonally between hunted (= 54% ± 3%) and nonhunted sites (= 46% ± 5%). Our spring density estimates on both sites (i.e., hunted vs. nonhunted) were similar through the first 2 years but diverged in 2020–2021, with bobwhite densities that were 129% higher on the nonhunted site. Comparing our annual spring density results to the means reported from population models (i.e., 100-year simulations) used to create the 20% harvest recommendation, we found that the mean spring density of the model simulations was higher than our mean field estimates on both our hunted (+59%) and nonhunted sites (+77%). We recommend a conservative approach to prescribing a bobwhite harvest in South Texas, such as using the lower 95% confidence interval of a bobwhite abundance estimate for calculating harvest prescriptions, due to variability within density estimates and bobwhite survival in semiarid ranges.

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Key words: bobwhite hunting, *Colinus virginianus*, harvest rate recommendations, northern bobwhite, sustainable quail harvest

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Northern bobwhites (*Colinus virginianus*) have been studied intensively for a century (Sandercock et al. 2008). Despite such attention, populations have declined across their geographic ranges (Rosene 1969, Klimstra 1982, Brennan 1991). These population declines have been attributed to changes in land use (Klimstra 1982, Brennan 1991) and loss of usable space (Guthery 1997). However, questions regarding the effects of hunting and the sustainability of populations exposed to hunting remain unanswered (Brennan 1991, Brennan et al. 2014a).

Early research by Errington and Hamerstrom (1935) found a biological justification for northern bobwhite harvest through the compensatory relationship between natural mortality and hunting-related mortality that they deemed a "doomed surplus." This theory was supported by research for nearly 40 years (Guthery 2002), but later investigations revealed this historical theory to be potentially misleading (Roseberry and Klimstra 1984, Guthery 2002). The primary challenge is that northern bobwhite harvest tends to vary along a gradient between being entirely compensatory to natural mortality and entirely additive to natural mortality (Roseberry 1979, Roseberry and Klimstra 1984, Curtis et al. 1989, Pollock et al. 1989, Robinette and Doerr 1993, Dixon et al. 1996). This gradient is influenced by the rate and timing of harvest (Lehmann 1984, Roseberry and Klimstra 1984, Pollock et al. 1989, Robinette and Doerr 1993, Kokko 2001, Brennan et al. 2014*a*).

Rates of harvest imposed on bobwhite populations can also vary annually and regionally. Early researchers documented a relationship between population abundance and fluctuations in hunting pressure from year to year (Stoddard 1931, Vance and Ellis 1972). Peterson and Perez (2000) confirmed this relationship with national and statewide bobwhite survey data, considering it a "self-limiting" function of harvest. However, Guthery et al. (2004*b*) found that bobwhite hunter efficiency and average hunter skill can increase during population lows, which can have impacts on localized densities. State regulations regarding bobwhite harvest are constructed to allow maximum flexibility and opportunity, providing only a general framework (e.g., season dates, daily bag limits) for management decisions at fine scales (Cooke 2007). Changes to these regulations, such as reductions to bag limits and shorter season lengths, may have limited effects on local populations (Peterson and Perez 2000, Peterson 2001, Guthery et al. 2004*a*, Tomeček et al. 2015). Therefore, harvest itself must be managed at the individual property or pasture scale (Lehmann 1984, Williams et al. 2004, Sands et al. 2012, Tomeček et al. 2015).

To this day, there is still considerable uncertainty regarding recommended northern bobwhite harvest rates. Proposed northern bobwhite harvest rates have varied across the species' geographic range from 0% to 70% (Guthery et al. 2000). In the 1930s, Stoddard (1931) considered a harvest rate of less than 50% sustainable depending on environmental conditions and the control of predators. Likewise, Rosene (1969) recommended a maximum harvest of 45% for the southeastern United States. In Illinois, USA, Vance and Ellis (1972) argued that a 70% harvest compensates for natural mortality. However, according to northern bobwhite population simulations by Roseberry (1979), harvest beyond 40–45% of fall populations was detrimental to maintaining sustainable breeding populations, a result that was supported by subsequent work by Sands (2010) and Guthery et al. (2000).

Theoretically, a sustained yield harvest should be prescribed to meet a desired spring density that will maximize the rate of population gain from spring to fall through density-dependent production (Guthery 2002). In areas with highly variable and unpredictable weather patterns (e.g., South Texas, USA), underlying density-dependent processes act inconsistently through time and space (DeMaso et al. 2013), and more conservative approaches to harvest are thus recommended (Sands et al. 2013). Therefore, maintaining a viable northern bobwhite population should be the harvest management focus. A viable breeding density of bobwhites should persist after total fall-to-spring mortality, including harvest (Sands 2010, DeMaso et al. 2011).

The current harvest recommendation for South Texas is a 20% harvest, including factoring for crippling loss (Brennan et al. 2014*a*). This recommendation is based on simulated population responses to various harvest prescriptions and stochastic environmental conditions over a 100-year time frame (Guthery et al. 2000, Sands 2010). Population simulations have been useful in determining key variables that affect bobwhite population persistence (Roseberry 1979, Guthery et al. 2000, Sandercock et al. 2008, DeMaso et al. 2011, Rader et al. 2011, Sands et al. 2012, DeMaso et al. 2013). According to Sands (2010), a 20% annual harvest in South Texas achieved the highest yield with greater than 95% probability of population persistence over 100 years. Guthery et al. (2000) found similar results with their simulations, recommending a harvest rate of 20–25%. Reed et al. (1998), Guthery (2002), and Brennan (2002) recommended testing the results from such models in the field using empirical data.

Many researchers have called for studies regarding the effects of bobwhite harvest intensity and timing on subsequent breeding densities (Roseberry 1979, Brennan 1991, Burger et al. 1994, Peterson 1999, Peterson and Perez 2000, Rollins 2002). The controlled manipulation of bobwhite harvest intensity, timing, and distribution compared to carefully selected nonhunted control populations permits evaluations of harvest (Brennan 1991, Burger et al. 1994), but quantifying the effects requires a time series of fall density, spring density, natural mortality, and total harvest (Guthery 2002, Sands et al. 2013).

The aim of this study was to evaluate the effects and feasibility of implementing the sustainable harvest rate recommendation for bobwhite populations in South Texas and compare bobwhite density trends from field estimates of hunted and nonhunted study areas, as well as comparisons to outputs from model simulations. We used density estimates obtained from line-transect distance sampling from a

helicopter platform, which is the recommended method for estimating bobwhite density in Texas rangelands (DeMaso et al. 2010) and is widely used across South Texas. We controlled bobwhite harvest timing, intensity, and spatial distribution while making monthly density estimates of hunted and nonhunted bobwhites to compare seasonal population trends and mortality. We hypothesized that a 20% harvest is attainable using standard South Texas hunting practices at densities <1.0 bobwhite/hectare. Second, we hypothesized that hunting-related mortality consisting of 16% retrieved and 4% assigned crippling loss based on the fall abundance estimate would result in mean spring breeding densities within 95% confidence intervals (CIs) of both a nonhunted site with a similar fall density and the mean of spring density from simulations by Sands (2010).

STUDY AREA

The study took place on two ranches located in Jim Hogg County, Texas (Figure 1). The ranches are approximately 35 km south of Hebbronville, Texas, within the South Texas Plains Ecoregion (Gould 1975). The ranches are owned and operated by the East Foundation, established in 2007 from the estate of Robert C. East. The hunted site was the entire Buena Vista Ranch, with a total of 6,118 hectares. Our designated nonhunted area consisted of 3 separate sites (1,265 hectares, 1,593 hectares, and 1,518 hectares) totaling 4,376 hectares within the San Antonio Viejo Ranch (60,290 ha). We adopted these sites from Bruno (2018), which served as refence areas for a long-term quail and grazing study. Bruno (2018) selected multiple sites to mitigate any unforeseeable circumstance where a single area would no longer serve as a control (e.g., wildfire). Quail hunting was prohibited within the San Antonio Viejo Ranch; any potential quail hunting or baiting that may have occurred near the nonhunted sites would have been on adjacent property not owned by the East Foundation. The distance between hunted and nonhunted areas was 19 km. The primary land use for both ranches has been cattle production for over 100 years.

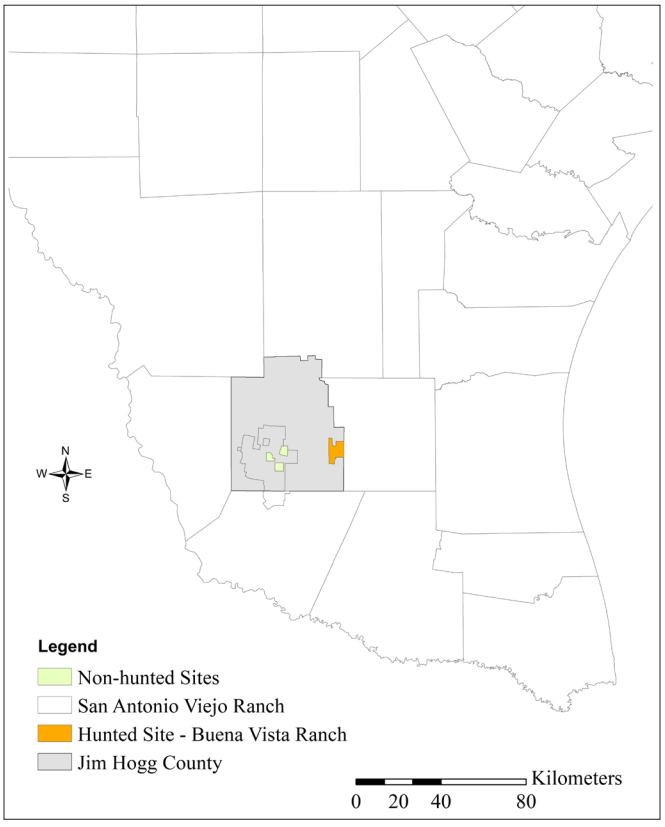

Fig. 1. Locations of hunted (Buena Vista Ranch) and nonhunted sites (3 reference pastures within the San Antonio Viejo Ranch) in Jim Hogg County, Texas, USA.

According to Sanders et al. (1974), the mean annual rainfall for Jim Hogg County is 47 cm. The annual rainfall on the hunted site was 92.2 cm in 2018, 50.1 cm in 2019, and 74.3 cm in 2020. The annual rainfall on the nonhunted area was 72.1 cm in 2018, 39.9 cm in 2019, and 79.3 cm in 2020. The mean daily temperature is 23° C, with a summer average of 30.5° C and a winter average of 15° C (Sanders et al. 1974). Predominant soil on both sites ranged from deep fine sands to sandy loams (Sanders et al. 1974, Gould 1975). Dominant woody vegetation consisted of honey mesquite (*Prosopis glandulosa*), brasil (*Candalia hookeri*), granjeno (*Celtis pallida*), and catclaw acacia (*Acacia greggi*). The herbaceous plant community was dominated by seacoast bluestem (*Schuzachyrium scoparium* var. *littorale*), Lehman love grass (*Eragrostis lehmanniana*), purple threeawn (*Aristida purpurea*), Texas broomweed (*Gutierrezia texana*), and croton (*Croton* spp.).

METHODS

Abundance Estimates and Population Trends

We estimated bobwhite abundance for our study sites using line-transect distance sampling from a helicopter platform. We contracted a Robinson R44 helicopter (Robinson Helicopter Co., Torrance, CA, USA) and pilot for each survey. We created the survey transects using ArcMap 10.8.0 (Esri, Inc., Redlands, CA, USA), spacing transects 200 meters apart to simulate 100% coverage (Figure 2). We oriented the transects on the hunted site from north and south to account for the geographical shape of the property boundary, while the transects on the nonhunted site were oriented east and west, as established during the long-term monitoring project on this area that began in 2014 (Bruno 2018). Pilots followed transect routes loaded into Garmin Nuvi 52LM (Garmin Corp., Lenexa, KS, USA) using Mapwell 11.0 software (BALARAD, Slovak Republic). We traversed every other transect until all transects were surveyed to reduce the probability of double counts (Rusk et al. 2007, Schnupp et al. 2013).

Following the protocols outlined by Schnupp et al. (2013) and DeMaso et al. (2010), we maintained 3 observers and 1 pilot, flying at average speeds of 37 km/hr and an altitude

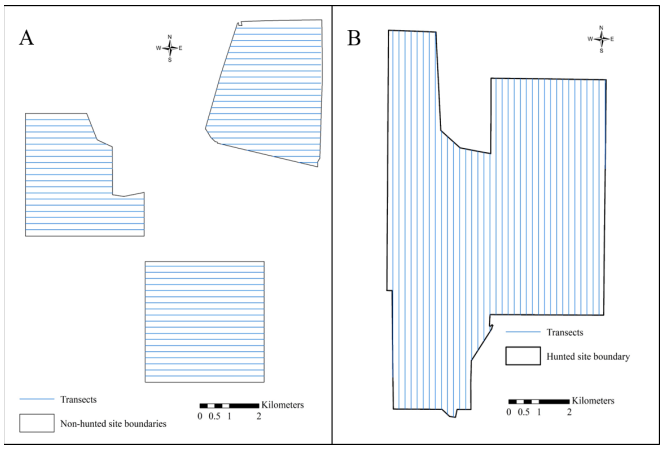

Fig. 2. Line transects for distance sampling from a helicopter platform on A) nonhunted and B) hunted sites in Jim Hogg County, Texas, USA.

of 7–10 meters. Northern bobwhite locations were obtained from laser range finders (Trimble Laser Ace 1000, Trimble Navigation Ltd., Sunnyvale, CA, USA) and stored on a Juno Handheld unit (Trimble 5 series, Trimble Navigation Ltd.). In December 2020, we incorporated a TruePulse 360r laser rangefinder (Laser Technology Inc., Centennial, CO, USA) after evaluating our equipment's accuracy from the helicopter platform (Montalvo et al. 2022: under review). During the survey, the front-seat observer detected coveys directly in front of the helicopter while the two rear-seat observers detected coveys to the left and right of the helicopter (DeMaso et al. 2010, Schnupp et al. 2013). Upon detecting a covey, the pilot held position by hovering (Schnupp et al. 2013) while the observer marked the location of the initial observation with a laser range finder and estimated the number of birds within the covey. Rear-seat observers would mark locations on their respective sides, and the front-seat observer operated the Juno. The pilot would signal a covey when detected, but was not considered an observer (Schnupp et al. 2013).

We conducted the first line-transect distance sampling survey in December of the 2017–2018 hunting season (28 Oct–25 Feb) to obtain baseline bobwhite densities prior to any harvest on study sites. During the subsequent years, the surveys reflected critical times associated with our evaluation of harvest and overwinter mortality of northern bobwhite populations (Rosene 1969:180, Lehmann 1984:306, Roseberry and Klimstra 1984:5, Burger et al. 1994, DeMaso et al. 2010). We conducted the pre-hunt survey at the onset of the statewide hunting season (i.e., early November) and a pre-breeding survey in early March (DeMaso et al. 2010, Brennan et al. 2014*a*), before covey breakup and reproductive efforts. We flew two additional surveys during the hunting season to compare mortality rates (i.e., harvest and natural mortality) between 3 designated periods representing the early, middle, and late months of the hunting seasons. Therefore, we conducted 4 flights/year on both hunted and nonhunted sites, occurring in early November, mid-December, late January, and early March.

Harvest Methods and Structure

We prescribed a northern bobwhite harvest of 20% to the hunted area as recommended by Brennan et al. (2014*a*), using the abundance estimates from the November surveys. The calculated prescription included both bobwhites retrieved and the estimated number of bobwhites shot but not retrieved (i.e., crippled [downed, legged, feathered]) while hunting. The projected figure of crippled bobwhites was according to Haines et al. (2009), who estimated losses to be on average 20% of the bobwhites brought to bag. Therefore, the 20% harvest recommendation represented a 16% retrieved and a 4% figure of crippling loss (i.e, harvest rate [20%] × crippling rate [20%] = 4%, or 25% of total harvest). However, researchers documented all hunter-covey interactions, including the detected number of crippled bobwhites harvested during each covey encounter. When the number of crippled bobwhites exceeded the 4% projection for the year, additional crippled bobwhites counted towards the total harvest.

We calculated harvest prescriptions for each pasture (i.e., 5 pastures ranging from 1,093 hectares to 3,077 hectares) to distribute harvest based on local density (Williams et al. 2004, Sands et al. 2012, Brennan et al. 2014*a*, Tomeček et al. 2015). Additionally, the pasture quotas were divided evenly across our early (early November–mid-December), middle (mid-December–late January), and late periods (late January–early March). However, the quota per period was considered a "target" for our hunting cooperators without penalty for falling short of the monthly quota.

The bobwhite hunting methods were standard for South Texas (Howard 2007). Hunters followed pointed dogs in modified hunting vehicles until a covey was pointed, where hunters approach the covey on foot (Hernández and Guthery 2012). Hunters were not allowed to use supplemental feed or bait along roadsides. However, they could pursue any covey found within the hunted area, without limits to the number of bobwhites harvested per covey or the number of pursuits following the covey rise. Therefore, we limited hunters only according to state game regulations and the total annual harvest prescription.

We recorded all hunting activities and harvest using detailed hunting logs (see Woodard et al. this volume). A trained observer would ride with the hunting party or follow the hunting party in a utility task vehicle (UTV), staying within a close proximity (i.e., <9 meters directly behind the hunting party). Observers documented each covey interaction, including an estimate of covey size, shots fired, bobwhites retrieved, and bobwhites crippled.

Age and Sex Ratios

We estimated the age and sex ratios of bobwhites on both the hunted and nonhunted sites. We determined age (i.e., juvenile or adult) and sex (i.e., male or female) according to Rosene (1969). When possible, we determined the estimated hatch date for juvenile bobwhites within our samples (Hernández and Guthery 2012). We determined sex and age

ratios for our hunted site from the hunter-harvested bobwhites, and we obtained age and sex ratios on the nonhunted sites from trapped and released northern bobwhites. We used standard funnel traps (Stoddard 1931) baited with grain sorghum (*Sorghum bicolor*) for capture. We followed all animal care and use guidelines according to Institutional Animal Care and Use Committee approval number 2018-01-31-A3 and Texas Parks and Wildlife Department scientific research permit number SPR-0413-044.

ANALYSES

Abundance Estimates

We estimated bobwhite density for each helicopter survey using the length of transects, covey detections, covey sizes, and perpendicular distances within Program Distance version 7.2, release 1 (Thomas et al. 2010). We analyzed the bobwhite abundance from our November survey for each year and site using the Conventional Distance Sampling (CDS) engine within Program Distance to determine the annual bobwhite harvest quotas for that specific hunting season. Upon completion of the last survey of the year (i.e., March survey), we analyzed seasonal density trends per site using CDS with a pooled detection function, CDS stratified by month, and multiple covariate distance sampling (MCDS) with the month as a covariate within Program Distance (Marques et al. 2007). This approach allowed for improved precision of our time-series analysis and our original November density estimate (Marques et al. 2007, Buckland et al. 2015). We fit probability detection functions from perpendicular distance measurements and examined frequency histograms for outliers and truncation points (Buckland et al. 2001). We fit models to the detection function and assigned a key function (i.e., Half normal, Hazard, or Uniform) along with a series expansion term if required (i.e., Cosine, Simple polynomial, Hermite polynomial), evaluating each model based on the three goodness of fit tests (i.e., Cramer VonMises with cosine and uniform, Kolmogorov-Smirnov) and Akaike's Information Criterion (Buckland et al. 2001; see Appendices A, B, C, D).

Hunted vs. Nonhunted Comparisons

We compared densities between hunted and nonhunted sites using the Z-test for independent samples outlined in Buckland et al. (2001:eqn. 3.102). We estimated survival and mortality (i.e., population decline) across hunting seasons (i.e., fall–spring) and within seasons (i.e., early, middle, late periods of the hunting seasons) by measuring changes in density on both the hunted and nonhunted sites (Roseberry and Klimstra 1984, DeMaso et al. 2010). Under this approach, we assumed density changes represent mortality and a balance between immigration and emigration (i.e., immigration + emigration = 0). This assumption is supported by Teinert et al. (2013), who analyzed mark-recapture data of radio-collared bobwhites during the fall–spring periods in South Texas.

Specifically, we calculated the total mortality (i.e., percent decline; equation 2.1) from prehunting to posthunting (Nov–Mar; Roseberry and Klimstra 1984, DeMaso et al. 2010) and for each period (i.e., early, middle, late), along with the percentage of natural mortality (NM) not accounted for by harvest (K; Roseberry and Klimstra 1984). Total mortality (Q) of a study site during a period of interest can be described as the difference between the prehunting bobwhite abundance (N_i) and the posthunting abundance (N_{i+1}). Subsequently, we estimated percent mortality (M) or percent decline and percent mortality not accounted for by harvest using the following:

Equation 2.1 $M = Q/N_i$, or $M = (N_i - N_{i+1})/N_i$

Equation 2.2 $NM = M - (K/N_i)$, or $(Q - K)/N_i$

We used the additive model of harvest mortality to determine the nature of harvest (equation 3; Ricker 1958). Furthermore, we estimated the rate of bobwhites lost to bobwhites harvested (α–additivity, equation 4), the proportional reduction in post-hunt population (p_a, equation 5), and the proportional reduction in one fall population to the next (β–additivity, equation 6). The α–additivity was calculated for each period by dividing the difference in estimated abundances on the nonhunted sites (N_{po}) and the abundance estimate of the hunted site (N_{ph}) by the total harvest (K) for the period (Guthery 2002). Proportional reduction in post-hunt population due to harvest (p_a) was calculated for the periods (Guthery 2002), while the proportional reduction in one fall population ($N_{po\text{-}f}$) to the next (β–additivity) was calculated only annually (Guthery 2002).

Equation 3 $Q = V_0 + K_0 - V_0K_0$

Equation 4 $\alpha\text{–additivity} = (N_{po} - N_{ph})/K$

Equation 5 $p_a = (N_{po} - N_{ph})/N_{po}$

Equation 6 $\beta\text{–additivity} = [N_{po\text{-}f} + 1 - N_{ph\text{-}f} + 1\ ]/N_{po\text{-}f}$

where,

V_0 = natural mortality in the absence of harvest mortality

K_0 = harvest mortality in the absence of natural mortality

K = harvest mortality in the presence of natural mortality

HR = harvest rate (periodic or seasonal)

We calculated percent summer gain (i.e., population increase from spring to fall) and adult summer mortality (ASM) annually for hunted and nonhunted areas. Percent summer gain (PSG) is derived from the proportional increase in net production of northern bobwhites from spring (N_b) to fall (N_f) using equation 7 (Roseberry and Klimstra 1984). Adult summer mortality is derived from the percent summer gain and the ratio of juveniles to adults (J:A) from our study sites (equation 8; Guthery 2002).

Equation 7 $PSG = [(N_f - N_b)/N_b] \times 100$

Equation 8 $ASM = 1 - (PSG + 1)/(J{:}A + 1)$

RESULTS

Based on our November bobwhite abundance estimates, the 20% harvest prescription for the hunted site was 422 bobwhites during the 2018–2019 hunting season (27 Oct–24 Feb), 852 bobwhites during the 2019–2020 season (26 Oct–23 Feb), and 1,005 bobwhites during the 2020–2021 season (31 Oct–28 Feb; Table 1). The harvest prescription was reached

for each of the 3 hunting seasons, requiring 59 bobwhite hunts (163.2 hours) in 2018–2019, 74 bobwhite hunts (254.4 hours) in 2019–2020, and 78 bobwhite hunts (250.5 hours) in 2020–2021 (Table 2). The number of crippled and lost bobwhites detected by hunting parties was above the 4% prescription (i.e., predicted crippling losses) during 2 years, representing 30% of overall harvest mortality in 2019–2020 and 35% of the overall harvest in 2020–2021.

Our bobwhite density estimates on both the hunted and nonhunted sites were similar during our baseline survey in December of the 2017–2018 hunting season (Table 3, Figure 3). In 2018–2019, we detected an increase in bobwhite density from November to December on both sites, along with evidence of a late-season hatch (Woodard et al. 2019). However, from December through March, bobwhite populations on both hunted and nonhunted sites had similar monthly trends and similar pre-breeding densities. During the 2019–2020 hunting season, we detected a sharp population decline on our nonhunted site between November and December. The spring breeding population (i.e., March) on our nonhunted site was 35% lower than our hunted site. During the 2020–2021 hunting season, our bobwhite density estimates were lower on the hunted site for each survey. Spring bobwhite density on our hunted site following the 2020–2021 hunting season was 55% lower than our nonhunted site. The mean spring density estimate across years and sites was 0.33 ± 0.003 bobwhites/hectare. Compared to simulations from Sands (2010), our observed spring densities were 59% (49–78%) lower than simulated densities on the hunted site and 77% (73–82%) lower on the nonhunted sites (Table 4).

The seasonal analysis conducted using MCDS improved the model fit of our detection functions and precision in density estimates for both sites, allowing us to reevaluate our annual (Table 5) and periodic (Table 6) harvest rates. According to our seasonal analysis, the realized harvest rate was 12% during the 2018–2019 hunting season, 17% in 2019–2020, and 22% in 2020–2021.

The mean seasonal mortality (i.e., population decline from November to March) was 54% (range = 32–77%) on our hunted site and 46% (range = 13–66%) on our nonhunted site (Table 7). Mortality per period (i.e., early, middle, late) varied between years and from site to site (Table 8). The greatest variation in mortality per period between the hunted and the nonhunted site occurred during the late period of 2020–2021, with total periodic mortality on the hunted site 10% greater than the nonhunted site (21% vs. 31%).

The estimated seasonal mortality varied from predictions using the additive harvest model. Mortality on our hunted site was greater than predicted in the 2018–2019 and 2020–2021 hunting seasons and less than the predicted mortality in the 2019–2020 season (Table 9). Mortality per period also varied between our observed rate and predicted. The additive model underpredicted mortality by as much as 16.4% and overpredicted mortality by up to 16.8% (Table 10). Our evaluations of the

Table 1. Annual harvest prescriptions for northern bobwhites (*Colinus virginianus*) on designated hunted site based on November abundance estimates calculated from line-transect distance sampling from a helicopter platform during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. The 20% harvest prescription represents a 16% retrieved and 4% crippling loss as recommended by Brennan et al. (2014*a*).

Year	Abundance (95% CI)	% CV	20% Harvest	Retrieved; crippled
2018–2019	2,100 (1,588–2,803)	14.5%	422	(338; 84)
2019–2020	4,262 (3,302–5,501)	13.0%	852	(682; 170)
2020–2021	5,026 (3,792–6,661)	14.4%	1,005	(804; 201)

Table 2. Summary of annual northern bobwhite (*Colinus virginianus*) hunting pressure and harvest according to designated periods: early (Nov–mid-Dec), middle (mid-Dec–late Jan), and late (late Jan–late Feb). The hunting parameters were collected during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA.

Year	Period	Hunts	Hunting hours	Total harvest	Retrieved; crippled
2018–2019	Early	10	24.9	30	(23; 7)
	Middle	33	91.6	269	(213; 56)
	Late	16	46.7	124	(102; 22)
	Total	59	163.2	423	(338; 85)
2019–2020	Early	23	70.8	201	(154; 47)
	Middle	35	124.7	413	(322; 91)
	Late	16	58.9	238	(182; 56)
	Total	74	254.4	852	(658; 194)
2020–2021	Early	24	73.7	201	(150; 51)
	Middle	37	118.4	548	(422; 126)
	Late	17	58.4	250	(170; 80)
	Total	78	250.5	999	(742; 257)

Table 3. Comparisons of northern bobwhite (*Colinus virginianus*) densities ($\hat{D}$, 95% CIs, coefficients of variation [CVs]) between hunted and nonhunted sites obtained from line-transect distance sampling surveys via helicopter platform conducted in 1) early November, 2) mid-December, 3) late January, and 4) early March during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA.

		Hunted site		Nonhunted site				
Year	Survey	$\hat{D}$ (± 95% CI)	% CV	$\hat{D}$ (± 95% CI)	% CV	Difference ± SE[a]	z-score[a]	*P*-value[b]
2017–2018[c]	2	0.61 (0.46–0.81)	14.2%	0.62 (0.48–0.79)	12.5%	- 0.01 ± 0.12	0.06	0.952
2018–2019	1	0.45 (0.33–0.62)	15.6%	0.35(0.27–0.44)	12.3%	+ 0.11 ± .08	1.38	0.167
	2[d]	0.59 (0.43–0.80)	15.6%	0.45 (0.33–0.58)	14.5%	+ 0.14 ± 0.57	0.24	0.812
	3	0.48 (0.36–0.63)	13.8%	0.43 (0.29–0.53)	15.0%	+ 0.05 ± 0.08	0.56	0.575
	4	0.40 (0.30–0.53)	14.1%	0.39 (0.27–0.44)	12.3%	< 0.00 ± 0.09	0.04	0.964
2019–2020	1	0.84 (0.70–1.02)	9.6%	0.76 (0.46–1.24)	25.5%	+ 0.08 ± 0.19	0.43	0.664
	2	0.53 (0.43–0.66)	10.9%	0.39 (0.29–0.53)	15.5%	+ 0.14 ± 0.08	1.79	0.073
	3	0.50 (0.38–0.66)	13.9%	0.38 (0.28–0.50)	14.5%	+ 0.12 ± 0.09	1.43	0.153
	4	0.40 (0.31–0.51)	12.3%	0.26 (0.17–0.39)	21.2%	+ 0.14 ± 0.07	2.07	0.039
2020–2021	1	0.73 (0.61–0.88)	9.3%	0.93 (0.78–1.12)	9.2%	- 0.20 ± 0.10	1.90	0.057
	2	0.63 (0.53–0.76)	9.2%	0.84 (0.68–1.04)	10.9%	- 0.21 ± 0.11	1.97	0.048
	3	0.35 (0.29–0.42)	9.7%	0.45 (0.34–0.61)	15.0%	- 0.10 ± 0.06	1.66	0.097
	4	0.17 (0.12–0.22)	16.2%	0.38 (0.29–0.50)	13.5%	- 0.22 ± 0.05	3.97	< 0.001

[a] Standard error of the difference and z-score calculated according to Buckland et al. (2001).
[b] H_0: $D_1 - D_2$; or $D_1 - D_2 = 0$
[c] Single density estimates were completed during the 2017–2018 hunting season for baseline density comparisons.
[d] Survey 2 during the 2018–2019 hunting season was conducted on 1–2 February 2019.

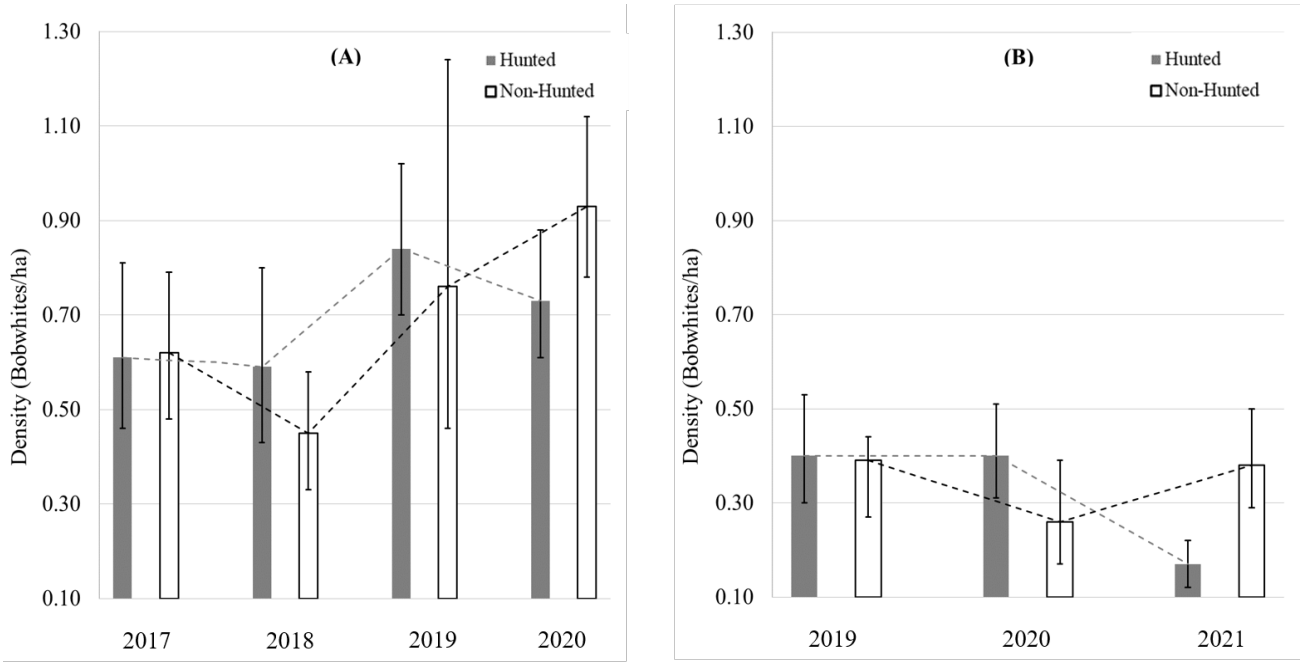

Fig. 3. Trends and comparisons of northern bobwhite (*Colinus virginianus*) densities ($\hat{D}$, 95% confidence intervals) in A) fall and B) spring between hunted and nonhunted sites obtained from line-transect distance sampling surveys via helicopter platform in Jim Hogg County, Texas, USA. Fall density estimates were calculated from November (2019 and 2020) and December (2017 and 2018) bobwhite surveys. Spring density estimates were calculated from March surveys conducted in 2019, 2020, 2021.

Table 4. Comparisons of spring northern bobwhite (*Colinus virginianus*) densities ($\hat{D}$, 95% CIs, coefficients of variation [CVs]) between field observations and means of 100-year simulations from stochastic model by Sands (2010). Observed density estimates obtained from line-transect distance sampling surveys via helicopter platform conducted in early March of 2019, 2020, and 2021 in Jim Hogg County, Texas, USA.

		Observed		Simulated		
Site	Year	$\hat{D}$ ± SE	(95% CI)	$\hat{D}$ ± SE	(95% CI)	Difference
Hunted	2018–2019	0.40 ± 0.07	(0.30–0.53)	0.78 ± 0.03	(0.71–0.84)	-0.38
Hunted	2019–2020	0.40 ± 0.04	(0.31–0.51)	0.78 ± 0.03	(0.71–0.84)	-0.38
Hunted	2020–2021	0.17 ± 0.02	(0.12–0.22)	0.78 ± 0.03	(0.71–0.84)	-0.61
Nonhunted	2018–2019	0.39 ± 0.06	(0.27–0.44)	1.46 ± 0.04	(1.39–1.54)	-1.07
Nonhunted	2019–2020	0.26 ± 0.05	(0.17–0.39)	1.46 ± 0.04	(1.39–1.54)	-1.20
Nonhunted	2020–2021	0.38 ± 0.05	(0.29–0.50)	1.46 ± 0.04	(1.39–1.54)	-1.08

Table 5. Comparisons of November northern bobwhite (*Colinus virginianus*) densities ($\hat{D}$, 95% CIs, coefficients of variation [CVs]) using a conventional distance sampling (CDS) analysis (November only) and results from the seasonal analysis (i.e., 4 surveys per hunting season). Density estimates were obtained from sites obtained from line-transect distance sampling surveys via helicopter platform during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons on the hunted and nonhunted sites in Jim Hogg County, Texas, USA. Seasonal analysis included conventional distance sampling with a pooled detection function, conventional distance sampling with a fully stratified detection function, and multiple-covariate distance sampling (see Appendix A and Appendix B).

		CDS analysis		Seasonal analysis				
Site	Year	($\hat{D}$ ± 95% CI)	% CV	($\hat{D}$ ± 95% CI)	% CV	Difference ± SE[a]	z-score[a]	P-value[b]
Hunted	2018–2019	0.34 (0.26–0.46)	14.8%	0.45 (0.33–0.62)	15.6%	- 0.11 ± 0.08	1.32	0.188
Hunted	2019–2020	0.70 (0.54–0.90)	13.0%	0.84 (0.70–1.02)	9.6%	- 0.15 ± 0.10	1.52	0.129
Hunted	2020–2021	0.82 (0.62–1.09)	14.4%	0.73 (0.61–0.88)	9.3%	+ 0.09 ± 0.13	0.66	0.510
Nonhunted	2018–2019	0.39 (0.29–0.53)	15.4%	0.35(0.27–0.44)	12.3%	+ 0.05 ± 0.07	0.64	0.525
Nonhunted	2019–2020	0.68 (0.44–1.04)	17.4%	0.76 (0.46–1.24)	25.5%	- 0.08 ± 0.22	0.36	0.721
Nonhunted	2020–2021	0.92 (0.76–1.11)	9.6%	0.93 (0.78–1.12)	9.2%	- 0.01 ± 0.15	0.08	0.940

[a] Standard error of the difference and z-score calculated according to Buckland et al. (2001).
[b] H_0: $D_1 - D_2$; or $D_1 - D_2 = 0$

Table 6. Comparisons of annual harvest rates and range (harvest rate × 95% CIs), according to November northern bobwhite (*Colinus virginianus*) abundance estimates ($\hat{D}$, 95% CIs) using a conventional distance sampling (CDS) analysis (November only) and results from the seasonal analysis (i.e., 4 surveys per hunting season) from line-transect distance sampling surveys via helicopter platform during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons on the hunted and nonhunted sites in Jim Hogg County, Texas, USA.

		CDS analysis		Seasonal analysis	
Year	Harvest	Abundance (95% CI)	% Harvest	Abundance (95% CI)	% Harvest
2018–2019	423	2,100 (1,588–2,803)	20.0 (15.1–26.6)	3,594 (2,630–4,911)[a]	11.8 (8.6–16.1)
2019–2020	852	4,262 (3,302–5,501)	20.0 (15.5–25.8)	5,153 (4,264– 6,226)	16.5 (13.7–20.0)
2020–2021	999	5,026 (3,792–6,661)	19.9 (15.0–26.3)	4,484 (3,728–5,395)	22.3 (18.5–26.8)

[a] December abundance used for realized harvest due to the increase in density from early November to mid-December (Woodard et al. 2019).

Table 7. Seasonal mortality (M; %) comparisons of northern bobwhites (*Colinus virginianus*) between hunted and nonhunted sites and percentage of natural mortality not accounted for by harvest (% NM) during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Seasonal mortality represents the difference in density estimates from November to March according to line-transect distance sampling via helicopter platform. Range values represent differences between lower 95% CI, upper 95% CI, and max difference (lower 95% CI – upper 95% CI) from November to March.

	Nonhunted site		Hunted site		
Year	M	ranges	M	ranges	NM[a]
2018–2019[b]	13.0	(16.7, 23.6, 53.1)	32.4	(30.3, 34.4, 62.7)	20.6
2019–2020	65.6	(62.7, 68.3, 86.2)	52.9	(55.4, 50.3, 69.4)	36.4
2020–2021	59.0	(62.2, 55.4, 73.8)	77.4	(80.3, 74.7, 86.4)	55.1

[a] Percentage of natural mortality not accounted for by harvest (% NM) on hunted site = total mortality rate – harvest rate.
[b] Seasonal mortality was calculated using difference between mid-December (peak density) to March density estimates due to increase in density from early November to mid-December (Woodard et al. 2019).

Table 8. Periodic mortality (M, %) comparisons of northern bobwhites (*Colinus virginianus*) between hunted and nonhunted sites, and percentage of natural mortality not accounted for by harvest (% NM) during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Periodic mortality represents the difference in density estimates between 4 seasonal surveys (early November, mid-December, late January, and early March) according to line-transect distance sampling via helicopter platform representing early, middle, and late hunting season periods. Range values represent differences between lower 95% CI, upper 95% CI, and max difference (lower 95% CI – upper 95% CI) from between seasonal surveys.

		Nonhunted site		Hunted site		
Year	Period	M	Ranges	M	Ranges	NM[a]
2018–2019	Early[b]	-	-	-	-	-
	Middle	3.9	(10.3, 8.6, 49.5)	18.4	(15.3, 21.4, 54.6)	10.9
	Late	9.5	(7.2, 16.5, 48.7)	17.2	(17.8, 16.6, 52.5)	12.9
2019–2020	Early	48.8	(38.1, 57.7, 77.0)	36.8	(38.4, 35.1, 57.8)	30.6
	Middle	2.3	(0.4, 4.2, 45.9)	5.5	(11.0, 0.0, 42.2)	-7.9
	Late	31.2	(39.5, 21.7, 65.8)	21.2	(18.5, 23.7 ,53.0)	11.3
2020–2021	Early	9.7	(12.7, 6.7, 39.3)	14.0	(13.8, 14.2, 40.4)	8.8
	Middle	46.3	(50.4, 41.8, 67.8)	44.5	(45.0, 44.0, 61.9)	18.9
	Late	15.4	(12.8, 17.9, 51.7)	52.6	(58.4, 47.4, 71.6)	28.9

[a] NM (%) on hunted site = total mortality rate – harvest rate.
[b] Bobwhite mortality was not estimated during the early period of 2018–2019 due to an increase in overall density from early November to mid-December (Woodard et al. 2019).

rate of bobwhites lost to bobwhites harvested (α–additivity), the proportional reduction in post-hunt population (p_α), and the proportional reduction in one fall population to the next (β–additivity) proved unrealistic (i.e., >1, or < 0). These models required identical starting densities and did not function when mortality on the nonhunted site was higher than on the hunted sites (Guthery 2002; see Appendix E).

The mean percentage of females across both hunted and nonhunted sites was 47%, ranging from 44% to 51.9%. The percentage of juveniles on hunted and nonhunted sites was similar during the 2018–2019 and 2020–2021 hunting seasons (Table 11). During the 2019–2020 hunting season, the percentage of juveniles on the nonhunted site was 16% lower than the hunted site. The percent summer gain (PSG) was positive for each summer analyzed (2019 and 2020) on both the hunted and nonhunted sites (Table 12). The estimated ASM on the hunted site was 24% higher than the nonhunted site during summer 2019 and 42% higher in summer 2020.

Table 9. Seasonal mortality (M, %) estimates of northern bobwhites (*Colinus virginianus*) as predicted using the additive harvest model and the observed mortality. Observed seasonal mortality was calculated using the difference in density estimates from November to March according to line-transect distance sampling via helicopter platform during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA.

	Predicted[a]	Observed[b]	
Year	M	M	Difference
2018–2019[c]	23.3	32.4	-9.1
2019–2020	71.3	52.9	18.4
2020–2021	68.1	77.4	-9.3

[a] Predicted mortality using the additive model of harvest mortality (equation 3; Ricker 1958): $Q_a = H_o + V_o + H_oV_o$.
[b] Observed mortality on the hunted site.
[c] Observed seasonal mortality was calculated using difference between mid-December (peak density) to March density estimates due to increase in density from early November to mid-December (Woodard et al. 2019).

Table 10. Periodic mortality (M, %) comparisons of northern bobwhites (*Colinus virginanus*) as predicted using the additive harvest model and the observed mortality during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Observed periodic mortality calculated using the difference in density estimates between 4 seasonal surveys (early November, mid-December, late January, and early March) according to line-transect distance sampling via helicopter platform representing early, middle, and late hunting season periods.

		Predicted[a]	Observed[b]	
Year	Period	M	M	Difference
2018–2019	Early[c]	-	-	-
	Middle	11.4	18.4	-7.0
	Late	13.3	17.2	-3.9
2019–2020	Early	52.0	36.8	15.2
	Middle	15.4	5.5	9.9
	Late	37.9	21.2	16.8
2020–2021	Early	14.4	14.0	0.5
	Middle	60.1	44.5	15.5
	Late	36.2	52.6	-16.4

[a] Predicted mortality using the additive model of harvest mortality (equation 2, Ricker 1958): $Q_a = H_o + V_o + H_oV_o$.
[b] Observed mortality on the hunted site.
[c] Bobwhite mortality was not estimated during the early period of 2018–2019 due to an increase in overall density from early November to mid-December (Woodard et al. 2019).

Table 11. Sex (M = male, F = female) and age (A = adult, J = juvenile) ratios of northern bobwhites (*Colinus virginianus*) from hunted and nonhunted sites during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Ratios were collected using hunter-harvested bobwhites along with trapped and released bobwhites.

				Sex			Age		
Year	Site	Method	*n*	M	F	% F	A	J	% J
2017–2018[a]	Hunted	Trap	133	72	61	45.9%	48	85	63.9%
	Nonhunted	-	-	-	-	-	-	-	-
2018–2019	Hunted	Harv	337[b]	185	149	44.6%	126	211	62.6%
	Nonhunted	Trap	61	31	30	49.2%	23	38	62.3%
2019–2020	Hunted	Harv	658	346	312	47.4%	193	465	70.7%
	Nonhunted	Trap	297[c]	163	129	44.2%	133	164	55.2%
2020–2021	Hunted	Harv	742[d]	388	353	47.6%	159	583	78.6%
	Hunted[e]	Trap	213[f]	104	90	46.4%	29	184	86.4%
	Nonhunted	Trap	245	117	126	51.9%	56	189	77.1%

[a] 2017–2018 was baseline year on hunted area, with hunting initiated during the 2018–2019 season.
[b] Three juveniles harvested of unknown sex.
[c] Five juveniles trapped and released of unknown sex.
[d] One juvenile harvested of unknown sex.
[e] Bobwhites were trapped and released on the hunted site in October 2020, prior to hunting season.
[f] Nineteen juveniles trapped and released of unknown sex.

DISCUSSION

Reaching the annual bobwhite harvest prescription was a matter of hunting efficiency and effort. For instance, covey encounter rates and harvest per covey varied between seasons and periods (see Woodard et al. this volume), but harvest prescriptions were reached by the addition of more hunts (i.e., effort). However, our harvest results revealed a potential discrepancy regarding total crippling loss. Our crippling rates (i.e., 20–26% of the total harvest, 25–35% of the retrieved harvest) were greater than reported by Rosene (1969) in Alabama, USA, Doster et al. (1982) in Florida, USA, and Roseberry and Klimstra (1984) in Illinois, USA. Haines et al. (2009) defined the total crippling loss as mortality in which 1) bobwhites are noticeably shot and downed, but not retrieved, 2) bobwhites are noticeably shot but not downed or retrieved (i.e., feathered), and 3) bobwhites are not noticeably shot or downed, but subsequently died from wounds undetected.

Table 12. Estimates of percent summer gain (PSG), adult summer mortality (ASM), and finite rate of increase (spring and fall) for northern bobwhites (*Colinus virginianus*) on hunted and nonhunted sites in Jim Hogg County, Texas, USA. Density was estimated using line-transect distance sampling via helicopter platform during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons.

Site	Year	Spring $\hat{D}$	Fall $\hat{D}$	J:A[a]	PSG[b]	ASM[c]	λ[d] (spring)	λ[d] (fall)
Hunted	2017[e]	-	0.61	1.77	-	-	-	-
	2018[e]	-	0.59	1.67	-	-	-	0.96
	2019	0.40	0.84	2.41	112.1%	37.8%	-	1.43
	2020	0.40	0.73	3.67	84.8%	60.4%	1.00	0.87
	2021	0.17	-	-	-	-	0.42	-
Nonhunted	2017[e]	-	0.62	-	-	-	-	-
	2018[e]	-	0.45	1.65	-	-	-	0.73
	2019	0.39	0.76	1.23	92.8%	13.5%	-	1.68
	2020	0.26	0.93	3.37	257.7%	18.2%	0.66	1.23
	2021	0.38	-	-	-	-	1.47	-

[a] Juvenile to adult ratio.
[b] Percent summer gain = $(D_{fall} - D_{spring})/D_{spring}$; see Roseberry and Klimstra (1984).
[c] Adult summer mortality = 1 – (PSG +1)/(J:A + 1); see Guthery (2002:53).
[d] Finite rate of increase (λ) = Dt +1/Dt
[e] Bobwhite densities were not estimated in March 2017 or March 2018.

During this study, hunters reached or exceeded the assigned crippling rate assumed by Brennan et al. (2014*a*) in all 3 years, without factoring for any bobwhites that were not noticeably downed or feathered (i.e., undetected cripples; Haines et al. 2009). Therefore, an unknown amount of crippling loss remains unaccounted for in addition to our total harvest.

Another challenge we found was related to our estimates of bobwhite density. Distance sampling from a helicopter has been shown to be a reliable method for estimating bobwhite densities (Shupe et al. 1987, Rusk et al. 2007, DeMaso et al. 2010), but changes within populations occurring after the calculation of a harvest prescription along with the variation within individual estimates evidently influenced results. For instance, during the 2018–2019 hunting season, our seasonal abundance estimate for December was 30% higher than our November estimate, changing our harvest prescription from 20% of the fall population to only 12%. In fact, the November density estimates from each initial survey (i.e., single November surveys) were different from the estimates from our seasonal analyses, despite statistical similarities (e.g., z-score *P*-values). According to Guthery (1988), the acceptable variation within a density estimate for bobwhites with proper survey distance sampling design is anything with less than a 20% coefficient of variation (% CV). The level of uncertainty with density estimates is a fundamental issue regardless of the species being sampled. However, this level of uncertainty seems to be heightened when prescribing bobwhite harvests. Using the November abundance estimate from 2020–2021 (CV = 14.4%, 95% CI = 3,792–6,661) as an example, the 20% harvest prescription (i.e., 1,005 bobwhites) was potentially 15% or 27% of harvest rate (i.e., 20% × 95% CIs).

Our average overwinter mortality on the hunted site (54% ± 3%) and the nonhunted site (46% ± 5%) was similar to those reported by Robinette and Doerr 1993 and Guthery (2002:101), and with scaled quail (*Callipepla squamata*) in New Mexico, USA by Campbell et al. (1973). The variation of overwinter mortality within sites and the similarities of overwinter mortality between sites provide evidence that the nature of harvest is a gradient between compensatory and additive, as Roseberry (1979) and many others have suggested. Our spring density and mortality rate estimates were similar between the hunted and nonhunted sites during the first 2 hunting seasons but diverged during the 2020–2021 hunting season. We assume that this was potentially influenced by the combination of harvest and environmental conditions. South Texas was exposed to below-freezing conditions that lasted 13 February–20 February 2021, which are highly unusual circumstances for bobwhites in this region. Roseberry and Klimstra (1984:62) reported a 230% increase in daily mortality during intense winter storms in Illinois. Stanford (1972) also reported lower spring densities and lower reproductive efforts following severe winters in Missouri, USA. However, whether the freeze of February 2021 factored into the total mortality rate on our hunted site remains unknown.

Another discrepancy we found was between our observed spring densities and the spring density of simulated populations from Sands (2010). However, Sands (2010:Table 3) also reported discrepancies between simulated results and the spring densities of his field observations. The Sands (2010) population model and models by Guthery et al. (2000) and DeMaso et al. (2011) were constructed from a hypothetical population within 800 hectares of 100% usable space (Guthery 1997). We assumed that the amount of usable space within our study sites is less than 100% but represents bobwhite habitat in South Texas. Additionally, Sands (2010) constructed his model using a mean annual mortality of 70% (Hernández et al.

2007), estimating natural mortality per season (i.e., period 4) by drawing a random value from normal distribution (±1 SD = 10%) with a mean mortality rate of 26%. Our results indicate that 26% natural mortality (range = 16%–36%) may have underpredicted mortality during the winter period within both hunted and nonhunted simulations. Therefore, the densities and outcomes reported from simulated models by Sands (2010) and the 20% harvest rate recommended by Brennan et al. (2014*a*) may require additional analyses. More recently, Sisson et al. (2017) recommended a 15% harvest in the southeastern United States (Alabama, Florida, Georgia, South Carolina), a figure they believe limits the additive effects of both harvest and translocation.

In summary, our 3-year evaluation of a sustainable harvest has provided valuable insight regarding bobwhite populations during the hunting season on relatively large areas (i.e., >4,000 hectares). Additional research using multiple harvest rates over longer temporal scales and multiple study sites would improve our understanding of the underlying nature of harvest and the long-term sustainability of populations exposed to hunting pressure.

MANAGEMENT IMPLICATIONS

Our results suggest that prescribing a 20% harvest to an estimate of density requires consideration for the variation within a density estimate. This variation can have a considerable influence on the realized harvest rates and total mortality. We found that annual and periodic differences in overwinter mortality varied between hunted and nonhunted populations. Average spring densities across both sites were less than those from the model simulations by Sands (2010), on which the 20% harvest recommendation was based. Therefore, we recommend applying a conservative approach when calculating a harvest prescription, using a reduced harvest rate (e.g., 15%) or calculating harvest prescriptions using the lower confidence intervals of density estimates.

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APPENDIX A. Model selection and results from season analysis (November, December, January, March) using conventional distance sampling with a pooled detection function, conventional distance sampling with a stratified detection function, and multiple covariate distance sampling with month as covariate for line-transect distance sampling surveys via helicopter platform on the hunted site during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Results include key function, parameters, Akaike's Information Criterion (AIC), and differences in AIC (ΔAIC), and three goodness of fit tests (GOF) recommended by Buckland et al. (2001): CvM = Cramer VonMises (cosine and uniform); K-S = Kolmogorov-Smirnov.

Year	Analysis[a]	Covariate[b]	Key function[c]	# parameters	ΔAIC	AIC	CvM (cos)	CvM (unif)	K-S
2018–2019	MCDS	Date	HR	5	0.00	2,549.10	0.60	0.60	0.55
	CDS	Stratified f(0)	HN+cos	5	0.87	2,549.97	-	-	-
	MCDS	Date	HN	4	2.13	2,551.23	0.70	0.60	0.51
	CDS	Stratified f(0)	HN+hp	4	2.17	2551.27	-	-	-
	CDS	Stratified f(0)	HR+sp	8	3.47	2552.57	-	-	-
	CDS	-	HN+cos	2	3.61	2552.71	0.90	1.00	0.95
	CDS	Stratified f(0)	UN+cos	5	3.74	2552.84	-	-	-
	CDS	-	HN+hp	1	3.90	2553.00	0.70	0.60	0.73
	CDS	-	HR+sp	2	4.12	2553.22	1.00	1.00	0.98
	CDS	-	UN+cos	2	5.18	2554.28	1.00	1.00	0.87
	CDS	-	HR+sp	3	0.49	5089.94	0.90	1.00	0.96
	CDS	Stratified f(0)	HN+hp	5	1.34	5090.79			
	MCDS	Date	HN	4	1.34	5090.79	0.70	0.80	0.70
	CDS	-	UN+cos	2	1.39	5090.85	0.90	0.80	0.80
	CDS	Stratified f(0)	HN+cos	4	1.54	5090.99			
	CDS	Stratified f(0)	UN+cos	5	3.10	5092.56			
	MCDS	Stratified f(0)	HR	5	9.69	5099.15	0.70	0.60	0.64
2020–2021	CDS	-	HN	1	0.00	5336.61	0.80	0.90	0.77
	CDS	-	HR+sp	2	1.20	5337.81	1.00	1.00	0.891
	CDS	-	UN+cos	2	1.52	5338.14	1.00	1.00	0.842
	CDS	Stratified f(0)	UN+cos	5	2.68	5339.29	-	-	-
	CDS	Stratified f(0)	HR+sp	8	2.68	5339.29	-	-	-
	MCDS	Date	HN	4	3.24	5339.85	0.70	0.80	0.78
	CDS	Stratified f(0)	HN+hp	5	3.34	5339.95	-	-	-
	CDS	Stratified f(0)	HN+cos	6	3.81	5340.42	-	-	-
	MCDS	Date	HR	5	5.24	5341.86	1.00	1.00	0.88

[a] Analysis: CDS = Conventional Distance Sampling; MCDS =Multiple Covariate Distance Sampling
[b] Covariate Date = month of survey (early November, mid-December, late January, early March).
[c] Key function [HN = Half-normal; HZ = Hazard-rate; UN = uniform] and adjustment terms [cos = cosine, sp = simple polynomial, hp=hermite polynomial].

APPENDIX B. Model selection and results from season analysis (November, December, January, March) using conventional distance sampling with a pooled detection function, conventional distance sampling with a stratified detection function, and multiple covariate distance sampling with month as covariate for line-transect distance sampling surveys via helicopter platform on the nonhunted site during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Results include key function, parameters, Akaike's Information Criterion (AIC), and differences in AIC (ΔAIC), and three goodness of fit tests (GOF) recommended by Buckland et al. (2001): CvM = Cramer VonMises (cosine and uniform); K-S = Kolmogorov-Smirnov.

Year	Analysis[a]	Covariate[b]	Key function[c]	# parameters	ΔAIC	AIC	CvM (cos)	CvM (unif)	K-S
2018–2019	CDS	Stratified f(0)	HN	4	0.00	2188.04	-	-	-
	CDS	Stratified f(0)	UN+cos	3	0.22	2188.26	-	-	-
	MCDS	Date	HR	5	4.20	2192.24	0.90	0.80	0.81
	CDS	Stratified f(0)	HR+sp	8	7.69	2195.73	-	-	-
	CDS	-	HN	1	30.48	2218.52	0.70	0.70	0.44
	CDS	-	UN	1	31.21	2219.25	0.70	0.80	0.56
	CDS	-	HR+sim	3	33.64	2221.69	1.00	1.00	0.81
2019–2020	CDS	Stratified f(0)	HR+sim	8	0.00	2472.66	-	-	-
	CDS	Stratified f(0)	UN+cos	6	2.42	2475.08	-	-	-
	CDS	-	HR+sim	2	2.43	2475.09	0.80	0.80	0.52
	CDS	-	UN+cos	1	2.53	2475.19	0.50	0.50	0.12
	CDS	-	HN	1	2.88	2475.54	0.70	0.60	0.24
	CDS	Stratified f(0)	HN+cos	7	3.67	2476.33	-	-	-
	CDS	Stratified f(0)	HN+hp	5	4.84	2477.50	-	-	-
	MCDS	Date	HN	4	5.97	2478.63	0.70	0.70	0.48
	MCDS	Date	HR	5	8.19	2480.85	0.80	0.80	0.67
2020–2021	MCDS	Date	HN	4	0.00	4695.94	1.00	1.00	0.95
	CDS	Stratified f(0)	UN+cos	5	0.06	4696.00	-	-	-
	CDS	Stratified f(0)	HN	4	0.13	4696.07	-	-	-
	MCDS	Date	HR	5	2.19	4698.13	1.00	1.00	0.95
	CDS	Stratified f(0)	HR+sp	9	4.73	4700.68	-	-	-
	CDS	-	UN+cos	1	5.12	4701.06	1.00	1.00	0.97
	CDS	-	HN	1	6.52	4702.46	1.00	1.00	0.97
	CDS	-	HR	2	8.25	4704.19	1.00	1.00	0.93

[a] Analysis: CDS = Conventional Distance Sampling; MCDS =Multiple Covariate Distance Sampling
[b] Covariate Date = month of survey (early November, mid-December, late January, early March).
[c] Key function [HN = Half-normal; HZ = Hazard-rate; UN = uniform] and adjustment terms [cos = cosine, sp = simple polynomial, hp=hermite polynomial].

APPENDIX C. Model selection and results of conventional distance sampling (CDS) estimates of bobwhite density per periodic survey (individual CDS per month) from November to March on the hunted site during the 2017–2018, 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Results include key function, parameters, Akaike's Information Criterion (AIC), and differences in AIC (ΔAIC), and 3 goodness of fit tests (GOF) recommended by Buckland et al. (2001): CvM = Cramer VonMises (cosine and uniform); K-S = Kolmogorov-Smirnov.

Year	Month	Key function[a]	# parameters	ΔAIC	AIC	CvM (cos)	CvM (unif)	K-S
2017–2018	December	UN+cos	1	0.00	1027.40	0.90	0.90	0.87
		HN	1	0.59	1027.99	1.00	1.00	0.89
		HR	2	0.86	1028.26	1.00	1.00	0.97
		UN	0	51.26	1078.66	0.00	0.00	0.00
2018–2019	November	UN+cos	1	0.00	1101.11	0.90	0.90	0.93
		HN	1	0.24	1101.35	0.90	1.00	0.95
		HR+sim	2	1.01	1102.12	1.00	1.00	0.98
		UN	0	44.19	1145.29	0.00	0.00	0.00
	December	HR	2	0.00	818.67	1.00	1.00	1.00
		HN+cos	2	0.98	819.95	1.00	1.00	1.00
		UN+cos	3	2.63	821.30	1.00	1.00	0.99
		HN	1	7.66	826.33	0.10	0.10	0.10
		UN	0	96.37	915.04	0.00	0.00	0.00
	February	HN	1	0.00	644.29	0.80	0.80	0.94
		UN+cos	1	0.36	644.65	0.50	0.50	0.69
		HR	2	0.58	644.87	1.00	1.00	0.93
		UN	0	37.11	681.41	0.00	0.00	0.00
	March	UN+cos	1	0.00	509.42	0.60	0.70	0.73
		HN	1	0.77	510.19	0.70	0.70	0.76
		HR	2	0.77	510.19	1.00	1.00	1.00
		UN	0	17.87	527.29	0.00	0.00	0.00
2019–2020	November	UN+cos	1	0.00	1956.38	0.30	0.30	0.16
		HN+cos	2	1.17	1957.55	0.60	0.70	0.55
		HN+hp	2	1.44	1957.82	0.70	0.80	0.64
		HN	1	1.77	1958.15	0.30	0.30	0.14
		HR	2	3.45	1959.83	0.70	0.70	0.69
		UN	0	91.74	2048.12	0.00	0.00	0.00
	December	HN	1	0.00	1251.09	0.90	0.90	0.89
		UN+cos	1	0.74	1251.83	0.90	0.90	0.83
		HR+sp	3	3.41	1254.50	1.00	0.90	0.89
		HR	2	3.73	1254.82	0.60	0.70	0.78
		UN	0	49.97	1301.06	0.00	0.00	0.00
	January	HN	1	0.00	1013.39	0.90	0.90	0.61
		UN+cos	1	0.57	1013.96	0.70	0.80	0.42
		HR	2	2.34	1015.73	0.50	0.60	0.46
		UN	0	18.68	1032.07	0.00	0.00	0.00
	March	UN+cos	1	0.00	869.53	0.90	1.00	0.91
		HN	1	0.26	869.80	0.90	0.90	0.82
		HR	2	2.02	871.56	1.00	1.00	1.00
		UN	0	12.00	881.53	0.00	0.00	0.00
2020–2021	November	UN+cos	1	0.00	1980.92	0.80	0.90	0.86
		HR	2	1.28	1982.20	1.00	1.0	0.93
		HN+cos	2	2.11	1983.03	1.00	1.0	0.93
		HN	1	2.18	1983.10	0.50	0.6	0.60

APPENDIX C. Continued.

Year	Month	Key function[a]	# parameters	ΔAIC	AIC	CvM (cos)	CvM (unif)	K-S
		UN	0	31.33	2012.25	0.00	0.00	0.00
	December	HN	1	0.00	1663.73	0.50	0.60	0.52
		HR	2	0.02	1663.74	1.00	1.00	0.98
		UN+cos	2	0.94	1664.67	0.70	0.80	0.78
		UN	0	20.03	1683.75	0.00	0.00	0.00
	January	UN+cos	1	0.00	1058.49	0.70	0.70	0.68
		HN	1	0.45	1058.94	0.80	0.90	0.87
		HR	2	0.63	1059.11	1.00	1.00	0.99
		UN	0	25.35	1083.84	0.00	0.00	0.00
	March	HN	1	0.00	631.41	0.90	1.00	0.83
		HR	2	0.37	631.78	0.90	0.90	0.96
		UN+cos	1	1.12	632.52	0.90	0.90	0.77
		UN	0	4.90	636.31	0.05	0.05	0.07

[a] Key function [HN = Half-normal; HZ = Hazard-rate; UN = uniform] and adjustment terms [cos = cosine, sp = simple polynomial, hp=hermite polynomial].

APPENDIX D. Model selection and results of conventional distance sampling (CDS) estimates of bobwhite density per periodic survey (individual CDS per month) from November to March on the nonhunted site during the 2017–2018, 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Results include key function, parameters, Akaike's Information Criterion (AIC), and differences in AIC (ΔAIC), and 3 goodness of fit tests (GOF) recommended by Buckland et al. (2001): CvM = Cramer VonMises (cosine and uniform); K-S =Kolmogorov-Smirnov.

Year	Month	Key function[a]	# parameters	ΔAIC	AIC	CvM (cos)	CvM (unif)	K-S
2017–2018	December	UN+cos	1	0.00	880.01	0.80	0.90	0.91
		HN	1	0.98	881.00	0.70	0.80	0.85
		HR	2	1.36	881.37	1.00	1.00	1.00
		UN	0	25.04	905.05	0.00	0.00	0.00
2018–2019	November	HN+cos	2	0.00	739.13	0.70	0.80	0.58
		HN	1	0.38	739.51	0.30	0.40	0.36
		HR	2	1.26	740.39	0.50	0.60	0.40
		UN+cos	3	1.29	740.42	0.70	0.80	0.60
		UN	0	58.99	798.12	0.00	0.00	0.00
	December	UN+cos	1	0.00	564.08	0.70	0.70	0.60
		HR	2	1.02	565.10	1.00	1.00	1.00
		HN	1	1.15	565.23	0.70	0.70	0.61
		UN	0	19.51	583.59	0.00	0.00	0.00
	February	HN	1	0.00	532.91	0.90	1.00	0.86
		UN+cos	1	0.06	532.97	0.80	0.80	0.70
		HR	2	1.80	534.71	1.00	1.00	0.93
		UN	0	9.71	542.62	0.00	0.01	0.01
	March	HR	2	0.00	601.12	0.150	0.20	0.14
		UN	0	1.97	603.10	0.300	0.15	0.08
		HN	1	2.06	603.19	0.150	0.20	0.21
2019–2020	November	UN+cos	2	0.00	809.40	0.90	0.90	0.84
		HR	2	0.37	809.77	1.00	1.00	0.97
		HN+cos	2	2.72	812.12	0.90	0.80	0.87
		HN	1	3.88	813.28	0.20	0.30	0.26
		UN	0	19.25	828.65	0.00	0.00	0.00

APPENDIX D. Continued.

Year	Month	Key function[a]	# parameters	ΔAIC	AIC	CvM (cos)	CvM (unif)	K-S
	December	UN+cos	1	0.00	605.18	0.50	0.60	0.49
		HN	1	0.38	605.56	0.70	0.70	0.74
		HR	2	1.04	606.22	0.90	1.00	0.75
		UN	0	8.17	613.34	0.01	0.01	0.00
	January	HR	2	0.00	545.80	0.40	0.40	0.18
		UN+cos	2	2.71	548.52	0.30	0.30	0.15
		HN+cos	3	3.64	549.44	0.40	0.50	0.25
		HN+hp	2	3.88	549.68	0.30	0.30	0.12
		HN	1	4.54	550.34	0.15	0.15	0.09
		UN	0	19.12	564.92	0.00	0.00	0.00
	March	HN	1	0.00	498.75	1.00	1.00	1.00
		UN+cos	1	0.01	498.76	1.00	1.00	1.00
		HR	2	2.24	500.99	1.00	1.00	1.00
		UN	0	3.00	501.75	0.05	0.05	0.06
2020–2021	November	UN+cos	1	0.00	1731.07	0.50	0.60	0.45
		HN	1	0.29	1731.35	0.70	0.80	0.56
		HR	2	0.88	1731.94	0.70	0.90	0.72
		UN	0	36.31	1767.37	0.00	0.00	0.00
	December	HN	1	0.00	1302.70	0.80	0.90	0.76
		UN+cos	1	0.47	1303.17	0.60	0.70	0.56
		HR+sp	3	2.72	1305.42	1.00	1.00	0.99
		HR	2	2.77	1305.47	1.00	1.00	0.99
		UN	0	65.63	1368.33	0.00	0.00	0.00
	January	HN	1	0.00	891.65	0.80	0.80	0.75
		UN+cos	1	0.21	891.86	0.70	0.80	0.56
		HR	2	1.46	893.11	0.80	0.90	0.92
		UN	0	8.44	900.09	0.01	0.01	0.00
	March	UN+cos	1	0.00	593.93	1.00	1.00	0.80
		HN	1	0.29	594.22	1.00	1.00	0.90
		HR	2	2.40	596.33	0.70	0.80	0.79
		UN	0	15.79	609.71	0.00	0.00	0.00

[a] Key function [HN = Half-normal; HZ = Hazard-rate; UN = uniform] and adjustment terms [cos = cosine, sp = simple polynomial, hp=hermite polynomial].

APPENDIX E. The ratio of bobwhites lost to bobwhites harvested (α–additivity), the proportional reduction in posthunt population (p_α), and proportional reduction in one fall population to the next (β–additivity) on the hunted site during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Population changes calculated using the difference in density estimates between the various seasonal surveys (early November, mid-December, late January, and early March) according to line-transect distance sampling via helicopter platform.

Year	Period	α–additivity[a]	p_α[b]	β–additivity[c]
2018–2019	Season	1.96	-0.30	-1.22
2019–2020	Season	0.61	-0.11	1.43
2020–2021	Season	-1.22	0.21	
2018–2019	Early[d]	-	-	-
	Middle	1.03	-7.0	-
	Late	0.20	-3.9	-
2019–2020	Early	4.40	15.2	-
	Middle	1.84	9.9	-
	Late	3.49	16.8	-
2020–2021	Early	-6.62	0.5	-
	Middle	-1.14	15.5	-
	Late	-5.31	-16.4	-

[a] α–additivity = $[N_{nonhunt} – N_{hunt}] / Harvest$, see Guthery (2002)

[b] $p_\alpha = [N_{nonhunt} – N_{hunt}] / N_{nonhunt}$, see Guthery (2002)

[c] β–additivity = $[N_{nonhunt\ fall\ yr2} – N_{hunt\ fall\ yr2}] / N_{nonhunt\ fall\ yr1}$, see Guthery (2002)

[d] Rates not estimated during the early period due to an increase in overall density from early November to mid-December (Woodard et al. 2019).

SPATIAL AND TEMPORAL ANALYSES OF NORTHERN BOBWHITE HUNTING DYNAMICS

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ABSTRACT

A variety of factors influence the harvest of northern bobwhites (*Colinus virginianus*) and where that harvest occurs on a landscape. Many of these factors can be quantified and manipulated to distribute harvest pressure across time and space to meet desired spring densities. We collected spatial hunting metrics using global positioning system units on trucks and hunting dogs, along with detailed hunting logs from 211 quail hunts during the 2018–2019, 2019–2020, and 2020–2021 statewide hunting seasons in Jim Hogg County, Texas, USA. We found that hunting parties effectively covered 23.8 ± 0.3 hectares per hour, with hunts lasting 3.5 ± 0.1 hours in the morning and 1.7 ± 0.1 hours in the evening. Hunts were less productive during the early season (November–mid-December), with 13% fewer encounters per hour and 31% lower harvest per encounter. We expected daily harvest to increase with hunt velocities, but found no significant relationship with the velocity of either pointing dogs or vehicles. However, as we predicted, total hunting pressure (hunts per 50-meter × 50-meter area) decreased by 12% (range = 7–17) for every 5% increase in brush density and every 10-meter increase in the distance to the nearest access road. Our findings can assist landowners and managers in the distribution of harvest and hunting pressure across properties and hunting seasons.

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Key words: bobwhite hunting, *Colinus virginianus*, hunting variables, northern bobwhite, quail hunting

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A modern realization in northern bobwhite (*Colinus virginianus*; hereafter, bobwhite(s)) conservation is that harvest must be managed at the individual property or pasture scale (Williams et al. 2004, Sands et al. 2012, Tomećek et al. 2015). At these scales, scientists recommend using a sustained yield harvest strategy (SYH; Roseberry 1982, Peterson 1999, Guthery et al. 2004, Brennan and Guthery 2007:412), where annual harvest prescriptions are constructed and assumed to leave sustainable spring densities (DeMaso 1999, Guthery 2002) that ensure maximum yield over time (Sands et al. 2013).

Incorporating a SYH prescription also involves managing the spatial and temporal distribution of the harvest. The spatial distribution of hunting pressure can affect seasonal hunting success (Radomski and Guthery 2000, Palmer et al. 2002, Brooke et al. 2017), daily movements patterns (McGrath et al. 2018), and local population persistence of bobwhites (Sands 2010). Guthery (2002:121) suggested that coveys learn avoidance responses after repeated exposure to hunting. McGrath et al. (2018) recorded instances where coveys altogether avoided heavily hunted areas after repeated encounters.

Researchers have suggested that bobwhite harvest adds to natural mortality when it occurs closer to breeding season (Roseberry 1979, Robinette and Doerr 1993, Williams et al. 2004, Hernández et al. 2007). This is especially concerning in South Texas, USA, where the hunting season concludes at the onset of the breeding season (i.e., late Feb–early Mar), and hunting pressure is geared toward the latter half of the hunting season (Hernández and Guthery 2012, Brennan et al. 2014).

However, a common goal for bobwhite managers is to control harvest without reducing the overall numbers of hunts and hunters (Howard 2007). This goal is particularly challenging in South Texas, where harvest objectives (e.g., meeting spring density goals) can fluctuate drastically with annual precipitation and reproductive success (i.e., fall density; Guthery 2002). Many quail hunting operations place self-imposed regulations to limit harvest, including limiting the number of bobwhites harvested per covey and hours spent hunting, and reduced bag or truck limits (Guthery et al. 2004, Howard 2007, Schnupp and Delaney 2012, Brennan et al. 2014, Brooke et al. 2017). Hardin et al. (2005) found that daily harvest increased linearly with increases in the hunt velocity and area hunted. Regulating hunting parameters such as hunting method (e.g., walking vs. vehicle), the area available to hunt, hunt velocity (Guthery 2002, Brennan 2012), and the number of pursuits per covey (i.e., relocating flushed coveys and re-engaging with a firearm) can assist the distribution of harvest across long seasons.

The aim of this study was to analyze the spatial and temporal aspects of quail hunts to provide insight for landowners and managers regarding the implementation of a sustainable harvest. Specifically, we estimated bobwhite hunting variables associated with South Texas quail hunts that can be used to strategically plan hunts across properties and hunting seasons to meet desired harvest prescriptions and spring density objectives. We assumed that hunters would frequently select areas within a pasture that are easiest to access and where brush densities provide the least obstruction for shooting. According to Hernández and Guthery (2012), quail hunters become dissatisfied with hunting leases that have brush densities exceeding 30%. Therefore, we hypothesized that hunters would select areas within a pasture nearest access roads (e.g., quail lanes, ranch roads) containing <25% brush canopy cover. Second, we hypothesized that daily harvest would increase as the velocity of the hunt (i.e., dogs and truck) increases, similar to the models from Hardin et al. (2005).

STUDY AREA

This study took place on the Buena Vista Ranch (6,118 ha) in Jim Hogg County, Texas. The ranch is located approximately 35 km south of Hebbronville, Texas, within the South Texas Plains Ecoregion (Gould 1975). The property is owned and operated by the East Foundation, established in 2007 from the estate of Robert C. East. The primary land use is cattle production, and until the start of this project, quail hunting was prohibited on the property. For the last 30 years, the average annual rainfall for the study site was 55.6 cm, with a mean daily temperature of 22.9° C (PRISM Climate Group 2020). Predominant soils ranged from deep fine sands to sandy loams (Sanders et al. 1974, Gould 1975). Dominant woody vegetation consisted of honey mesquite (*Prosopis glandulosa*), brasil (*Candalia hookeri*), granjeno (*Celtis pallida*), and catclaw acacia (*Acacia greggi*). The herbaceous plant community was dominated by seacoast bluestem (*Schuzachyrium scoparium*), Lehman love grass (*Eragrostis lehmanniana*), purple threeawn (*Aristida purpurea*), Texas broomweed (*Gutierrezia texana*), and croton (*Croton* spp.).

METHODS

Harvest Methods and Structure

We prescribed annual bobwhite harvest quotas for the hunting cooperators, with hunts ongoing until quotas were reached. The annual harvest quotas represented 20% of the prehunting abundance estimate as recommended by Brennan et al. (2014). Prehunting surveys were conducted in early November using line-transect distance sampling from a helicopter platform and following protocols described in Rusk et al. (2007), DeMaso et al. (2010), and Schnupp et al. (2013). We analyzed surveys and calculated density estimates using Conventional Distance Sampling (Buckland et al. 2001, Rusk et al. 2007, Schnupp et al. 2013) within Program Distance version 7.2, release 1 (Thomas et al. 2010).

The harvest quota was calculated for each pasture within the study area to distribute harvest based on local density (Guthery et al. 2000, Brennan et al. 2014, see Woodard et al. this volume). The total harvest quota was 422 northern

bobwhites for the 2018–2019 hunting season, 852 in 2019–2020, and 1,005 in 2020–2021. These figures included both bobwhites bagged (i.e., harvested and retrieved) and an estimate of bobwhites crippled and not recovered. The estimated crippling loss was according to Haines et al. (2006), who estimated losses to be on average 20% of the birds brought to bag. Therefore, the 20% harvest recommendation was represented by 16% birds retrieved to bag and 4% crippling loss. Additionally, researchers recorded all crippled bobwhites detected by hunting parties (i.e., including researcher) in the field. When the number of detected cripples surpassed the 4% designation, the detected cripples were tallied towards harvest quota to maintain a maximum annual harvest of 20%.

Hunting cooperators used standard hunting methods for South Texas (Howard 2007), where hunters followed pointing dogs in vehicles cross-country (i.e., off-road) throughout pastures until a covey is pointed, and then hunters approached the pointed covey on foot (Hernández and Guthery 2012). The only restriction to the hunting method was that hunting cooperators could not provide supplemental feed or bait roadsides within the study area. We placed no limit on the number of birds harvested per covey or pursuit of coveys following the initial covey rise. Hunters were also free to hunt anywhere within the study area throughout the hunting season and were limited only by the annual estimated harvest quota (i.e., total harvest prescription distributed by pasture).

We divided the statewide hunting season into 3 periods to examine the potential for within-season variation of harvest and hunting variables. The 3 periods were:

1. Early (Nov–mid-Dec).
2. Middle (mid-Dec–late Jan).
3. Late (late Jan–late Feb).

We gave a harvest "target" per period to the hunting cooperators to distribute hunting pressure throughout the hunting season. However, hunting cooperators were not penalized for falling short of monthly harvest targets, and annual harvest quotas were cumulative across periods.

We recorded detailed hunting logs from each hunt, excluding 10 hunts during the 2018–2019 hunting season (i.e., only Global Positioning System [GPS] spatial data recorded). Hunts were half-day excursions that took place in either the morning or the afternoon. Each hunt's start and end times were manually recorded and stored within the Garmin (Garmin Ltd., Olathe, KS, USA) tracklogs. We also documented the start and end time for each brace (i.e., 1 or 2 dogs hunting simultaneously), covey found, travel (e.g., hunting without dogs by driving roads), and nonhunting activity (e.g., snack breaks, nonhunting travel). We estimated covey size, pursuits, shots fired, bobwhites retrieved, and bobwhites crippled during each covey interaction. Like Mecozzi and Guthery (2008), we recorded the breeds, ages, and sexes of all individual dogs used during each hunt.

SPATIAL HUNTING EFFORT AND ANALYSIS

We collected hunting location data using Garmin Dog Tracking Systems (Garmin Ltd., Olathe, KS, USA). Tracking systems consisted of a GPS hand-held unit for the dog handler and GPS collars to be attached to the dogs. We used a combination of Garmin Astro 430 hand-held units, Garmin Alpha 100 hand-held units, T5 GPS dog collar, and TT 15 dog collars. Tracklogs were stored within the hand-held devices with track location intervals on default setting for hand-held units (i.e., 5 seconds) and GPS dog collars (i.e., 2.5 seconds). Prior to each hunt, tracking systems were turned on and left in the open area for 15 minutes to allow for proper satellite connection and accuracy. Garmin currently reports the tracking systems' accuracy to be within 3.65 meters (personal communication, Garmin Ltd., 8 Jun 2021). Hunting tracklogs were downloaded as text files upon completion of each hunt and analyzed for nonhunting related activity (e.g., nonhunting travel; Brooke et al. 2017).

Waypoints for each covey interaction and associated data (i.e., shots fired, harvested bobwhites, crippled bobwhites) were collected manually from stored tracklogs using corresponding event times documented within hunting logs. These waypoints represented the location of the individual dog credited with each specific covey found; if coveys were jumped by the truck and not pointed by dogs, the GPS hand-held unit location was used. Each waypoint was designated as a covey encounter location, evaluated for accuracy and covey interaction behavior (e.g., multiple waypoints with exact locations resembling dogs pointed).

We processed and analyzed all tracklogs using ArcMap 10.8.0 (Esri Inc., Redlands, CA, USA). To start, we converted interval locations to Universal Transverse Mercator (UTM) coordinates before transforming each tracklog from individual points to a line, thus calculating total distance traveled and velocity (i.e., length divided by time). The track lines from GPS hand-held units were buffered by 7.2 meters, representing the effective search width without dogs, derived from Rusk et al. (2007). Each track line from GPS dog collars was buffered by 13.2 meters (Guthery and Mecozzi 2008), representing the standardized width of the hunting zone for each dog track. This figure was the average effective search area as determined from point to flush estimates by Guthery and Mecozzi (2008). We combined tracklogs of dogs and hunting vehicles per hunt into a classified raster (i.e., hunted or nonhunted; McGrath et al. 2018). We combined each hunt raster using the Raster Calculator function in ArcMap 10.8.0, creating a cumulative raster with 50-meter resolution (Brøseth and Pedersen 2000), with values representing the total hunting pressure. We consider this resolution the observed scale (Hernández 2020) of bobwhite hunters, representing the maximum range of firearms used during quail hunts and the resolution at which quail hunters analyze habitats (e.g., perceive landscape features to yield covey contact and feasible

shooting opportunities). We defined landscape following the definition of Turner et al. (2002) as an area that is spatially heterogeneous in at least one factor of interest.

The covariates used for our analysis were the distance of hunters from roads and the percentage of brush canopy cover on hunted and nonhunted areas of the landscape. Due to the style of quail hunting in South Texas, managers strategically design access roads (i.e., quail lanes, mowed paths) for fire prevention in the semiarid landscape and to increase covey contacts in optimal locations (e.g., where visibility allows viable shooting). Although no baiting was permitted in this study, quail lanes were hunted and utilized to access various locations within the study area. Therefore, we calculated the nearest distance to a quail lane for the cell center of each 50-meter × 50-meter pixel of our hunting raster, using the near function in ArcMap 10.8.0.

We assessed the influence of brush canopy coverage using imagery from the U.S. National Agriculture Imagery Program (NAIP; 0.6-meter resolution). The 2020 imagery for Jim Hogg County was downloaded from Texas Natural Resources Information System (2020) and processed within Program ERDAS IMAGINE (Hexagon Geospatial, Madison, AL, USA). Pixels were classified into 200 clusters, then subcategorized into 2 categories: brush and non-brush. We analyzed the accuracy of our classifications according to methods outlined in Mata et al. (2018) by generating 200 random points within our boundary and comparing land cover classifications to visual observations in Google Earth 7.1 (Google, Menlo Park, CA, USA). In addition, a field assessment was conducted in March 2021. We calculated the brush canopy coverage of the observed scale for bobwhite hunters by resampling the classified raster to 1-meter resolution and aggregating the resampled raster to 50-meter resolution using the Resample and Aggregate tools in ArcMap 10.8.0.

We used Program R (R package version 4.1.0, www.r-project.org, accessed 15 Jun 2021) for data analysis. We determined the influence of brush canopy coverage and distance from a road using negative binomial regression, accounting for overdispersion and zero inflation, and compared the performance of models using Akaike's Information Criterion (Burnham and Anderson 2002). We used Spearman's Rank Correlation to analyze the correlation between brush canopy coverage and distance from the road and the correlation between daily harvest and hunting velocities (i.e., dog velocity and truck velocity) due to non-normality (Shapiro and Wilk 1965).

RESULTS

We documented 59 half-day quail hunts during the 2018–2019 Texas quail hunting season (27 Oct–24 Feb), 74 hunts during the 2019–2020 season (26 Oct–23 Feb), and 78 hunts during the 2020–2021 season (31 Oct–28 Feb; Table 1). In total, we recorded 668 hours of quail hunting activity, consisting of 595 hours in the morning (i.e., between 0700 and 1400 CST, start time = 07:46 ± 0:25 standard deviation [SD]) and 73 hours in the afternoon (i.e., between 1400 and 1900 CST, start time = 16:00 ± 0:39 SD). On average, morning hunts lasted 3.5 ± 0.1 hours and evening hunts lasted 1.7 ± 0.1 hours.

Total hunting pressure was greatest during the middle period (i.e., mid-December–late January), accounting for 50% of the total hunts, 53% of total covey encounters, and 55% of the total harvest (Table 2). We found harvest rate per covey encounter during the early period was significantly lower than the middle and late periods (>30% lower), as was the encounter rate per hour (>13% lower).

We recorded details from braces, dogs, and overall running times for 201 of the 211 hunts. We recorded tracklogs and hunting parameters from 153 individual dogs (n females = 67; n males = 86) belonging to 9 different professional dog handlers. Forty dogs were recorded in two different hunting seasons, and 32 dogs were recorded in all three hunting seasons. The mean age of dogs across all years was 4.6 ± 0.04 years, and the majority of these were the English pointer breed (n = 143), with 10 English setters participating in the hunts. We recorded the details of 836 separate braces. Overall, dog handlers ran 4.2 ± 0.1 braces per hunt, lasting 40.7 ± 0.7 minutes per brace and covering 17.8 ± 0.3 hectares.

Table 1. Annual summary of hunting effort and harvest for morning (0700–1400 CST) and afternoon (1400–2000 CST) hunts for northern bobwhites (*Colinus virginianus*) recorded during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA.

Year	Time	Hunts	Hours	Encounters	Harvest	Crippled
2018–2019	AM	41	131.3	375	271	64
	PM	18	31.9	81	67	21
	Totals	59	163.2	456	338	85
2019–2020	AM	61	232.8	672	611	181
	PM	13	21.6	50	47	13
	Totals	74	254.4	722	658	194
2020–2021	AM	67	231.1	589	719	247
	PM	11	19.4	38	23	10
	Totals	78	250.5	627	742	257

Morning braces lasted 42.9 ± 0.8 minutes per brace (n = 707 braces) and covered 18.7 ± 4.6 hectares, with evening braces averaging 28.8 ± 1.2 minutes (n = 129 braces) and covering 12.4 ± 0.6 hectares. We found that individual dogs had 32.8 ± 0.3% redundancy of search area, and the redundancy between dogs (i.e., brace) was 39.5 ± 0.3%. The average vehicle velocity across all recorded hunting activities was 3.8 ± 0.1 kilometers per hour, and the average velocity of dogs was 10.6 ± 0.1 kilometers per hour (Table 3). We found no relationship between daily harvest and the velocity of dogs or trucks (Figure 1).

The hunters had a total of 1,805 quail encounters (= 9.3 ± 0.1 bobwhites per covey), including all points by bird dogs (n = 1,653 coveys) and coveys jumped by vehicle (n =155 coveys) undetected by the dogs. Hunting parties averaged 9.7 ± 0.3 encounters per morning at a rate of 2.8 ± 0.1 per hour and 4.0 ± 0.3 encounters per afternoon at a rate of 2.4 ± 0.2 per hour. Hunters pursued 90.1% of total quail encounters with a firearm (i.e., attempted harvest by discharged firearm), presenting a total of 15,394 targets (i.e., individual quail). Unpursued encounters (n = 179 coveys) were due to the nature of flush (e.g., flushed by a dog, beyond gun range), size of covey (e.g., singles and pairs), hunter experience, and brush densities around encounter locations. On average, 1.0 ± 0.04 quail were retrieved per encounter (i.e., averaged by hunt), with an additional 0.3 ± 0.02 quail wounded per encounter. The number of shots per encounter was recorded for 199 hunts, resulting in 1,685 encounters with gunfire documented and 8,220 gunshots recorded. The average number of shots per encounter (i.e., rates derived from individual hunts) was 4.87 shots. Hunters retrieved a bird for every 5.1 shots and crippled one quail for every 15.3 shots (i.e., detected cripples).

Table 2. Summary of annual bobwhite hunting parameters according to designated periods: early (Nov–mid-Dec), middle (mid-Dec–late-Jan), and late (late Jan–late Feb). The hunting parameters were collected during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Encounters per hour were significantly lower during the early period (t = -2.78, $P < 0.01$), as was harvest per covey encounter (t = -3.45, $P < 0.01$).

		Hunts	Hours	Encounters		Harvest		Crippled	
Period	Year	(n)	(n)	rate[a]	SE	rate[b]	SE	rate[c]	SE
Early	2018–2019	10	24.9	2.3	0.14	0.4	0.13	0.2	0.08
	2019–2020	23	70.8	2.7	0.13	0.8	0.13	0.3	0.04
	2020–2021	24	73.7	2.2	0.20	0.8	0.10	0.3	0.05
	pooled	57	169.4	2.4	0.10	0.7	0.07	0.3	0.03
Middle	2018–2019	33	91.6	2.9	0.19	0.8	0.08	0.2	0.04
	2019–2020	35	124.8	2.9	0.14	0.9	0.09	0.3	0.03
	2020–2021	37	118.4	2.7	0.13	1.4	0.11	0.4	0.05
	pooled	105	334.8	2.8	0.09	1.04	0.06	0.3	0.02
Late	2018–2019	16	46.7	2.9	0.29	0.7	0.08	0.2	0.06
	2019–2020	16	58.9	2.8	0.18	1.1	0.13	0.4	0.06
	2020–2021	17	58.4	2.3	0.22	1.3	0.19	0.7	0.08
	pooled	49	164.0	2.7	0.14	1.0	0.09	0.4	0.05

[a] Mean covey encounters per hour.
[b] Mean bobwhites harvested and retrieved per covey encounter.
[c] Mean crippled bobwhites detected and not recovered per covey encounter.

Table 3. Velocities and area covered by northern bobwhite hunting parties recorded during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA.

			Truck velocity (km/hr)		Dog velocity (km/hr)		Coverage rate[a] (ha/hr)	
Year	Time	n	$\bar{x}$	95% CI	$\bar{x}$	95% CI	$\bar{x}$	95% CI
2018–2019	AM	41	4.4	3.9–4.9	11.7	11.2–12.2	27.7	26.2–29.1
	PM	18	4.1	3.3–4.9	11.1	10.1–12.0	24.0	20.2–27.8
2019–2020	AM	61	3.6	3.4–3.8	10.6	10.2–10.9	24.6	23.7–25.5
	PM	13	3.8	2.7–4.9	9.8	9.2–10.5	22.6	19.4–25.9
2020–2021	AM	67	3.8	3.5–4.1	9.6	9.2–9.9	21.2	20.2–22.1
	PM	11	3.1	2.3–3.8	9.3	8.1–10.6	21.4	18.8–24.0

[a] Area effectively hunted by pointing dogs and hunting vehicle in hectares per hour.

Hunting occurred on 77% of the total study area. Bobwhite hunting parties effectively hunted 23.8 ± 0.3 hectares per hour (e.g., area effectively hunted with dogs and truck) on average across 3 hunting seasons. Morning hunts covered 83.8 ± 1.6 hectares on average at a rate of 24.0 ± 0.4 hectares per hour. The evening hunts covered less area, averaging 39.9 ± 2.3 hectares per hunt at 22.9 ± 1.0 hectares per hour.

According to the spatial hunting distributions at the observed scale (i.e., 50-meter resolution, Figure 2), 10% of grid cells were not hunted through 3 hunting seasons, 11% only hunted once, and 79% hunted more than once (range = 2–24), with only 9% of grid cells hunted on more than 10 occasions (Figure 3). The nonhunted cells had a mean brush canopy coverage of 44.7 ± 0.6%, and the mean distance to a quail lane was 163.9 ± 1.9 meters, while brush canopy coverage of hunted cells was 21.71 ± 0.12% (see Appendix A) and mean distance to a quail lane was 84.2 ± 0.5 meters (see Appendix B). We found that mean brush canopy cover and mean distance to road decreased as total hunting pressure increased (Figure 4). Our top model, according to Akaike's Information Criterion with a correction for sample size, was our full model with an interaction term (Table 4), which we included due to a correlation between our brush canopy coverage and distance to roads. Therefore, we found that total hunting pressure had a negative relationship with percent brush coverage, distance to a road, and their interaction (Table 5), suggesting hunters are selecting areas to hunt based on lower brush densities and proximity to access roads.

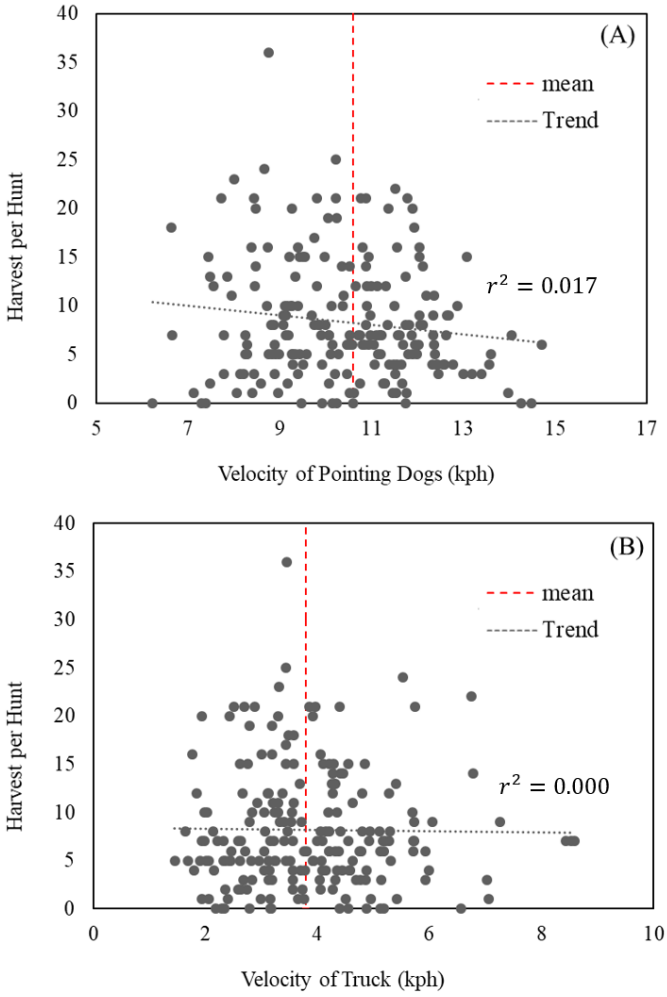

Fig. 1. Relationship between northern bobwhite (*Colinus virginianus*) harvest per hunt and hunting velocity (km/hr), categorized by mean velocity of pointing dogs (A; $\bar{x}$ = 10.6 ± 0.1 km/hr ; rs = -0.09, P = 0.1786) and mean velocity of hunting vehicles (B; $\bar{x}$ = 3.8 ± 0.1 km/hr; rs = -0.01, P = 0.9194) from 211 quail hunts in Jim Hogg County, Texas, USA.

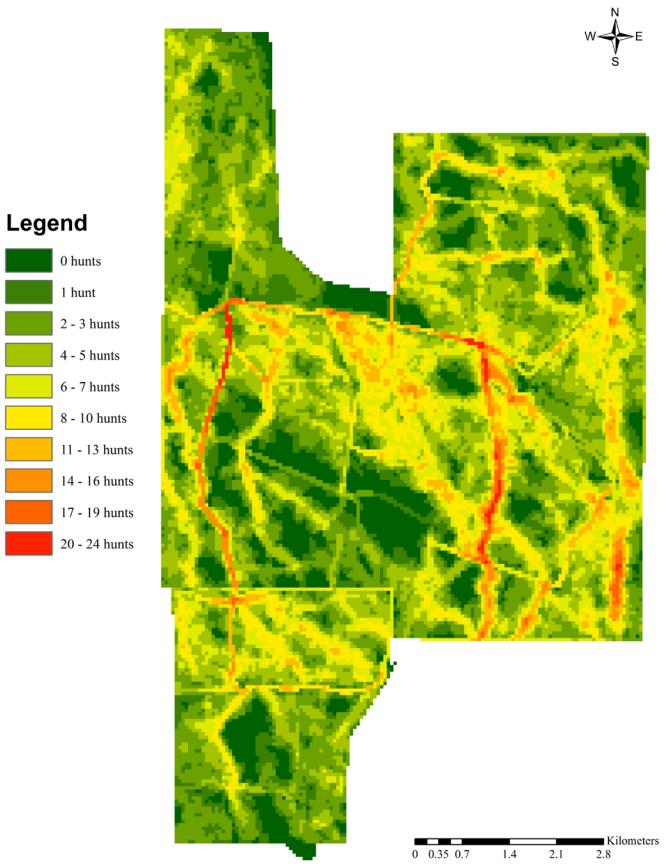

Fig. 2. Spatial distribution of 211 quail hunts at 50-meter resolution, recorded during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA.

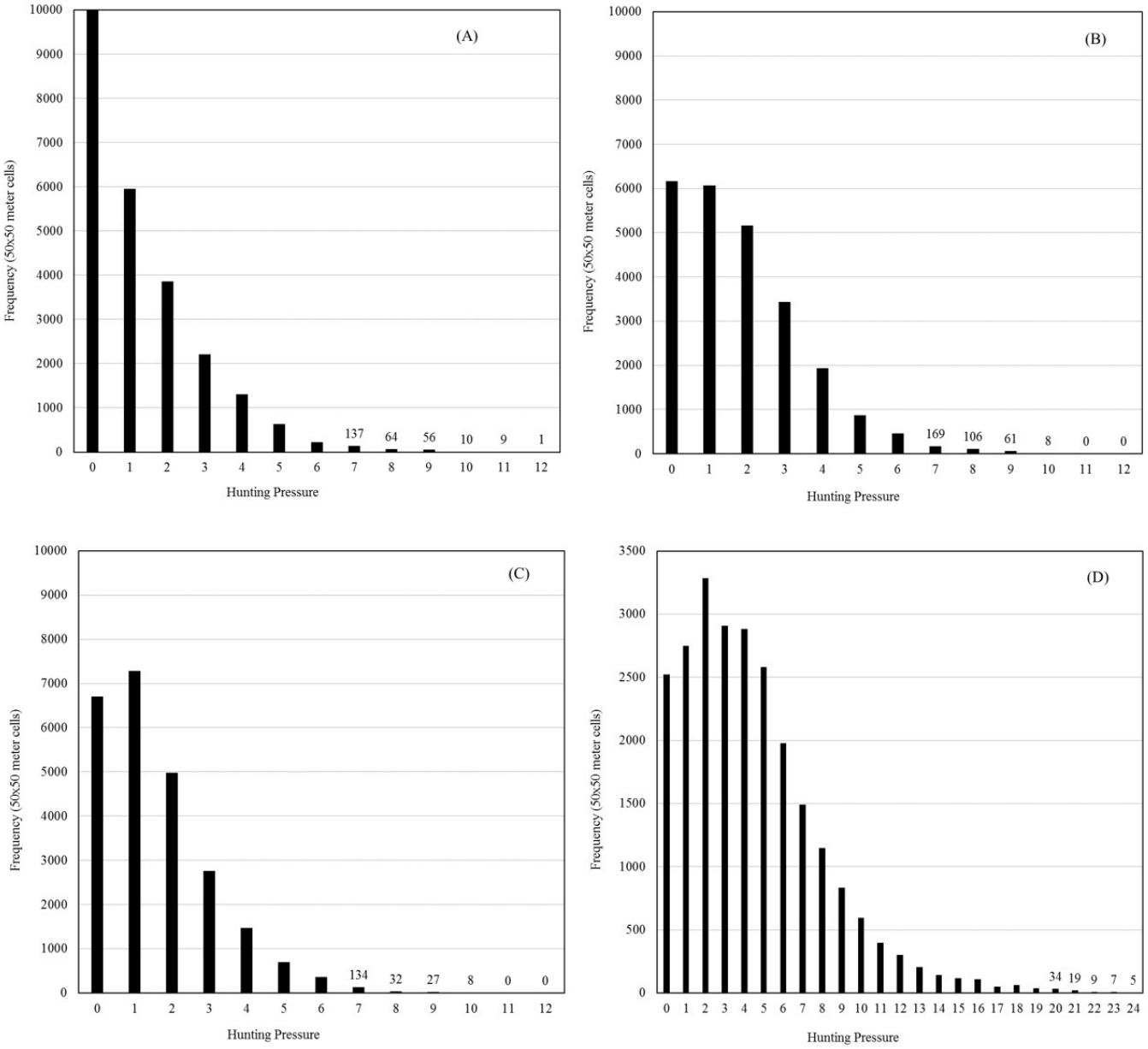

Fig. 3. Frequency of 50-meter grid cells categorized by total hunting pressure for the A) 2018–2019, B) 2019–2020, and C) 2020–2021 seasons, and D) cumulative across the 3 seasons from quail hunts in Jim Hogg County, Texas, USA.

Table 4. Model selection results for total hunting pressure over the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA. Negative binomial regression used percent brush canopy coverage (Brush) and distance to access road (Road) per 50-meter × 50-meter grid cell.

Model	*K*	log(L)	AIC_c[a]	ΔAIC_c	W_i
Brush + Road + Interaction	5	-57,815.3	115,640.6	0.00	1.0
Brush + Road	4	-57,960.1	115,928.3	287.69	0.0
Road	3	-59,137.8	118,281.6	2,641.05	0.0
Brush	3	-60,327.5	120,661.0	5,020.4	0.0

[a] Akaike's Information Criterion with a correction for sample size.

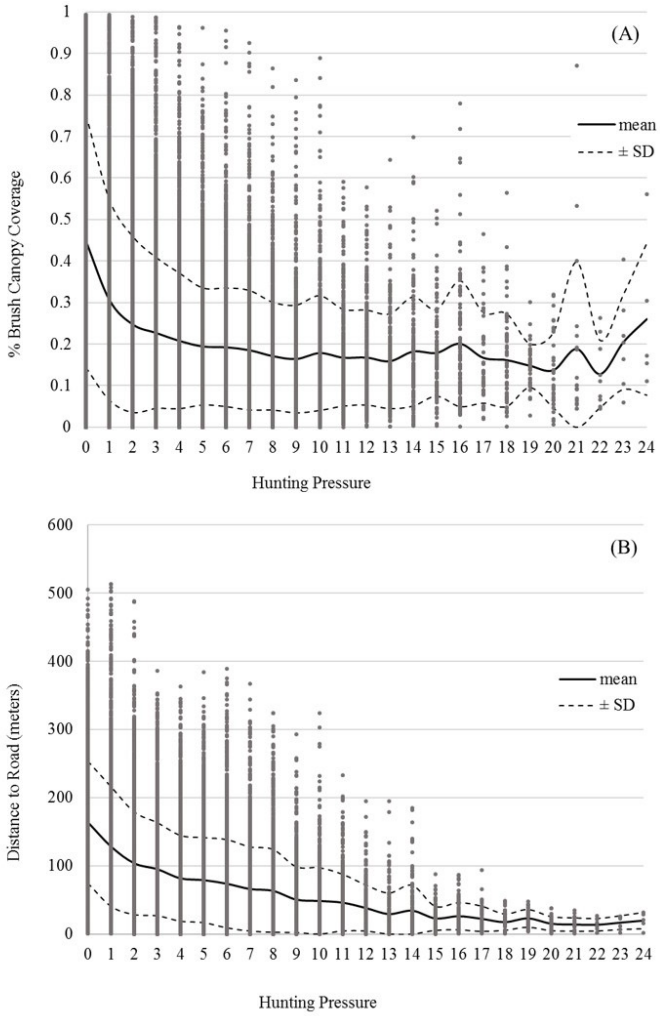

Fig. 4. A) Percent brush canopy cover and B) distance to road per 50-meter × 50-meter grid cell, categorized by total hunting effort from quail hunts recorded during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA.

Table 5. Parameter estimates of top-ranking model for total hunting pressure over the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA.

Variable	*β*-estimate	SE	Z-value
(Intercept)	2.0168	0.0106	189.92
Brush	-0.6887	0.0417	-16.50
Road	-0.0035	0.0001	-34.79
Interaction[a] (Brush × Road)	-0.0063	0.0003	-16.82

[a] $r_s = 0.13$, $P < 0.01$

DISCUSSION

According to daily harvest predictions from Hunter Covey Interface models by Hardin et al. (2005) and similarities between our velocity rates, we expected to find a relationship between daily harvest and hunting velocity. We found no such relationship; however, Hardin et al. (2005) predicted daily harvest using constant parameters for harvest rate (i.e., 2.0 per encounter) that was 50% higher than our results. In fact, our mean harvest rate per covey encounter was lower than those reported by Bennitt (1951; $\bar{x}$ = 1.9 ± 0.02), Guthery (2002; $\bar{x}$ = 1.7 ± 0.07), Hardin et al. (2005; $\bar{x}$ = 1.8 ± 0.04), and Mecozzi and Guthery (2007; $\bar{x}$ = 1.4 ± 0.16). The 5.1 shots per bobwhite retrieved were 2 shots higher than reported from Doster et al. (1982; $\bar{x}$ = 3.1) and 3 shots higher than Mecozzi and Guthery (2007; $\bar{x}$ = 2). Therefore, our hunting participants were significantly less efficient when presented with harvest opportunities. However, we feel this harvest rate and shooting efficiency are an honest representation of the current trends in bobwhite hunting participants (Rollins 2002, Johnson et al. 2012) and diversity of hunters in South Texas. Quail hunters in South Texas are composed of a variety of ages and experiences. Some hunting parties are composed of seasoned veterans, while others focus on the entertainment of families and corporate customers, ranging from novice to expert. Second, the model by Hardin et al. (2005) did not account for the time constraints when hunters find and engage with a covey and as the daily number of covey encounters increases more time will be spent with dogs on point (i.e., 0 kilometers per hour; Mecozzi and Guthery 2007). Our results support the findings of Mecozzi and Guthery (2007), who found a weak negative relationship between dog velocity and encounter per kilometer during walk-hunts in Oklahoma, USA, northern Texas, and eastern Missouri, USA.

Several studies have examined how access or road systems influence hunting distributions. For instance, when analyzing willow ptarmigan (*Lagopus lagopus*) hunters in central Norway, Brøseth and Pedersen (2000) found that the access point (i.e., hunter's cabin) strongly influenced spatial hunting distributions. Richardson (2006) found that the distance from a road system significantly influenced walk-only quail hunts in Oklahoma and recommended designing road systems within average walking distance to maintain huntable area. However, Tanner et al. (2016) found that the risk of mortality for northern bobwhites in Oklahoma decreased as the distance from roads increased, regardless of hunting pressure. The relationship we found between percent brush canopy cover and access roads is straightforward. Hunters focus on areas with the highest rate of return (i.e., shooting efficiently and harvest per covey), or one could say the path of least resistance, which is heavily influenced by brush configurations and access roads throughout landscapes in South Texas. Hernández and Guthery (2012) indicated the landowners will "lose the goodwill" of hunters when brush exceeds 30%. If hunters cannot walk or drive through particular areas due to brush densities, they are less likely to hunt there. Likewise, if hunters find quail in dense brush but have no viable shooting opportunities, they are more likely to avoid such areas in the future.

Our results differ from those of Kellogg et al. (1982) in Florida, USA, as well as Wellendorf et al. (2012), who reported a 17% higher covey encounter rate during evening

hunts in Georgia, USA. We attribute this discrepancy to 2 possible explanations: first, the temperature typically increases throughout the day, limiting bobwhite activity (Carroll et al. 2015) and reducing overall variability in scenting conditions for pointing dogs (Gutzwiller 1990, Wellendorf et al. 2012). Second, our hunters consistently started at legal shooting light to take advantage of scenting conditions in the early morning and to maximize the time spent in the field. This is unlike most quail hunters, and on average 2 hours earlier then starting times reported by Wellendorf et al. (2012), who rarely begin morning hunts at daybreak.

The differences we found during the early season (i.e., Nov–mid-Dec) regarding covey encounter rates (≥13% lower) and harvest per encounter (≥30% lower) are likely why quail hunting in South Texas is geared towards the later portions of season dates. Wellendorf et al. (2012) reported no differences in encounter rate between their early (Nov–Dec) and late (Jan–Feb) periods. Bobwhite populations should be highest at the start of the season and decrease throughout winter (Guthery 2002). With fewer bobwhite available for detection, we would naturally expect to see a declining trend in covey encounter rate as the season progresses. Radomski and Guthery (2000) predicted an increase in covey avoidance behavior throughout the season as naïve coveys learn from repeated contact with hunting parties, resulting in lower hunting success, a trend detected by Palmer et al. (2002) in Florida and Brooke et al. (2017) in Kentucky, USA. McGrath et al. (2018) also found evidence of avoidance behavior while analyzing forage and movement patterns of bobwhites after being exposed to hunting parties. However, we predict that our discrepancy is likely due to climatic factors, with typical weather patterns in early winter unfavorable for quail hunting and cooler weather with optimal scenting conditions more common throughout January and February in South Texas.

MANAGEMENT IMPLICATIONS

We suggest time of day, period of the bobwhite hunting season (i.e., early, middle, late), and length of time spent hunting influence the within-season variation of covey encounter rates and subsequent harvest in South Texas. Adjusting these parameters can increase or decrease harvest depending on management objectives. For instance, hours spent hunting are more influential to the total area covered and daily harvest than minor variations in hunting velocities. Our results also indicate that brush densities of areas selected by quail hunters are at the lower end of brush density thresholds utilized by bobwhites, according to various findings in the region. We strongly recommend that landowners and managers focus on strategic placement of road systems and combating brush encroachment to optimize the huntable area available and spatially distribute hunting pressure.

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APPENDIX A. Summary statistics for percent brush canopy cover per 50-meter × 50-meter grid cell, categorized by total quail hunting effort recorded during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA.

		% Brush canopy coverage			
Hunted[a]	n[b]	$\bar{x}$	SD	SE	95% CI
0	2,520	0.45	0.30	0.01	0.44–0.46
1	2,747	0.31	0.24	0.00	0.30–0.32
2	3,283	0.25	0.21	0.00	0.24–0.25
3	2,907	0.23	0.18	0.00	0.22–0.23
4	2,884	0.21	0.16	0.00	0.20–0.21
5	2,579	0.19	0.14	0.00	0.19–0.20
6	1,978	0.19	0.14	0.00	0.19–0.20
7	1,492	0.19	0.14	0.00	0.18–0.19
8	1,149	0.17	0.13	0.00	0.16–0.18
9	834	0.16	0.13	0.00	0.16–0.17
10	596	0.18	0.14	0.01	0.17–0.19
11	399	0.17	0.12	0.01	0.16-0.18
12	301	0.17	0.11	0.01	0.15–0.18
13	204	0.16	0.11	0.01	0.14–0.17
14	142	0.18	0.13	0.01	0.16–0.20
15	115	0.18	0.10	0.01	0.16–0.20
16	109	0.20	0.15	0.01	0.17–0.23
17	48	0.17	0.11	0.02	0.14–0.20
18	63	0.16	0.11	0.01	0.13–0.19
19	37	0.15	0.05	0.01	0.13–0.17
20	34	0.14	0.09	0.02	0.11–0.17
21	19	0.19	0.21	0.05	0.09–0.29
22	9	0.13	0.08	0.03	0.07–0.19
23	7	0.21	0.11	0.04	0.10–0.31
24	5	0.26	0.18	0.08	0.03–0.49

[a] Hunted value represents the total hunting pressure per grid cell.
[b] Total number of grid cells per Hunted category.

APPENDIX B. Summary statistics for distance to roads per 50-meter × 50-meter grid cell, categorized by total quail hunting effort recorded during the 2018–2019, 2019–2020, and 2020–2021 hunting seasons in Jim Hogg County, Texas, USA.

		Distance from road			
Hunted[a]	n[b]	$\bar{x}$	SD	SE	95% CI
0	2,520	163.9	89.5	1.8	160.4–167.4
1	2,747	128.3	87.7	1.7	125.0–131.6
2	3,283	103.8	75.3	1.3	101.3–106.4
3	2,907	95.1	68.2	1.3	92.6–97.6
4	2,884	81.7	62.9	1.2	79.4–84.0
5	2,579	79.1	62.3	1.2	76.7–81.5
6	1,978	73.8	64.7	1.5	70.9–76.6
7	1,492	66.1	61.7	1.6	62.9–69.2
8	1,149	63.3	60.7	1.8	59.8–66.8
9	834	50.5	48.2	1.7	47.2–53.8
10	596	48.5	48.8	2.0	44.6–52.4
11	399	46.1	41.5	2.1	42.0–50.2
12	301	38.2	33.8	1.9	34.4–42.0
13	204	29.4	30.8	2.2	25.2–33.7
14	142	34.3	37.2	3.1	28.1–40.5
15	115	23.0	17.6	1.6	19.8–26.3
16	109	26.2	19.9	1.9	22.4–30.0
17	48	22.4	18.5	2.7	17.0–27.8
18	63	17.5	12.0	1.5	14.5–20.6
19	37	23.0	13.0	2.1	18.7–27.3
20	34	15.3	10.3	1.8	11.7–18.9
21	19	14.0	9.8	2.2	9.3–18.7
22	9	13.7	9.2	3.1	6.6–20.7
23	7	16.8	10.1	3.8	7.4–26.1
24	5	19.8	12.0	5.4	4.9–34.7

[a] Hunted value represents the total hunting pressure per grid cell.
[b] Total number of grid cells per Hunted category.

A SIMULATION MODEL OF SUSTAINED-YIELD HARVEST FOR NORTHERN BOBWHITE IN SOUTH TEXAS

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ABSTRACT

Recommended sustainable harvest rates for northern bobwhite (*Colinus virginianus*) vary greatly and range from 25% to 70% of the prehunt population. Because northern bobwhite populations have declined across their geographic range, determining sustainable harvest levels is critical for effective management. Our objectives were to use simulation modeling to identify sustainable rates of bobwhite harvest, probability of population persistence, and minimum viable population estimates. We also conducted a sensitivity analysis to evaluate the impacts of harvest on northern bobwhite populations in Texas, USA. We constructed a simulation model using Program STELLA 9.0 for a hypothetical northern bobwhite population on 800 ha in the South Texas Plains USA and modeled population dynamics to 100 years over a range of harvest rates (0–40%). A 20% harvest rate produced the greatest average yields (mean ± standard error = 231 ± 10 bobwhites harvested/year). Given a quasi-extinction

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criterion of ≤40 bobwhites (≤0.05 bobwhite/ha), a 30% harvest rate resulted in a high probability of quasi-extinction (PE = 0.75) within 47.8 ± 2.3 years. A 40% harvest rate was not sustainable (PE = 1.0), with quasi-extinction occurring within 15.5 ± 2.6 years. Harvesting northern bobwhite populations in the South Texas Plains at rates of 20−25% of the prehunt population should maximize long-term harvest while minimizing the probability of population extinction. Spring densities of 0.60−0.80 bobwhite/ha may represent minimum viable spring densities for northern bobwhite populations in the South Texas Plains as these are the densities associated with sustainable 20-25% harvest rates. Harvest rates >30% are likely to be excessive with respect to long-term population persistence for northern bobwhite populations in the South Texas Plains.

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Sustained-yield harvest is a recommended but untested management philosophy for northern bobwhite (*Colinus virginianus;* hereafter, bobwhite(s); Roseberry 1982). Recommended rates for sustainable harvest of northern bobwhite range from 25% to 70% of the prehunt population (Stoddard 1931, Rosene 1969, Vance and Ellis 1972, Roseberry 1979, Lehmann 1984). Identifying the appropriate harvest rate for bobwhites is important because harvest is considered to be partially additive to natural mortality (Roseberry 1979, Roseberry and Klimstra 1984, Guthery 2002, Yeiser et al. 2021) and therefore hunting can lead to excessive harvest pressure, overharvest, and unsustainable survival rates (Brennan and Jacobson 1992, Rolland et al. 2010). A possible reason for the wide variation in recommended harvest rates is that study-specific conditions (e.g., interactions between density-dependent and density-independent phenomena, population trends, and landscape context) are dynamic, and bobwhites exist in a diverse array of habitat types which occur in varying degrees of availability across the landscape. Bobwhite populations are declining across most of their geographic range (Brennan 1991, Williams et al. 2004*a*). However, where habitat exists, population trends are often stable or increasing (Veech 2006). Fragmented habitats are likely to be associated with declining populations (Veech 2006), and declining populations are more sensitive to changes in survival rates than stable or increasing populations (Sandercock et al. 2008, DeMaso et al. 2011).

Minimum viable spring density is the minimum density necessary to produce a population that persists over time. Given highly variable bobwhite abundance in semiarid environments (Kiel 1976) and the importance of reproduction in compensating for additive harvest mortality under sustained-yield harvest (Roseberry 1979, Roseberry and Klimstra 1984), it is intuitive that the target spring density should be greater than or equal to minimum viable spring density, as this value represents the threshold beyond which harvest would be detrimental to population persistence. Current knowledge of desired spring density is speculative (DeMaso 1999, Peterson 1999), or estimates are based on maximum percent summer gain, which assumes density-dependent production (Guthery 2002).

Systems modeling and analysis provide a tool for addressing problems within complex systems and allow investigators to examine the interplay among factors that impact system dynamics (Grant et al. 1997, Sage et al. 2003). A systems modeling approach to problem solving fosters recognition of potential causal relationships within complex systems that may otherwise remain unidentified. Furthermore, such an approach permits the testing of predictive ecological theory through inductive and deductive reasoning (Grant et al. 1997:6–7). Systems and simulation modeling can be used as a tool for studying avian ecology and population dynamics (e.g., Martinez et al. 2005, Tichit et al. 2007), including research specific to Galliformes (Potts et al. 1984; Rader et al. 2011; DeMaso et al. 2011, 2013). Simulation models have been applied to evaluate the impacts of harvest on bobwhite (Roseberry 1979), wild turkey (*Meleagris gallopavo*; Lobdell et al. 1972, Suchy et al. 1983, Rolley et al. 1998, Schwertner 2005, McGhee et al. 2008), and gray partridge (*Perdix perdix;* Potts 1986). Simulation models where values can be adjusted based on available estimates of population parameters (e.g., survival and mortality rates, production, and dispersal rates) can be a powerful tool for evaluating the effects of harvest on populations and providing harvest recommendations to managers.

Bobwhite populations are declining throughout the majority of their range, and quantifying sustainable harvest rates represents an important component of effective management. Applying a systems approach to bobwhite population dynamics in Texas, USA requires knowledge of the factors that directly impact bobwhite population parameters. The objectives of this study were to 1) construct a data-based systems model of bobwhite population dynamics using a dynamic modeling approach, 2) determine optimal harvest rates and minimum viable spring densities of northern bobwhite via stochastic simulations, and 3) conduct a sensitivity analysis designed to evaluate the impacts of model parameters on abundance of the winter (hunted) population. We defined optimal harvest rates as those that maximize probability of long-term population persistence within the context of sustained-yield harvest while optimizing yield (number of bobwhites harvested per year) and hence hunting opportunity. Based on the results of Guthery et al. (2000) our research hypotheses were that 1)

bobwhite harvest rates of 25−30% of the prehunt population would represent sustainable rates of harvest for bobwhites in the South Texas Plains and produce the largest average yield, and 2) harvest rates >30% would reduce the probability of population persistence below 95% over 100 years.

STUDY AREA

We collected field data for this research in the South Texas Plains Ecoregion of Texas (Gould 1975). The South Texas Plains experiences high annual and seasonal variability in rainfall amount and distribution, and quail populations therein exhibit irruptive population behavior (Lehmann 1984). Historical accounts of the region vary greatly (e.g., barren desert or lush grassland) depending on the rainfall conditions at the time (Lehmann 1984).

The study area was located on private rangeland in Brooks County, Texas within a landscape composed predominantly of suitable quail habitat. Fieldwork was located primarily on 3 core areas distributed north to south and separated by approximately 5 km. The northernmost area (North Viboras) was 1,966 ha, the center area (La Loba) was 1,379 ha, and the southernmost area (Cuates) was 1,240 ha. Land uses on the study area included wildlife management for commercial hunting (primarily bobwhite and white-tailed deer [*Odocoileus virginianus*]) and cattle production, as well as oil and gas production. Bobwhite hunting on the study sites was conducted by following dogs from vehicles. Average annual rainfall was 617 mm (NOAA National Climatic Data Center 2008). Mean winter (Nov–Mar) temperature was 16.7º C and summer (Apr–Aug) temperature was 30.0º C (NOAA National Climatic Data Center 2008). Soils were primarily sands (USDA Natural Resources Conservation Service 2008).

The plant community was a mixed-brush community characteristic of the South Texas Plains (McLendon 1991). Common brush and cactus species included mesquite, huisache (*Acacia farnesiana*), granjeno (*Celtis pallida*), brasil (*Condalia hookeri*), and Texas prickly pear (*Opuntia lindheimeri;* Hernández et al. 2002). Common forbs included doveweed (*Croton* spp.) and sunflower (*Helianthus* spp.; Hernández et al. 2002). Common grasses were seacoast bluestem (*Schizachyrium scoparium*), gulf cordgrass (*Spartina spartinae*), sandbur (*Cenchrus incertus*), and purple threeawn (*Aristida purpurea*; Hernández et al. 2002).

METHODS

Demographic Data

We used data from the South Texas Quail Research Project, a long-term telemetry study in the South Texas Plains (DeMaso 2008) to develop a simulation model of the impacts of harvest on bobwhite population dynamics. Radio-telemetry data collected from 2000−2005 provided information on reproductive ecology of bobwhites which were used to estimate parameters impacting bobwhite reproduction (Rader et al. 2007, DeMaso et al. 2011). Bobwhites were captured, handled, and marked within the guidelines of the Texas A&M University-Kingsville Animal Care and Use Committee (Approval No. 2003-3-3). DeMaso (2008) provides details regarding demographic parameter estimation from radio-marked bobwhites and independent parameter estimates.

Density

We used density (number of bobwhites/ha) estimates provided by Schnupp et al. (2013) for spring density, and estimates from Rusk et al. (2007) and Schnupp (2009) for fall density. Both Rusk et al. (2007) and Schnupp (2009) used helicopter-based distance sampling (Buckland et al. 2001) to estimate bobwhite density. Predetermined transects were traversed at a height of 7−10 m above ground level and velocity of 37 km/hour in a Robinson R-44 helicopter (Robinson Helicopter Co., Torrance, CA, USA). Rusk et al. (2007) and Schnupp (2009) provide details on estimation of density using Program Distance (Thomas et al. 2004).

Harvest and Age Ratios

We compiled harvest data from a commercial hunting camp on our study site for use as a comparison to our simulated harvest data. Harvest rates were estimated in the field on 2 pastures during the 2007−2008 and 2008−2009 hunting season (Sands 2010). Additionally, harvest data (birds harvested per pasture and age of harvested birds) were collected from 1983−2008 and used to estimate juvenile:adult age ratios. Bobwhites were identified as juvenile or adult by inspection of the primary coverts (Leopold 1939).

Model Development

Conceptual overview.—We constructed a stochastic, age- and sex-specific population model that estimated probability of population persistence under harvest rates ranging from 0−40% (Figure 1). The model followed the general approach of DeMaso et al. (2011) and Rader et al. (2011), where bobwhites were produced during the spring and summer and removed as a result of natural mortality during each season. The model represented a bobwhite population on a hypothetical property of 800 ha. Our model consisted of stocks (chicks, juveniles, and adult bobwhites), flows (transfer of chicks, juveniles, and adult bobwhites into or out of the model), and auxiliary variables (e.g., survival rates, reproduction) that influenced flows. We conceptualized (Figure 1) and programmed our model using STELLA version 9.0 (ISEE Systems, Lebanon, NH, USA).

We simulated the dynamics of the population and evaluated its probability of persistence in the presence of harvest over a 100-year period. Stochasticity was invoked during each 100-year simulation by randomly selecting values for production and survival from empirically determined Weibull probability distributions generated within SAS 9.1 (SAS Institute Inc.,

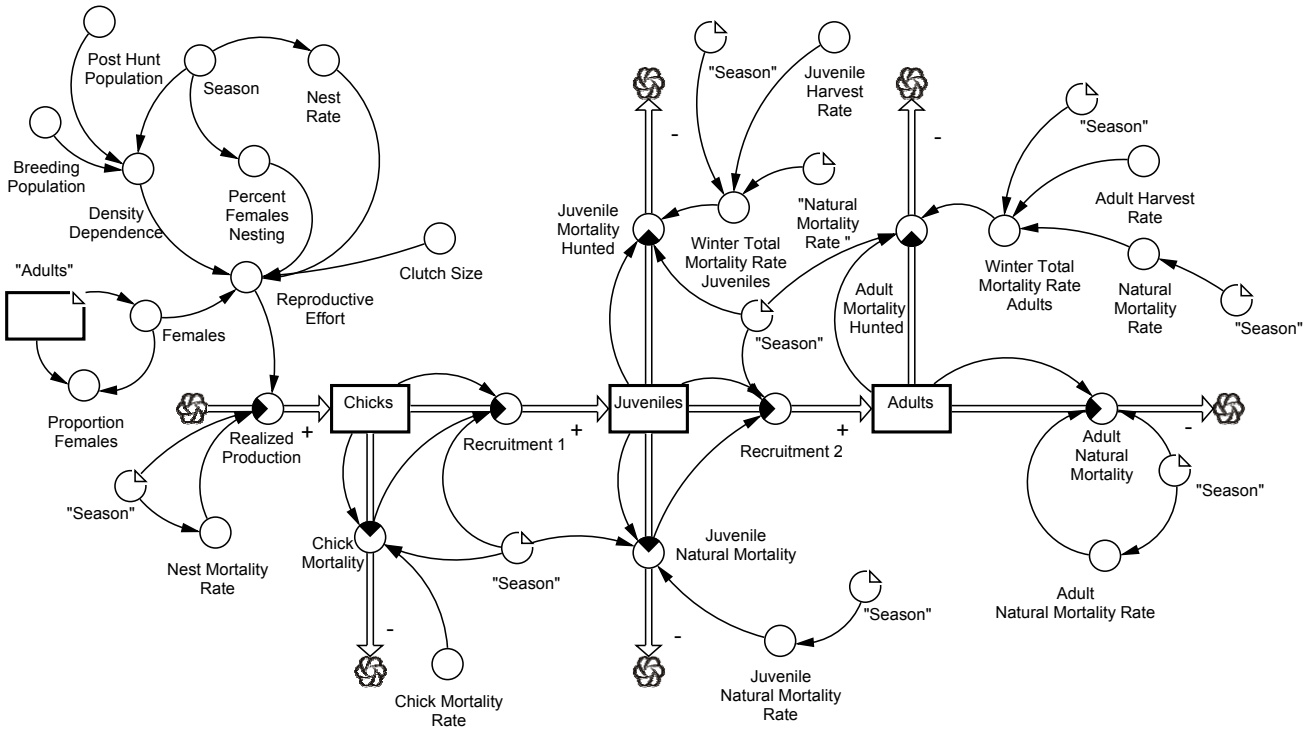

Fig. 1. A conceptual model of factors impacting northern bobwhite (*Colinus virginianus*) population dynamics in the South Texas Plains, USA. Boxes are state variables which represent stocks of northern bobwhites at different age classes (chicks, juveniles, and adults). Circles represent driving variables, auxiliary variables, or constants (e.g., natural mortality rates, density-dependence, harvest rates). Large arrows with centered circles represent flows. Flows transfer material into (+) or out of (–) state variables (e.g., production and mortality).

Cary, NC, USA). When Weibull parameters could not be estimated, we used normal distributions for stochastic variables (DeMaso et al. 2011).

Preliminary simulations.—Our reference value for determining population changes was 200 individuals in the simulated winter or spring populations, and change of 40 individuals in harvest at a significance level of $\alpha = 0.05$ with a probability of $P = 0.80$ that the difference would be detected if it existed (Grant et al. 1997). We estimated the number of simulations to run (n) using the formula provided by Sokal and Rohlf (1969:247) and Grant et al. (1997:61–64). We conducted 50 preliminary stochastic baseline simulations to obtain variance estimates for the following parameters: winter (hunted) population, spring (posthunt) population, and harvest. We used this information to calculate the required number of simulations. Preliminary simulations were conducted with a 20% harvest rate, and each model variable evaluated was simulated independently. Based on these calculations, we conducted 165 simulations for each level of harvest (0−40%) because it was the largest number of simulations considered necessary to achieve our objectives for model power (DeMaso et al. 2011).

Model Description and Specification

The model operated on a seasonal (quarterly) time step (Δt) of 3 months, where season 1 = spring (1 Mar−31 May), 2 = summer (1 Jun−31 Aug), 3 = fall (1 Sep−30 Nov), and 4 = winter (1 Dec–28 Feb), and was based on empirically derived relationships and hypothesized links between population parameters and population dynamics (Figure 1; Appendices A, B). The model assumed that the 800-ha area was composed of 100% usable space (Guthery 1997) and that either no immigration or emigration occurred or immigration and emigration were equal.

Production.—Bobwhites in the South Texas Plains do not exhibit age-specific reproduction (Hernández et al. 2007*a*). The model considered all females entering the breeding period to have the same probability of initiating a nest. Banding records from the South Texas Plains indicate that approximately 45% of the spring adult bobwhite population was composed of females (Caesar Kleberg Wildlife Research Institute Quail Research Program unpublished data). We calculated the number of females in the breeding population ($Females_t$) each season by drawing from a normal distribution at time t with a mean value of 0.45 ± 1 standard deviation of the mean (Table 1). Values for percent females nesting ($PropNest_t$), clutch size ($ClutchSize_t$), and number of nests per hen ($NestRate_t$) were drawn each year from the Weibull distributions developed and used by DeMaso et al. (2011; Tables 1, 2). Density-dependent reproduction ($DDependence_t$) was incorporated by using a theoretical weak linear relationship described by Guthery et al. (2000) and developed and used by DeMaso et al. (2011): Density-dependence = -0.00038386 × breeding population + 0.95250 (Table 2). Reproductive effort ($RepEffort_t$) was calculated as $ClutchSize_t \times Females_t \times NestRate_t \times DDependence_t$.

Table 1. Values of constants and parameters describing statistical distributions for stochastic variables in the population simulation model for northern bobwhites (*Colinus virginianus*) in the South Texas Plains, USA, during fall, winter, spring, and summer seasons. Parameters β, α, and γ represent the shape, scale, and location parameters of the Weibull distribution, and the parameters $\bar{x}$ and σ represent the mean and standard deviation of the normal distribution. Both Weibull and normal distributions were truncated at 0.0 and the highest estimate from telemetry data, and values of parameters controlling reproduction were equal to zero except during spring and summer seasons (DeMaso et al. 2011). See text for details.

Parameter	Season[a]	Distribution	Value	β	α	γ	$\bar{x}$	σ
Production								
DDependence	1, 2		-0.004					
$ClutchSize_t$	1, 2	Weibull		14.306	4.988	0.000		
$Females_t$	1,2	Normal					0.450	0.050
$NestRate_t$	1, 2	Weibull		0.766	1.361	0.975		
$PropNest_t$	1, 2	Weibull		25.289	1.569	42.827		
Mortality								
$ChickMortRate_t$	2, 3	Normal					0.4761	0.160
$JuvNatMortRate_t$	1, 2, 3, 4	Normal					0.2599	0.091
$AdultNatMortRate_t$	1, 2, 3, 4	Normal					0.2599	0.091
Harvest								
$JuvHarvestRate_t$	4	Constant	0–40% [b]					
$AdultHarvestRate_t$	4	Constant	0–40% [b]					

[a] 1 = spring (breeding), 2 = summer, 3 = fall, 4 = winter (hunted)

[b] Harvest was simulated at 0%, 10%, 15%, 20%, 25%, 30%, 40%, but remained constant during each set of simulations.

Table 2. Sample size (*n*), mean ($\bar{x}$), and 95% confidence interval (95% CI) for 7 model parameters used in the northern bobwhite (*Colinus virginianus*) sustained-yield harvest population model sensitivity analysis.

Category		Descriptive parameter values	
Parameter	*n*	$\bar{x}$	95% CI
Productivity			
$DDependence_t$ [a]		–0.0004	
$NestMort_t$ [b]	109	0.6150	0.491–0.710
$NestRate_t$ [c]	15	1.7000	1.400–2.000
$PropNest_t$ [c]	15	0.6560	0.574–0.739
Mortality			
$ChickMort_t$ [d]	119	0.4761	
$JuvNatMortRate_t$ [e]	50	0.2599	
$AdultNatMortRate_t$ [e]	50	0.2599	

[a] Slope of the theoretical, linear relationship between reproduction and spring and summer populations determined by DeMaso et al. (2011). No estimate of variance is associated with the intercept and slope of the regression line.

[b] Estimate derived from data in Rader et al. (2007) for 23-day incubation period.

[c] Estimate derived by DeMaso et al. (2011) based on empirical data from study site.

[d] Estimate derived from data in Lusk et al. (2005).

[e] Estimate based on 30% annual survival estimate for bobwhites in the South Texas Plains, USA (Hernández et al. 2007*a*, Sands et al. unpublished data)

Nest success was based on the daily nest survival rate (0.9593) estimated by Rader et al. (2007). We calculated the probability of nests surviving the incubation period (23 days) where survival = 0.9593^{23} = 0.3845. Nest mortality ($NestMort_t$) = 0.6155 or 1 – nest survival. We drew nest survival rates from a normal distribution ± 1 standard deviation of the mean. Realized reproduction ($RealReprod_t$) was calculated as the ($RepEffort_t$) – ($RepEffort_t \times NestMort_t$). $RealReprod_t$ became the number of chicks ($Chicks_t$) hatched into the population each spring and summer.

Natural mortality.—Chick mortality was calculated using the 150-day survival rate based on the daily survival rate (0.9957) from Lusk et al. (2005). Chick survival = 0.9957^{150} = 0.5229. Chick mortality rate ($ChickMortRate_t$) = 0.4771 or 1 – chick survival. This rate was also used by DeMaso et al. (2011) to estimate chick survival during summer. We drew chick mortality rates from a normal distribution, ± 1 standard deviation of the mean, and calculated chick mortality ($ChickMort_t$) as $ChickMortRate_t \times Chicks_t$. We calculated recruitment of Chicks to juveniles (*Recruitment1*)

using $Chicks_t - ChickMort_t$. Individuals remaining after this calculation were classified as juveniles (*Juveniles*).

We calculated natural mortality of adults and juveniles based on an annual survival estimate of 30% (Hernández et al. 2007*b*). Each seasonal mortality rate (juvenile natural mortality rates: $JuvNatMortRate_t$ and adult natural mortality rates: $AdultNatMortRate_t$) was drawn from a normal distribution ± 1 standard deviation of the mean (Table 1). Natural juvenile mortality ($JuvNatMort_t$) was calculated as $Juveniles \times JuvNatMortRate_t$ and juvenile mortality during the hunting season was calculated as $Juveniles_4 \times JuvHuntedMortRate_4$ (see following "Harvest" section). Recruitment of Juveniles to adults (*Recruitment2*) was calculated as $Juveniles_t - JuvNatMort_t$ or $Juveniles_4 - JuvHuntedMort_4$ (see "Harvest" section). Individuals remaining after this calculation were classified as adults ($Adults_t$). We calculated retention of adults from season to season as $Adults_t - AdultNatMort_t$ or $Adults_4 - AdultHuntedMort_4$ (see "Harvest" section).

Harvest.—The model included harvest effects to evaluate the impacts of harvest within a sustained-yield harvest context. The winter population was subject to harvest (H) and natural mortality rate with the survivors constituting the breeding population. The impact of H on bobwhite mortality was modeled using the additive mortality model (Ricker 1958, Roseberry 1979, Guthery 2002):

$$Q_a = H_o + V_o - H_o V_o$$

where,

Q_a=total mortality rate from start to end of hunting season

H_o=harvest rate in a population with no natural mortality

V_o=natural mortality in the absence of harvest

The additive harvest model predicts that increasing the rate of harvest will increase the overall mortality rate (Q_a) within a population during the period of harvest, but that this increase does not result in 1:1 additivity because it accounts for natural mortality (V_o) that occurs within the population during the time of harvest (Roseberry 1979, Guthery 2002). We assumed that H_o was equal to a harvest rate H in a population that was experiencing natural mortality. H has been considered a sufficient approximation of H_o by other researchers (Roseberry 1981, Guthery 2002).

We calculated mortality of juveniles and adults during the hunting season as $JuvHuntedMort_4$ and $AdultHuntedMort_4$, where $JuvHuntedMort_4 = Juveniles_4 \times JuvHuntedMortRate_4$. $JuvTotalMortRate_4$ was the total mortality rate for juveniles during the winter (hunted population) and was calculated as $JuvHuntedMortRate_4 = (JuvHarvestRate_4 + JuvNatMortRate_4) - (JuvHarvestRate_4 \times JuvNatMortRate_4)$. $AdultHuntedMortRate_4$ was the total mortality rate for adults during winter (hunted population) and was calculated as $AdultHuntedMortRate = (AdultHarvestRate + AdultNatMortRate_t) - (AdultHarvestRate_4 \times AdultNatMortRate_4)$. $JuvHarvestRate_4$ was the percentage of juveniles harvested each hunting season. $AdultHarvestRate_4$ was the percentage of adults harvested each hunting season. Finally, we calculated the number of bobwhites harvested each year ($Yield_4$) as $JuvHarvestRate_4 \times Juveniles_4 + AdultHarvestRate_4 \times Adults_4$. We recognize that juvenile and adult bobwhites may be harvested at different rates during hunting season (Pollock et al. 1989, Shupe et al. 1990, Roseberry and Klimstra 1992). However, because bobwhites do not exhibit age-specific reproduction (Hernández et al. 2007*a*), and the determination of either age class cannot be made prior to harvest (e.g., hunters cannot distinguish adult birds from juveniles at flushing), we considered it justifiable to model these age classes with equal harvest rates. Essentially, we were more concerned with modeling the abundance of bobwhites from year to year and the number of bobwhites harvested than we were with modeling which demographic class (age and sex) to which each bobwhite in the population belonged.

We constructed a model that would optimize the yield from bobwhite hunting in the South Texas Plains while minimizing probability of population extinction. Guthery et al. (2000) suggested that bobwhites in southern latitudes (e.g., South Texas Plains) could sustain harvest rates ≤30% and that 30−40% harvest rates would be excessive. Preliminary simulations indicated that 30−40% harvest could potentially impact population persistence, while harvest rates ≤10% had no impact on persistence. Therefore, we ran 7 scenarios of 100-year simulations: 1) a baseline model (i.e., 0% harvest), 2) 10% harvest, 3) 15% harvest, 4) 20% harvest, 5) 25% harvest, 6) 30% harvest, and 7) 40% harvest.

Model Evaluation and Application

Simulated dynamics.—We evaluated the model by 1) visually inspecting model output for evidence of "boom and bust" dynamics characteristic of the South Texas Plains; 2) comparing the trend (slope ± standard error [SE], 95% confidence interval [CI]) with an independent population index (i.e., August roadside counts conducted by Texas Parks and Wildlife Department [TPWD]); and 3) comparing our results with the observed estimates from our study site (Table 3). We estimated the winter (hunted) population and density, spring (posthunt) population and density, the total harvest (100-year total), population quasi-extinction (≤0.05 bobwhite/ha; DeMaso et al. 2011), mean harvest/year, finite rate of increase (λ), and proportion of density-based poor hunting conditions (winter population ≤0.60 bobwhite/ha; DeMaso et al. 2011) for each harvest scenario.

Model sensitivity.—We conducted a sensitivity analysis by using a deterministic version of the model. We made the model deterministic by assigning mean empirical values (DeMaso et al. 2011, Hernández unpublished data) to stochastic parameters (e.g., *PropNest*) and changing the value of one parameter by a consistent percentage. This was repeated for each variable used in the sensitivity analysis (Table 2). Mean variation of our stochastic parameters was approximately 17%; therefore, we varied each parameter in the sensitivity analysis by ±17% while holding the other parameters constant at their mean values.

Table 3. Comparisons between simulated and field estimated (observed) values of 5 population parameters of northern bobwhite (*Colinus virginianus*) populations in the South Texas Plains, USA. Simulated values are based on 165 stochastic baseline (0% harvest) runs; observed values are from the study area in Brooks County, Texas, 2001–2008.

	Simulated					Observed				
Parameter	*n*	$\bar{x}$	95% C	Min	Max	*n*	$\bar{x}$	95% CI	Min	Max
Spring density (bobwhites/ha)[a]	165	1.46	1.39–1.54	0.62	3.13	6	0.66	0.38–0.93	0.18	1.17
Winter density (bobwhites/ha)[b]	165	1.99	1.89–2.09	0.67	4.16	9	1.92	1.59–2.25	1.12	2.80
Juvenile:adult age ratio[c]	165	2.74	2.47–3.01	0.03	13.95	26	2.83	2.38–3.27	1.06	5.10
Finite rate of increase (λ)[d]	165	1.09	1.03–1.15	0.31	2.45	3	0.94	0.62–1.27	0.64	1.21

[a] Observed estimates from Schnupp (2009).
[b] Observed estimates from Rusk et al. (2007) and Schnupp (2009).
[c] Observed estimates from hunter-harvested wings on study site, 1983–2008 (R. Howard, San Tomas Hunting Camp, personal communication).
[d] Observed estimates calculated from Rusk et al. (2007) and Schnupp (2009) density estimates.

Bobwhite populations in the South Texas Plains are greatly impacted by production (Guthery et al. 2000, DeMaso et al. 2011). The simulation model constructed by DeMaso et al. (2011) was driven mostly by changes in nesting attempts per hen, nest survival, proportion of hens nesting, sex ratio at hatch, and density-dependent reproduction. We did not consider sex ratio at hatch as a model parameter, but we did evaluate the impacts of *NestMort*, *NestRate*, *PropNest*, and *DDependence* on the winter (hunted) population.

Sandercock et al. (2008) found that chick and adult survival parameters explained the greatest amount of variance in the λ of bobwhite populations. Thus, in addition to the production parameters, we tested the seasonal impacts of varying $JuvNatMortRate_t$, and $AdultNatMortRate_t$ on the winter population. It was not necessary to evaluate the impacts on spring population or yield as these parameters are correlated with the winter population (i.e., results would have been nearly identical).

Applied harvest management scenario.—Bobwhite managers in the South Texas Plains often discontinue harvest when they consider fall-winter populations too low to be safely harvested (e.g., 0.25 bobwhite/ha). We wanted to evaluate the effects of discontinuing harvest during population lows. Therefore, we conducted a series of simulations (n = 191) where no harvest was conducted (Q_a = 0) if the winter (season 4) density was <0.25 bobwhite/ha (200 birds). Otherwise, the population was harvested at rates of 20−30%. We determined the number of simulations necessary for this scenario using the methodology described earlier. Based on these results we ran 191 simulations of the harvest discontinuation scenario at 20%, 25%, and 30% harvest rates, and evaluated the impacts of these rates on winter and spring populations, probability of population persistence, yield, and frequency of hunting stoppage.

RESULTS

Model Dynamics

Visual inspection of our baseline model (Figure 2) indicated the dynamic "boom and bust" behavior typical of South Texas Plains bobwhite populations. Our baseline model was consistent (95% CIs overlapped) with 3 of 4 observed parameters (winter density adult:juvenile age ratio, and finite rate of increase) at our study site. Finite rate of increase from simulations indicated a 9% annual increase, whereas the observed estimate indicated a 6% annual decrease at our study site (Table 3). However, CIs of these estimates overlapped. Population trends (slope ± SE, 95% CI) based on TPWD survey data and model data were different. The TPWD data indicated a declining trend (-0.72 ± 0.22, 95% CI = -1.16− - 0.28), while our model output indicated a stable to slightly increasing trend (0.93 ± 0.94, 95% CI = -0.93−2.79). Our model remained generally consistent (e.g., 95% CIs overlapping with 3 of 4 observed parameters) as harvest increased from 0−15% (Table 3, Appendix C). Beyond 20% harvest rates, 95% CIs of model predictions overlapped only with spring density (20% harvest, 25% harvest) and finite rate of increase (20% harvest, 25% harvest, 30% harvest, and 40% harvest; Appendix C).

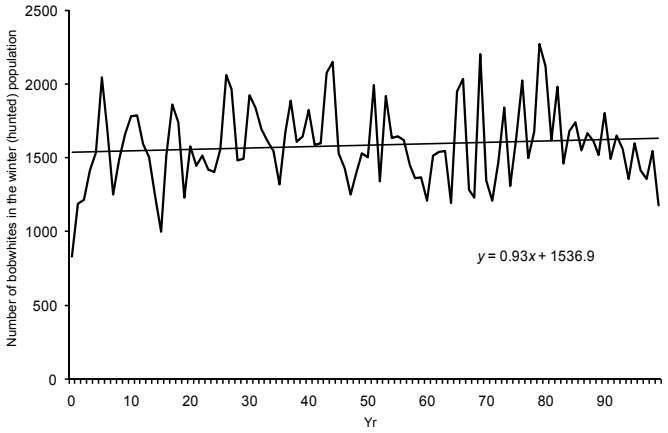

Fig. 2. Population projection and trend based on the mean of 5 randomly selected baseline (0% harvest) winter northern bobwhite (*Colinus virginianus*) populations simulated over a 100-year period.

Harvest Rates, Yield, and Population Persistence

Increasing harvest rates resulted in 11−94% decreases in mean winter (hunted) populations from the baseline population (Figure 3), and 21−95% decreases in mean spring (breeding) populations (Figure 4) as harvest increased from 0% to 40%. Our model indicated that bobwhite harvest rates ≤20% did not impact probability of quasi-extinction [P (quasi-extinction) ≤ 0.95] (Table 4). A 20% harvest rate resulted in a 7% probability of quasi-extinction within an average (±SE) of 53.0 ± 7.8 years, a 30% harvest rate resulted in a 75% quasi-extinction probability within an average 47.8 ± 2.3 years, and a 40% harvest rate resulted in population quasi-extinction in 100% of simulations within an average of 15.5 ± 2.6 years (Table 4).

Harvest rates of 20% and 25% produced the greatest annual yield ($\bar{x}$ ± SE: 231 ± 10 and 219 ± 11 bobwhites harvested/year, respectively), which also produced the greatest total harvest over the 100-year simulation (Table 5). Since the model included a density-dependent production component, age ratios (juveniles:adults) increased by 15−54% as harvest rates increased from 0−30%; however, this relationship collapsed at a 40% harvest rate due to the high frequency of quasi-extinction. Mean spring densities at 20% and 25% harvest rates were 0.78 bobwhite/ha (95% CI: 0.71−0.84) and 0.60 bobwhite/ha (95% CI: 0.55−0.65), respectively (Appendix C).

Proportion of simulations with density-based poor hunting conditions (<0.6 bobwhite/ha) increased from 111% to 184% as the annual harvest rate increased from 10 to 40% (Table 6), but density-based poor hunting conditions occurred at all levels of harvest (0−40%). As harvest increased from 15% to 25%, the mean number of years with poor harvest conditions increased from 5.53 ± 0.45 (95% CI: 4.65−6.41) to 26.41 ± 1.08 (95% CI: 24.29−28.53), a 378% increase per 100 years (Table 6).

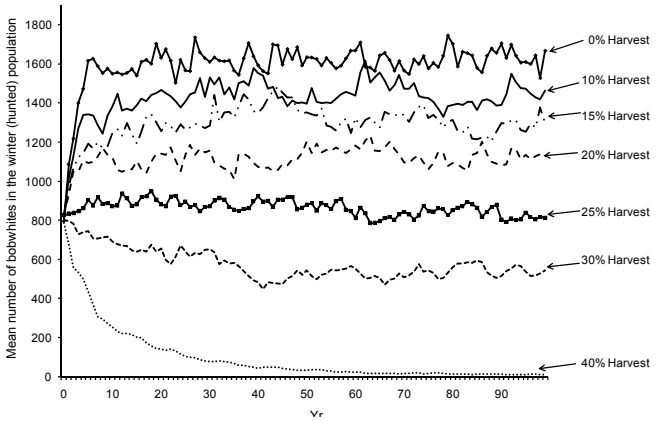

Fig. 3. Trends in simulated mean winter (hunted) northern bobwhite (*Colinus virginianus*) populations on an 800-ha area based on 165 simulations at 0%, 10%, 20%, 25%, 30%, and 40% harvest rates in the South Texas Plains, USA.

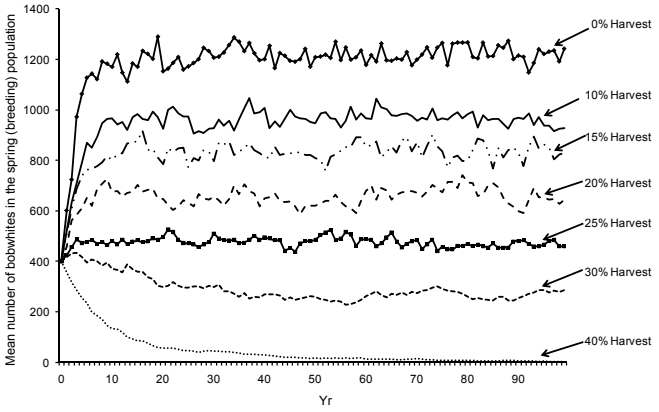

Fig. 4. Trends in simulated mean spring (breeding) northern bobwhite (*Colinus virginianus*) populations on an 800-ha area based on 165 simulations at 0%, 10%, 20%, 25%, 30%, and 40% harvest rates in the South Texas Plains, USA.

Table 4. Relationship between percent harvest, abundance (winter and spring), probability of population persistence (*P*), and time to quasi-extinction[a] in a simulated northern bobwhite (*Colinus virginianus)* population in the South Texas Plains, USA (n = 165, 100-year simulations).

	Seasonal abundance									Population persistence			
	Winter population[b]				Spring population[c]					Time to quasi-extinction (years)			
Harvest	$\bar{x}$ ± SE	95% CI	Min	Max	$\bar{x}$ ± SE	95% CI	Min	Max	*P*	$\bar{x}$ ± SE	95% CI	Min	Max
0%	1,509 ± 41	1,509–1,671	539	3,328	1,170 ± 30	1,112–1,229	497	2,501	1.00	–	–	–	–
10%	1,402 ± 51	1,302–1,503	320	3,781	952 ± 32	889–1,015	123	2,419	1.00	–	–	–	–
15%	1,347 ± 47	1,255–1,438	301	3,921	820 ± 33	755–886	107	2,304	1.00	–	–	–	–
20%	1,148 ± 45	1,059–1,237	260	3,163	621 ± 26	570–671	110	1,679	0.93	53.0 ± 7.8	37.6–68.2	10.5	92.5
25%	863 ± 41	784–943	43	3,185	480 ± 22	437–523	25	1,428	0.75	56.5 ± 4.0	48.6–64.3	16.3	99.5
30%	522 ± 35	453–591	13	2,525	260 ± 18	225–297	4	1,395	0.25	47.8 ± 2.3	43.3–52.3	4.5	97.5
40%	34 ± 7	20–48	0	844	16 ± 2	12–20	0	159	0.00	15.5 ± 2.6	10.4–20.6	3.5	53.3

[a] Quasi-extinction occurs when the population declines to ≤40 bobwhites (≤ 0.05 bobwhite/ha; DeMaso et al. 2011).

[b] Winter population (season 4) is the population subject to hunter harvest.

[c] Spring population (season 1) is the population immediately following hunting season and represents the initial breeding population for the next year.

Table 5. Simulated yield (mean [$\bar{x}$], standard error [SE], 95% confidence interval [CI], range, mean 100-year total yield) from a northern bobwhite (*Colinus virginianus*) population at 6 different rates of harvest in the South Texas Plains, USA (n = 165 simulations).

	Average annual yield				Mean total yield (100 years)			
Harvest Rate	$\bar{x}$ ± SE	95% CI	Min	Max	$\bar{x}$ ± SE	95% CI	Min	Max
10%	153 ± 5	143–164	22	357	14,428 ± 95	14,242–14,613	10,779	17,111
15%	189 ± 7	176–201	47	472	19,188 ± 154	18,885–19,490	14,484	24,333
20%	231 ± 10	211–252	43	888	22,461 ± 278	21,917–23,005	13,876	31,502
25%	219 ± 11	198–248	15	696	22,269 ± 342	21,599–22,938	9,692	32,032
30%	158 ± 10	137–179	2	737	16,822 ± 414	16,009–17,636	4,122	29,113
40%	18 ± 5	8–27	0	719	4,192 ± 236	3,730–4,654	519	17,671

Table 6. Proportion of simulations with density-based poor hunting conditions (≤0.60 bird/ha in the winter population; DeMaso et al. 2011) and mean number of years with density-based poor hunting conditions per 100-year simulation at 7 different rates of harvest in the South Texas Plains (n = 165*)*.

		Years with poor hunting conditions			
Harvest rate	Simulations with poor hunting conditions	$\bar{x}$ ± SE	95% CI	Min	Max
0%	35.2%	0.72 ± 0.11	0.51–0.92	0	6
10%	74.5%	2.78 ± 0.24	2.31–3.24	0	15
15%	87.2%	5.53 ± 0.45	4.65–6.41	0	39
20%	97.6%	12.12 ± 0.69	10.80–13.53	0	47
25%	100.0%	26.41 ± 1.08	24.29–28.53	2	72
30%	100.0%	52.67 ± 1.44	49.85–58.49	11	97
40%	100.0%	93.90 ± 0.46	92.99–94.81	67	100

Model Sensitivity

Changes in reproductive parameters had the greatest impacts on simulated winter (hunted) populations (Table 7). Specifically nest mortality ($NestMort_t$) had the largest impact on the winter population. A 17% increase in nest mortality resulted in a 93% decrease in the winter population (Table 7). The proportion of hens nesting ($PropNest_t$) and the number of nests per hen ($NestRate_t$) had the same impact on fall populations. Increasing either of these parameters by 17% resulted in a 37% population increase. Reducing either variable by 17% resulted in a 52% population decrease. Reducing density-dependence ($DDependence_t$) in reproduction by 17% resulted in a 20% population increase, and increasing density-dependence in reproduction by 17% resulted in a 14% decrease in the population.

With the exception of chick mortality ($ChickMort_t$), mortality parameters had a comparatively low impact on the winter population. Reducing chick mortality by 17% resulted in a 34% population increase, and increasing chick mortality by 17% resulted in a 47% population decrease (Table 7). Increasing spring adult mortality ($AdultNatMortRat_1$) by 17% resulted in an 11% population decrease (Table 7). Increasing or reducing the remaining mortality rates of adults and juveniles resulted in <10% population increases or declines (Table 7).

Despite relatively high sensitivity of our deterministic model, our stochastic model was generally consistent (95% CIs overlapping in 4 of 5 parameters) with observed parameters as harvest rates ranged from 0−25%, and appeared to be robust to changes in harvest rates ≤25% with respect to observed data. Given that estimated harvest rates on our study area averaged 15.6 ± 7.2% per year (Sands 2010), it should not necessarily be expected that model predicted population parameters would remain consistent with field estimates at relatively high (30% and 40%) harvest rates.

Model Applications: Harvest in an Applied Context

Our harvest management scenario indicated that when hunting was discontinued at 0.25 bird/ha, probability of population persistence increased for 20%, 25%, and 30% harvests (Table 8). However, despite decreased probability of quasi-extinction at 30% harvest rates, 20% and 25% harvest rates resulted in 21% and 23% greater annual yields of bobwhites, respectively (Table 9). Mean spring densities at 20% and 25% harvest rates were 0.81 (95% CI: 0.75−0.87) and 0.66 (95% CI: 0.61−0.72), respectively. This scenario also indicated harvest rates of 30% resulted in increased frequency of hunting season closure and reduced average yields compared to harvest rates <30% (Table 10). In 30% harvest simulations, hunting seasons were closed at least once in 96.3% of simulations, with a mean of 6.6 ± 0.3 seasons (Table 10).

Table 7. Northern bobwhite (*Colinus virginianus*) sensitivity analysis of 11 model parameters varied by ±17%, based on variation associated with empirical parameter estimates (if there was a measure of variation associated with the estimate), and the absolute difference between the winter (hunted) population, at –17% and +17%, and their percent difference from the baseline (mean values for all model parameters): winter population (1,351 bobwhites).

Category		Winter (hunted) population difference		
Parameter	Variation	Value	Absolute difference	% Difference
Productivity				
$DDependence_t$	+17%	1,155	472	–14.51
	–17%	1,627		20.43
$NestMort_t$	+17%	90	2,001	–93.34
	–17%	2,091		54.77
$NestRate_t$	+17%	1,854	1,213	37.23
	–17%	641		–52.55
$PropNest_t$	+17%	1,854	1,213	37.23
	–17%	641		–52.55
Mortality				
$ChickMort_t$	+17%	717	1,098	–46.93
	–17%	1,815		34.34
$JuvNatMortRate_3$	+17%	1,249	196	–7.55
	–17%	1,445		6.96
$JuvNatMortRate_4$	+17%	1,269	155	–6.07
	–17%	1,424		5.40
$AdultNatMortRate_1$	+17%	1,201	281	–11.10
	–17%	1,482		9.70
$AdultNatMortRate_2$	+17%	1,285	131	–4.89
	–17%	1,416		4.81
$AdultNatMortRate_3$	+17%	1,285	131	–4.89
	–17%	1,416		4.81
$AdultNatMortRate_4$	+17%	1,226	230	–9.25
	–17%	1,456		7.77

Table 8. Relationship between percent harvest, abundance (winter and spring), probability of population persistence (*P*), and time to quasi-extinction[a] in a simulated northern bobwhite (*Colinus virginianus*) population at 3 different rates of harvest in the South Texas Plains, USA (n = 191, 100-year simulations) when harvest is discontinued when winter populations are ≤0.25 birds/ha (200 birds).

	Seasonal abundance								Population persistence				
	Winter population[b]				Spring population[c]					Time to extinction (years)			
Harvest	$\bar{x}$ ± SE	95% CI	Min	Max	$\bar{x}$ ± SE	95% CI	Min	Max	*P*	$\bar{x}$ ± SE	95% CI	Min	Max
20%	1,114 ± 40	1,034–1,194	204	2,770	651 ± 24	604–698	98	2,121	0.99	51.0 ± 0.0	– 51.0	51.0	
25%	911 ± 38	836–986	126	3,220	531 ± 24	484–577	82	1,791	0.97	47.5 ± 8.6	30.6–64.4	26.5	77.5
30%	584 ± 27	530–638	116	2,200	321 ± 15	291–351	69	1,043	0.94	37.5 ± 8.1	21.6–53.5	6.8	88.5

[a] Quasi-extinction occurs when the population decline to ≤ 40 bobwhites (≤ 0.05 bobwhite/ha; DeMaso et al. 2011).

[b] Winter population (season 4) is the population subject to hunter harvest.

[c] Spring population (season 1) is the population immediately following hunting season and represents the initial breeding population for the next year.

Table 9. Simulated yield (mean [$\bar{x}$], standard error [SE], 95% confidence interval [CI], range, mean 100-year total yield) from a northern bobwhite population at 3 different rates in the South Texas Plains, USA (n = 191 simulations) when harvest is discontinued when winter populations are ≤0.25 bird/ha (200 birds).

	Average annual yield				Mean total yield (100 years)			
Harvest rate	$\bar{x}$ ± SE	95% CI	Min	Max	$\bar{x}$ ± SE	95% CI	Min	Max
20%	232 ± 9	214–249	0	681	22,393 + 223	21,956–22,829	13,145	29,770
25%	228 ± 11	207–250	0	994	22,106 ± 280	21,557–22,564	11,581	32,509
30%	188 ± 11	166–209	0	1,071	19,716 ± 308	19,113–20,319	11,659	35,697

Table 10. Proportion of simulations with ≥1 year harvest ending density ≤0.25 bobwhite/ha and mean number of years with a harvest ending per 100-year simulation at 3 different harvest rates in the South Texas Plains, USA (n = 165 simulations) when winter populations are ≤0.25 bird/ha (200 bobwhites).

		Mean number of years with ending			
Harvest rate	Simulations with ≥1 year ending	± SE	95% CI	Min	Max
20%	29.3%	0.68 ± 0.11	0.47–0.88	0	9
25%	70.7%	2.35 ± 0.19	1.98–2.71	0	13
30%	96.3%	6.61 ± 0.31	5.99–7.22	0	21

DISCUSSION

Sustainable Harvest Rates and Spring Population Goals

Sustainable harvest rates.—Harvesting bobwhite populations in the South Texas Plains at rates of ≤20% of the prehunt population may maximize long-term harvest while minimizing the probability of population extinction, at least on areas that represent fully usable habitat space and in populations that tend to be stable to increasing from year to year (as was the case for our simulated population). Additionally, our model indicated that harvest rates >30% would significantly decrease the probability of long-term population persistence, and that 40% harvest rates would result in population extinction. This represents sustainable harvest rates that are lower than those reported from other regions of the bobwhite range (e.g., Vance and Ellis 1972, Roseberry 1979).

Vance and Ellis (1972) suggested that harvest rates as high as 60−80% of the hunted population had no detrimental impact on bobwhite abundance. Based on our results and those of Roseberry (1979), we question these estimates in the absence of significant immigration that perhaps masked detrimental effects of these harvest rates. Simulations based on a 24-year dataset (Roseberry and Klimstra 1972) of demographic data from southern Illinois, USA (Roseberry 1979) indicated that harvest rates ≥50% of the population severely impacted the ability of bobwhite populations to compensate for losses from hunting. These harvest rates required exponential increases in summer gains to maintain stable population densities. However, harvest rates of 40−45% appeared to be acceptable for maintaining suitable densities in Illinois (Roseberry 1979).

Scale of hunting (i.e., property size) influences sustainable yields. For example, Guthery et al. (2000) reported that probability of persistence did not reach 0.95 for populations subject to summer catastrophes (e.g., severe droughts) and experiencing 40% harvest until demographic capacities exceeded 10,000. The density required to sustain a 40% harvest may be reasonable for a large property (e.g., ≥10,000 ha; 1 bobwhite/ha) but not for our hypothetical property (800 ha; 12.5 bobwhites/ha). It should be noted that given our model conditions (800-ha area, 0% immigration), 40% harvest rates were never sustainable over a 100-year simulation.

Spring population goals.—In arid and semiarid regions, New World quail population dynamics are influenced by weather (Heffelfinger et al. 1999, Hernández et al. 2005). Influences of rainfall and temperature are likely to obscure effects of density-dependent population mechanisms, and may result in weak density-dependent population growth. Using harvest rates to achieve spring (breeding) population goals is a longstanding component of sustained-yield harvest theory (Roseberry 1982). Our data indicate that spring densities of 0.60−0.80 bobwhite/ha are associated with harvest rates that optimize harvest and reduce probability of population extinction (20% and 25% harvest rates). The probability of extinction further declines when harvest is discontinued during years of poor production. To this end, the range of 0.60−0.80 bobwhite/ha represents a minimum viable spring density for bobwhites in the South Texas Plains. Mean field estimates of spring densities on our study sites were 0.66 bobwhite/ha (95% CI: 0.38−0.93), which may indicate that some bobwhite populations in this region currently occur near this density at the beginning of the breeding period.

The simulation model developed by Yeiser et al. (2021) based on data from bobwhites in the Red Hills region of the

Gulf Coastal Plain, USA, indicated that density-dependence was unlikely to fully compensate for harvest mortality even when density-dependence was relatively strong. In regions where density-dependent effects may be relatively weak relative to the impact of weather conditions (Sands 2010), the predictability of reproduction based on spring density may become even more tenuous. In declining bobwhite populations, hunting pressure may actually increase (Brennan and Jacobson 1992), and harvest can become an increasingly additive and unsustainable component of mortality (Rolland et al. 2010). In declining populations, sustainable harvest rates may be lower than the 15−25% range suggested by our model.

A more conservative and perhaps more appropriate approach to harvest management in these situations is to determine a long-term sustainable harvest rate (e.g., 15%), prescribe a harvest based on the prehunt population (e.g., 150 of 1,000 birds), and discontinue harvest when prehunt density is <0.25/ha. Weak density-dependence in the South Texas Plains populations of bobwhites decreases the benefits of harvesting in excess of 25% to reach the minimum viable spring density. This is because a positive density-dependent response in reproduction, as a result of reduced abundance, is likely to be less pronounced than in other regions. Successful implementation of either strategy depends on precise (e.g., ±5% of the true population) estimates of the hunted population.

Managing Hunting to Facilitate Sustainable Harvests

Timing of harvest.—Bobwhite harvest is considered additive to natural mortality (Roseberry and Klimstra 1984, Williams et al. 2004*b*), and timing of harvest impacts the degree of additive mortality that results from harvest (Kokko and Lindström 1998, Kokko 2001). The majority of harvest in the South Texas Plains occurs from December to February. Presumably, harvesting during the late winter (Jan−Feb) produces more additive mortality than if the majority of harvest occurred from October to December. Bobwhite hunting conditions are often less than optimal (i.e., temperatures >30° C; abundant, green cover conditions prior to a winter frost) during the early portions of legal hunting season in the South Texas Plains, and many hunters prefer to hunt late in the season. Given this, it is important to choose harvest rates that will not result in excessive additivity. Our model indicates that harvest rates <20% should be sustainable on a long-term basis.

Hunting pressure.—Hardin et al. (2005) recognized that hunting pressure and harvest could be managed by altering hunting behaviors within the context of hunter-covey interface theory (Radomski and Guthery 2000, Guthery 2002). Once a winter hunted population is estimated and a harvest prescription assigned, the level of daily harvest can be determined: daily harvest × number of days hunted = prescribed yield. Daily harvest can be controlled by regulating number of birds killed per covey (both bagged and wounded) or velocity (km/hour) of hunting parties, or both (Hardin et al. 2005). Conducting hunts at low velocities has potential to reduce daily harvest without reducing total hunting time (Hardin et al. 2005), which could impact hunter satisfaction.

Connecting Harvest Management to Habitat Management

The widespread decline of the bobwhite in the United States is primarily the result of broadscale habitat loss and degradation (Brennan 1991, 1999). Management of bobwhite habitat and harvest has traditionally been conducted at improper scales, which may have exacerbated this decline (Williams et al. 2004*a*), especially considering that unsustainable harvest rates and harvest pressure exist in locations where populations are declining (Brennan and Jacobson 1992, Rolland et al. 2010). Researchers who study migratory game birds have recognized that connecting population goals based on harvest and habitat management objectives would improve conservation of these species (Runge et al. 2006, Rappole et al. 2008). The reason for this is that where habitat is lost, sustainable annual yields decrease (Runge et al. 2006). Conversely, expansion of habitat increases the level of sustainable annual yields and improves hunting opportunity (Runge et al. 2006).

A parallel situation exists within the bobwhite management paradigm. For instance, in the South Texas Plains, a reduction in necessary habitat components (e.g., abundance of available nesting cover) resulted in simulated bobwhite populations decreasing by 75% from baseline conditions (Rader et al. 2011). Our model indicates that reducing the hunted population by 33% would result in a 28% decrease in mean annual harvest yield. Thus, it appears that the effect of maintaining usable bobwhite habitat space (Guthery 1997) on bobwhite population production, yield, and ultimately population viability is palpable. Given that rangewide bobwhite population recovery requires a landscape-scale approach to habitat management and a regional or local approach to harvest management (Peterson 2001, Williams et al. 2004*a*), bobwhite conservation would be best suited by unifying population recovery goals with habitat and harvest objectives.

MANAGEMENT IMPLICATIONS

Harvesting bobwhite populations in the South Texas Plains at rates of 20−25% of the prehunt population (based on accurate population estimates) may maximize long-term harvest while minimizing the probability of population extinction. Harvest rates >30% are excessive with respect to long-term population persistence. For high probability of population persistence and optimal yield, managers should harvest 15−20% of winter bobwhite populations and discontinue harvest when winter populations are ≤0.25 bird/ha. Managers must realize that even in the presence of optimal habitat and conservative harvest (15−25% mean annual harvest), density-based poor hunting conditions will occur in 5−25% of hunting seasons. However, maximizing usable habitat area within a landscape has the potential to increase annual yield of bobwhites.

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APPENDIX A.
Parameter and variable definitions used to simulate bobwhite harvest in the South Texas Plains.

Parameter or variable	Definition
$Adults_t$	Adult northern bobwhite (individuals ≥1 year old).
$AdultHarvestRate_4$	Proportion of adult northern bobwhites removed from the population by hunting during season 4.
$AdultHuntedMort_4$	Total mortality of adults during season 4.
$AdultHuntedMortRate_4$	Total mortality rate of adults during season 4 as calculated by the additive harvest model (see text).
$AdultNatMortRate_t$	The natural mortality rate of adults in seasons 1–4.
Area	Geographic area of interest in the model (800 ha).
$Chicks_t$	Number of eggs successfully hatched.
$ChickMort_t$	Number of chicks dying during season 2 and season 3.
$ChickMortRate_t$	Proportion of chicks dying during season 2 and season 3.
$ClutchSize_t$	Clutch size for northern bobwhites during the breeding season (season 1 and season 2).
Δt	Represents the time step of the model. Time step from t to t + 1 (3 months or 1 season).
$Density_t$	Number of northern bobwhites/ha.
$DDependence_4$	Density-dependent reproduction, a density-dependent feedback loop that the scales the relationship between the breeding population (season 1 and season 2). Study site-specific values were derived by DeMaso et al. (2011).
$Juveniles_t$	The number of chicks surviving to become juveniles in season 3 and season 4.
$JuvHarvestRate_4$	The proportion of juveniles removed from the population by hunting during season 4.
$JuvHuntedMortRate_4$	The total mortality rate of juveniles during season 4 as calculated by the additive harvest model (see text).
$JuvHuntedMort_4$	Total juvenile mortality during season 4.
$JuvNatMort_t$	Natural mortality rate of juveniles during season 3 and season 4.
$Females_t$	Number of females in the population during a given season.
$NestRate_t$	Number of nests initiated per female during the breeding season (season 2 and season 3).
$PropNest_t$	Proportion of females in the population nesting during the breeding season (season 2 and season 3).
$RealReprod_t$	Number of chicks (Chickst) hatched into the population each spring and summer (season 2 and season 3).
Recruitment1	Number of chicks becoming juveniles in season 2 and season 3.
Recruitment2	Number of juveniles becoming adults in season 3 and season 4.
$RepEffort_t$	Number of eggs produced each breeding period.
$Season_{1–4}$	Counter that represents 4 periods in a year as they relate to northern bobwhite phenology in the South Texas Plains: 1 = spring (1 Mar–31 May); 2 = summer (1 Jun–31 Aug); 3 = fall (1 Sep–30 Nov); 4 = winter (1 Dec–28 Feb).
$Yield_4$	The number of northern bobwhite harvested during winter (season 4).

APPENDIX B.

Difference equations used in STELLA 9.0 to parameterize and run harvest simulation model.

Hunter_Harvest =

Adults(t) = Adults(t - dt) + (Recruitment_2 - Adult_Mortality_Hunted - Adult_Mortality_Natural) * dt

INIT Adults = 200

INFLOWS:

Recruitment_2 = If (Season =3) then (Juveniles-Juvenile__Mortality__Natural) else if (Season = 4) then (Juveniles-Juvenile__Mortality__Hunted) else 0

OUTFLOWS:

Adult_Mortality_Hunted = If (Season = 4) then (Adults*Winter_Total__Mortality__Rate_Adults) else 0

Adult_Mortality_Natural = If (Season = 1) or (Season = 2) or (Season =3) then (Adults*Post_Hunt_through_Breeding__Mortality_Rate) else 0

Juveniles(t) = Juveniles(t - dt) + (Recruitment_1 - Recruitment_2 - Juvenile__Mortality__Hunted - Juvenile__Mortality__Natural) * dt

INIT Juveniles = 0

INFLOWS:

Recruitment_1 = If (Season = 2) then (Chicks-Chick__Mortality) else if (Season = 3) then (Chicks-Chick__Mortality) else 0

OUTFLOWS:

Recruitment_2 = If (Season =3) then (Juveniles-Juvenile__Mortality__Natural) else if (Season = 4) then (Juveniles-Juvenile__Mortality__Hunted) else 0

Juvenile__Mortality__Hunted = if (Season = 4) then ((Juveniles*Juvenile_Total_Mortality_Rate__Winter)) else 0

Juvenile__Mortality__Natural = If (Season = 3) then (Juveniles *Juvenile_Mortality_Rate) else 0

Adults__Harvested = Adults*Harvest__Rate

Age_Ratio = If (Season = 3) then (Juveniles/Adults) else if (Season = 4) then (Juveniles/Adults) else 0

Harvest__Rate = If (Season = 4) then 0.4 else 0

Hunted__Density = If (Season = 4) then (Hunted__Population/Area) else 0

Juveniles__Harvested = Juveniles*Harvest__Rate

Northern_Bobwhite__Harvested = Adults__Harvested+Juveniles__Harvested

Season = Counter (1,5)

Productivity =

Bounded_Density_Dependence = If (Density__Dependence <0) then 0 else (Density__Dependence) Clutch_Size = If (Season = 1) THEN (14.30617 * (-LN(RANDOM(0,1)))^(1/4.98768) + 0) ELSE

If (Season = 2) THEN (14.30617 * (-LN(RANDOM(0,1)))^(1/4.98768) + 0) ELSE 0

Eggs = Clutch_Size*Nests

Females = Adults*NORMAL(0.45, 0.05)

Nests = (Females*Nest__Rate*Percent_Females__Nesting)*Bounded_Density_Dependence

Nest__Rate = If (Season = 1) THEN (0.76644 * (-LN(RANDOM(0,1)))^(1/1.36121) + 0.97447) else if (Season = 2) THEN (0.76644 * (-LN(RANDOM(0,1)))^(1/1.36121) + 0.97447) ELSE 0

Percent_Females__Nesting = If (Season = 1) then ((25.28907 * (-LN(RANDOM(0,1)))^(1/1.56920) + 42.82725)/100) ELSE if (Season = 2) THEN ((25.28907 * (-LN(RANDOM(0,1)))^(1/1.56920) + 42.82725)/100) ELSE 0

Seasonal_Population_Parameters = Adults(t) = Adults(t - dt) + (Recruitment_2 - Adult_Mortality_Hunted - Adult_Mortality_Natural) * dt

INIT Adults = 400

INFLOWS:

Recruitment_2 = If (Season = 3) then (Juveniles-Juvenile__Mortality__Natural) else if (Season = 4) then (Juveniles-Juvenile__Mortality__Hunted) else 0

OUTFLOWS:

Adult_Mortality_Hunted = If (Season = 4) then (Adults*Winter_Total__Mortality__Rate_Adults) else 0

Adult_Mortality_Natural = If (Season = 1) or (Season = 2) or (Season = 3) then (Adults*Post_Hunt_through_Breeding__Mortality_Rate) else 0

Chicks(t) = Chicks(t - dt) + (Realized__Production - Recruitment_1 - Chick__Mortality) * dt

INIT Chicks = 0

INFLOWS:

Realized__Production = If (Season = 1) then (Reproductive_Effort)-(Reproductive_Effort*Nest_Mortality_Rate) else if (Season = 2) then (Reproductive_Effort)-(Reproductive_Effort*Nest_Mortality_Rate) else 0

Appendix B, continued

Difference equations used in STELLA 9.0 to parameterize and run harvest simulation model.

OUTFLOWS: Recruitment_1 = If (Season = 2) then (Chicks-Chick__Mortality) else if (Season = 3) then (Chicks-Chick__Mortality) else 0

Chick__Mortality = If (Season = 2) then (Chick_Mortality_Rate*Chicks) else if (Season = 3) then (Chick_Mortality_Rate*Chicks) else 0

Juveniles(t) = Juveniles(t - dt) + (Recruitment_1 - Recruitment_2 - Juvenile__Mortality__Hunted - Juvenile__Mortality__Natural) * dt

INIT Juveniles = 0

INFLOWS:

Recruitment_1 = If (Season = 2) then (Chicks-Chick__Mortality) else if (Season = 3) then (Chicks-Chick__Mortality) else 0

OUTFLOWS:

Recruitment_2 = If (Season = 3) then (Juveniles-Juvenile__Mortality__Natural) else if (Season = 4) then (Juveniles-Juvenile__Mortality__Hunted) else 0

Juvenile__Mortality__Hunted = if (Season = 4) then ((Juveniles*Juvenile_Total_Mortality_Rate__Winter)) else 0

Juvenile__Mortality__Natural = If (Season = 3) then (Juveniles *Juvenile_Mortality_Rate) else 0

Area = 800

Breeding_Density = If (Season = 2) then (Breeding__Population_Adults/Area) else 0

Breeding__Population_Adults = If (Season = 2) then (Adults) else 0

Density = Total__Population/Area

Density__Adults_and_Juveniles = Population_Adults_and__Juveniles/Area

Density_Acres = Density*0.4047

Density_Adults_and_Juveniles_Acres = Density__Adults_and_Juveniles*0.4047

Hunted__Population = If (Season = 4) then (Adults+Juveniles) else 0

Hunted__Density = If (Season = 4) then (Hunted__Population/Area) else 0

Population_Adults_and__Juveniles = Adults+Juveniles

Post_Breeding_Density = If (Season = 3) then (Post_Breeding_Population/Area) else 0

Post_Breeding_Population = If (Season = 3) then (Adults+Juveniles+Chicks) else 0

Post_Hunt_Density = If (Season = 1) then (Post_Hunt__Population/Area) else 0

Post_Hunt__Population = If (Season = 1) then (Adults) else 0

Season = Counter (1,5)

Total__Population = Adults+Juveniles+Chicks

Chick_Mortality_Rate = If (Season = 2) then NORMAL (0.4761, 0.16) else if (Season = 3) then NORMAL (0.4761, 0.16) else 0

Density__Dependence = If (Season = 1) Then (-0.00038386*Post_Hunt__Population + 0.95250) Else IF (Season = 2) Then (-0.00038386*Breeding__Population_Adults + 0.95250) else 0

Juvenile_Mortality_Rate = If (Season = 3) then NORMAL (0.2599, 0.091) else 0

Juvenile_Total_Mortality_Rate__Winter = If (Season = 4) then ((Harvest__Rate+Natural__Mortality)-(Harvest__Rate*Natural__Mortality)) else 0

Natural__Mortality = If (Season = 4) then NORMAL (0.2599, 0.091) else 0

Nest_Mortality_Rate = IF (Season= 1) then NORMAL(0.615, 0.07) else if (Season = 2) then NORMAL(0.615, 0.07) else 0

Post_Hunt_through_Breeding__Mortality_Rate = If (Season = 1) then NORMAL (0.2599, 0.091) else If (Season = 2) then NORMAL (0.2599, 0.091) else if (Season = 3) then NORMAL (0.2599, 0.091) else 0

Proportion_Females = If (adults = 0) then 0 else (Females/Adults)

Reproductive_Effort = If (Season =1) then (Clutch_Size*Females*Percent_Females__Nesting*Nest__Rate)*Bounded_Density_Dependence else If (Season = 2) then (Clutch_Size*Females*Percent_Females__Nesting*Nest__Rate)*Bounded_Density_Dependence else 0

Winter_Total__Mortality__Rate_Adults = If (Season = 4) then ((Harvest__Rate+Natural__Mortality)-(Harvest__Rate*Natural__Mortality)) else 0

APPENDIX C.
Simulated values of 4 bobwhite population parameters at 6 rates of harvest in the South Texas Plains.

Harvest Rate	Parameter	*n*	$\bar{x}$	95% CI	Min	Max
10%	Spring density (bobwhites/ha)	165	1.19	1.11–1.27	0.15	3.02
	Winter density (bobwhites/ha)	165	1.75	1.63–1.89	0.40	4.73
	Juvenile : adult age ratio	165	3.20	2.92–3.49	0.41	10.79
	Finite rate of increase (λ)	165	1.09	1.03–1.16	0.32	2.55
15%	Spring density (bobwhites/ha)	165	1.03	0.94–1.11	0.13	2.88
	Winter density (bobwhites/ha)	165	1.68	1.57–1.80	0.38	4.90
	Juvenile : adult age ratio	165	3.18	2.92–3.45	0.28	11.45
	Finite rate of increase (λ)	165	1.07	1.01–1.13	0.33	2.76
20%	Spring density (bobwhites/ha)	165	0.78	0.71–0.84	0.14	2.10
	Winter density (bobwhites/ha)	165	1.44	1.32–1.55	0.32	3.95
	Juvenile : adult age ratio	165	3.72	3.30–3.92	0.91	11.14
	Finite rate of increase (λ)	165	1.11	1.03–1.19	0.38	3.80
25%	Spring density (bobwhites/ha)	165	0.60	0.55–0.65	0.03	1.79
	Winter density (bobwhites/ha)	165	1.08	0.98–1.18	0.05	3.98
	Juvenile : adult age ratio	165	4.04	3.77–4.34	0.94	10.70
	Finite rate of increase (λ)	165	1.08	1.02–1.13	0.30	2.32
30%	Spring Density (bobwhites/ha)	165	0.33	0.28–0.37	<0.01	1.74
	Winter Density (bobwhites/ha)	165	0.65	0.57–0.74	0.02	3.16
	Juvenile : adult age ratio	165	4.11	3.80–4.41	0.91	11.6
	Finite rate of increase (λ)	165	1.10	1.03–1.17	0.27	3.43
40%	Spring density (bobwhites/ha)	165	0.02	0.01–0.03	0.00	0.20
	Winter density (bobwhites/ha)	165	0.04	0.02–0.06	0.00	1.06
	Juvenile : adult age ratio	165	4.98	4.59–5.38	1.33	18.57
	Finite rate of increase (λ)	165	0.94	0.90–0.98	0.41	2.26

EFFICACY OF A PREEMERGENCE HERBICIDE FOLLOWING POSTEMERGENCE CONTROL TO REDUCE SERICEA LESPEDEZA IN OLD FIELDS MANAGED FOR NORTHERN BOBWHITE

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ABSTRACT

Sericea lespedeza (*Lespedeza cuneata*; hereafter, sericea) is a nonnative forb that commonly invades sites managed for northern bobwhite (*Colinus virginianus*; hereafter, bobwhite). Sericea can reduce habitat quality for bobwhite as it outcompetes native plants that provide forage and cover. Bobwhite eat sericea seed, but seed are relatively indigestible and may limit nutrition intake and reduce the fecundity rate. Postemergence herbicides, including glyphosate, triclopyr, and fluroxypyr+triclopyr, control standing sericea, but do not provide preemergence control, which would increase long-term control because sericea annually produces large amounts of hard seed with high dormancy rates. Imazapic is labeled to provide preemergence control, but no study has evaluated preemergence applications of imazapic following postemergence herbicides to control sericea and promote native plants important for bobwhite. Additionally, data evaluating various rates of imazapic to control sericea are lacking. We currently are evaluating the efficacy of glyphosate and fluroxypyr+triclopyr, applied alone post-emergence and in conjunction with 3 preemergence rates of imazapic, to reduce coverage of sericea at 4 sites in Tennessee and Alabama, USA. We split each site into 8 treatment units and control and assigned the following treatments: glyphosate, fluroxypyr+triclopyr, glyphosate with 48, 96, and 144 ml/ha (4, 8, and 12 oz/acre) imazapic, and fluroxypyr+triclopyr with 48, 96, and 144 ml/ha imazapic. We applied 767 ml/ha (2 qt/acre) glyphosate and 192 ml/ha (16 oz/acre) fluroxypyr+triclopyr in August 2018 to control established sericea. We measured coverage of native forbs, native grasses, and sericea during the 2019 and 2020 growing seasons to determine the efficacy of treatments on sericea and the native plant community. Both glyphosate and fluroxypyr+triclopyr reduced sericea coverage 1 and 2 growing seasons following treatment, but we documented no difference in reduction of sericea coverage between postemergence treatments. We will apply imazapic in March 2021 at 3 different rates to determine whether a preemergence application improves sericea control. Our results on the effectiveness of a preemergence application after postemergence applications should provide valuable information to managers trying to control sericea on lands managed for bobwhite.

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Key words: *Colinus virginianus*, glyphosate, habitat management, herbicide, imazapic, invasive species, northern bobwhite, PastureGard®

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NORTHERN BOBWHITE RESPONSE TO POSTGRAZING VEGETATION MANAGEMENT AND RECOVERY IN SOUTH TEXAS

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ABSTRACT

The northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) requires habitat structure and composition with grass cover for nesting, predator avoidance, and thermal refuge and forb cover for feeding on phytophagous arthropods and seeds. During the past 2 decades, many land managers with interest in promoting quail hunting opportunities have reduced or completely eliminated livestock across South Texas, USA, rangelands. Resting the land from grazing allows vegetation—especially grasses and forbs—to recover and thus provide nesting and foraging habitat for bobwhite and other birds. How bobwhite respond to postgrazing vegetation recovery is of keen interest to rangeland quail managers, but this topic is poorly known because case histories with quantitative data are lacking. Our objective was to investigate how bobwhite respond to the vegetation changes following removal of cattle grazing. Our study was conducted on a private ranch in Jim Hogg County, Texas and involved 3 different categories of postgrazing recovery and management: 1 area at 15 years post-cattle grazing where the landscape has been brush-sculpted and is actively managed since removal of cattle, 1 area at 3 years post-grazing with a previous stocking density of 7 ha/animal unit (high stocking density), and 1 area at 3 years post-grazing with a previous stocking density of 14 ha/animal unit (moderate stocking density). We trapped, radio-marked, and located bobwhites from March to September during 2015–2016 on the 3 comparative units. We estimated nest survival, adult breeding-season survival, home range size, and early winter density. We hypothesized that the 15-year postgrazing site would have higher early winter density, higher adult breeding season survival, and higher nest survival along with smaller mean home range size compared to the 2 more recently grazed sites. On average, the probability of a nest surviving the 23-day incubation period was highest on the 15-year postgrazing site at 0.61 ± 0.12 (mean nest survival ± standard error), with estimates of 0.32 ± 0.12 on the 3-year moderate postgrazing site and 0.33 ± 0.12 on the 3-year high postgrazing site. Adult breeding season survival did not differ among the 3 sites, and was instead influenced mostly by month within the season, probably a result of summer heat. An adult bobwhite had a 0.48 ± 0.04 probability of surviving the breeding season. Early winter density, after summer and fall production was complete, increased on all sites from 2015 to 2016 and was consistently highest on the 15-year postgrazing site. Home range sizes on the 15-year and 3-year moderate postgrazing sites were significantly larger than on the 3-year high postgrazing site. Additionally, landscape features around nest sites suggest lingering differences among the sites, supporting higher nest survival on the 15-year postgrazing site. These findings suggest that in South Texas, bobwhite populations can attain densities of approximately 2.0–2.9 birds/ha within 5 years after removal or reduction of cattle, given adequate rainfall.

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Key words: *Colinus virginianus*, distance sampling, habitat, management, nest success, northern bobwhite, South Texas, survival, vegetation

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Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite(s)) and livestock have been coexisting in southern Texas, USA, rangelands for well over a century and a half, beginning with European settlement of this region. Over time, however, cattle grazing has altered much of the landscape in ways that can be detrimental to quail. Historically, brush in the region was limited to riparian corridors and areas protected from fire (Schmidly 2002). As the ranching industry grew, livestock populations and fire suppression efforts, in concurrence with rises in atmospheric carbon dioxide levels, led to vast increases in brush across the landscape (Van Auken 2000). By the mid-20th century, much of the open grassland areas had been lost (Johnston 1963, Archer and Smeins 1991). Grazing was historically viewed by biologists as detrimental to bobwhite abundance because bobwhites prefer habitat structure with grass cover for nesting and evading predators (Stoddard 1931, Lehmann 1937). Guthery (1997) proposed that the ideal goal of quail management was to maximize usable space, making all of an available area (such as an entire pasture, which on large South Texas ranches may be up to 4,000 ha) usable by bobwhite at all times. Although the encroachment of brush on a landscape may seem detrimental, brush is an important habitat component for bobwhite as it provides thermal refuge, which is especially important during dry years. It has been found that bobwhite can persist under a range of brush canopy cover conditions. Recommendations from 5% to 85% woody canopy can be found in the literature (Guthery 1986, Guthery et al. 2000). However, a landscape with too little (<5%) brush over the long term can lead to lower bobwhite densities (DeMaso et al. 2014).

Many studies have examined the response of bobwhite under different highly variable grazing regimes (Hammerquist-Wilson and Crawford 1981, Schulz and Guthery 1988, Wilkins and Swank 1992). However, the results of these studies were inconclusive as to which grazing regimes best benefit bobwhite. There has been increasing interest in managing landscapes to increase bobwhite populations for hunting purposes because the bobwhite has declined over much of its historical range (Brennan 1991, Hernández et al. 2013). Bobwhite hunting is of great economic importance to Texas, and many landowners have been reducing stocking densities or eliminating cattle completely to promote vegetation regrowth in hopes of improving quail habitat (Fulbright and Bryant 2002, Hernández and Guthery 2012). How bobwhite respond to these postgrazing landscapes is not well understood. Confounding factors such as stocking densities, different grazing systems, and precipitation patterns can make specific predictions about timing of recovery difficult.

The primary objective of our study was to quantify and compare variations in bobwhite responses on 3 different sites where cattle have been removed: 1 area of 15-years postgrazing where the landscape has been brush-sculpted and had been actively managed for bobwhite during this period; 1 area of 3 years postgrazing at a high stocking density (7 ha/animal unit [AU]), and 1 area of 3 years postgrazing at a moderate stocking density (14 ha/AU; Figure 1). We hypothesized that the 3 years postgrazing site which had been grazed at high intensity would have the lowest amount of usable space (Guthery 1997). Furthermore, we hypothesized that bobwhite nest survival, adult breeding season survival, and early winter population density estimates would be lowest on the site with 3 years postgrazing at high intensity and highest on the 15-year postgrazing site with restoration. Because of potentially lower proportions of usable space, we also hypothesized that home range size on the area of 3 years postgrazing at high intensity would be larger compared to the 3-year postgrazing at moderate intensity and 15-year postgrazing sites.

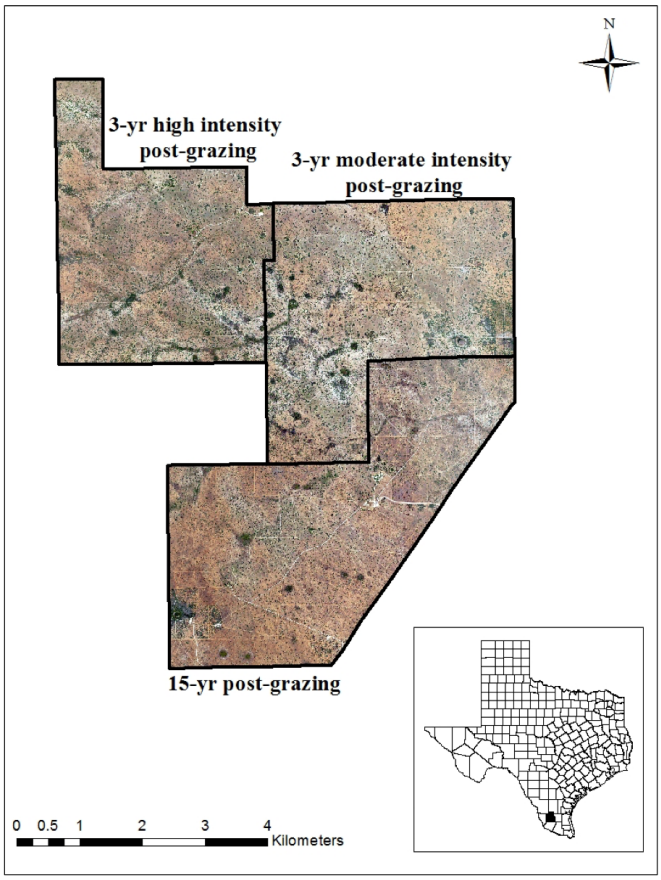

Fig. 1. Study area with 3 postgrazing sites in Jim Hogg County, Texas, USA.

STUDY AREA

Our research was conducted on a private ranch in Jim Hogg County, Texas (27°6'55.10"N, 98°47'41.01"W). This ranch is in the Rio Grande Plains ecoregion (Gould 1975). The production of wild bobwhite for hunting is the primary management priority of this ranch. Mean annual rainfall for the study area was 60.4 cm (1981–2010) with precipitation peaking in May and September (Western Regional Climate Center 2015). Temperatures range from an average low of 16.1º C to an average high of 28.8º C (Western Regional Climate Center 2015). The most common soil types are Delmita

loamy fine sand, Delmita fine sandy loam, and Nueces-Sarita association. Common woody species include honey mesquite (*Prosopis glandulosa*), brasil (*Condalia hookeri*), granjeno (*Celtis pallida*), Texas persimmon (*Diospyros texana*), Mexican olive (*Cordia boissieri*), catclaw acacia (*Acacia greggii*), and hogplum (*Colubrina texansis*). Common forbs include croton (*Croton* spp.), palafoxia (*Palafoxia* spp.), cowpen daisy (*Verbesina encelioides*), and partridge pea (*Chamaecrista fasciculata*). Common grasses in the area are Lehmann lovegrass (*Eragrostis lehmanniana*), red lovegrass (*Eragrostis secundiflora*), bufflegrass (*Pennisetum ciliare*), Texas grama (*Bouteloua rigidiseta*), hairy grama (*Bouteloua hirsuta*), seacoast bluestem (*Schizachyrium scoparium*), and purple threeawn (*Aristida purpurea*).

Additional study area details can be found in Smith (2017).

METHODS

Study Design

The study consisted of 3 sites of postgrazing vegetation recovery as follows: 1 area at 15 years postgrazing where the landscape has been brush-sculpted and is actively managed since removal of cattle, 1 area of 3 years post-cattle grazing with a previous stocking density of 7 ha/AU (high stocking density), and 1 area of 3 years post-cattle grazing at a previous stocking density of 14 ha/AU (moderate stocking density; Figure 1). Because our study sites lacked true replication, inferences should be restricted to these study areas (Wester 1992).

Fifteen years postgrazing site.—This site was approximately 1,552 ha and was subject to long-term continuous grazing until around 2000 when the previous owner removed cattle from the property. Long-term cattle stocking densities for this property are unknown prior to about 2000, after which for several years the landscape was dominated by leatherstem (*Jatropha dioica*) with some bufflegrass (*Pennisetum ciliare*) and sparse native bunch grasses (Brennan, observations from ranch visits prior to this study). After cattle were removed, the site was treated with herbicides to combat the leatherstem and promote the growth of native grasses. A large-scale brush-sculpting operation was done in 2013. On this site many roads are disked, and mesquite is treated using individual plant treatment (IPT) to control it. Of our 3 sites, this site was the most intensively managed for bobwhite throughout the year as it contains the primary hunting routes. Due to the repeated brush control and the length of time since grazing, this site also had the most herbaceous cover of the 3 sites.

Three years postgrazing site at moderate grazing density.—This site is approximately 1,248 ha and was grazed at a level of 14 ha/AU before cattle were removed in 2013. This area has largely been left to recover since cattle removal. It does have a larger amount of brush than the actively managed site, but less than the previously highly grazed site. Disking of hunting routes is done to promote forb production.

Three years postgrazing site at high grazing density.—This site is approximately 1,133 ha and was subjected to high grazing density at approximately 7 ha/AU before cattle were removed in 2013. This site has areas that were subjected to brush management techniques by the previous owner that were not suitable for creating quail habitat. These past management practices have resulted in areas of monotypic stands of young mesquite growth. This site has the largest amount of brush cover of the 3 areas. Routes on this site are also disked, but due to many inaccessible areas it is not heavily hunted.

Trapping and Radio-telemetry

We trapped bobwhites from March to July in 2015–2016 using funnel traps baited with grain sorghum (*Sorghum bicolor;* Stoddard 1931). During 2015, we trapped bobwhites along roads and monitored them only on the 15-year postgrazing site and the 3-year high density postgrazing site due to time constraints. During 2016, bobwhites were monitored on the 3-year moderate density postgrazing site, as well as on the other two sites monitored in 2015. During 2016, we created a 500-m buffer inside the boundaries of the 3 study sites to minimize the potential of bobwhites moving among study sites. We stratified trap sites using a 20-ha grid across the buffered area of each study site. One trap was placed near the center of each grid cell to achieve uniform trapping effort. We hid all traps under shrubs to provide canopy cover and help prevent predation and mitigate heat stress. If additional woody cover was needed, we placed freshly cut limbs over the trap. Traps were set before sunrise and checked every 2–3 hours until they were closed at sunset (Abbott et al. 2005). If the daily temperature rose above 35° C, we closed traps before noon and then reopened them in the evening when the temperature fell. After bobwhites were captured, we weighed them and determined age and sex (Rosene 1969). We fitted each bird with a size 7 aluminum band (Fair et al. 2010). We radio-marked 20–25 females that weighed ≥150 g with a 5–6.5 g necklace-style radio transmitter (American Wildlife Enterprises, Monticello, FL, USA) at each of the 3 study sites to maintain a sample size of 60–75 birds (Hernández et al. 2004). Males were radio-marked if we were not successful at trapping females. No more than 3 birds from each trap site were radio-marked so we could maximize the number of coveys with radio-marked birds. We located radio-marked birds 2–3 times/week using a hand-held, 3-element Yagi antenna. We took bobwhite locations (individual birds, activity unknown) and nest locations at the point of sighting a bobwhite using a hand-held Global Positioning System (GPS). If a bird was found to be in the same location twice during different days, we assumed it was incubating and placed flagging tape about 20 m from the nest in the 4 cardinal directions. Incubating birds were not approached closer than 20 m to limit disturbance to the nest site. Once a nest site was located, it was monitored every 2–3 days from a distance ≥20 m to determine nest fate. Usually because the incubating bobwhite moved away from the nest site without returning, we defined the outcome as either success or failure, based on the nest condition, shell

contents, and shell condition, all of which indicated whether the chicks hatched successfully or were lost to predation. Once nesting was completed, clutch size was determined from successful nests where possible. Bobwhite trapping, handling, and tracking were done in accordance with the Texas A&M University-Kingsville Institutional Animal Care and Use protocols 2013-04-16-A5 and 2016-02-26.

Vegetation Measurements

Macrohabitat.—We used 2014 National Agriculture Imagery Program natural color/color infrared aerial photography of our study sites at 1-m resolution to quantify the landscape structure of our study sites (Figure 2a). We performed an unsupervised classification (convergence threshold of ≥95%) in ERDAS IMAGINE 2015 (Hexagon Geospatial, Norcross, GA, USA) to classify the landscape into 3 categories (woody, herbaceous, and bare ground) (Figure 2b). Roads on the study site were digitized using ArcGIS 10.4 based on aerial photography definition at scale 1:500 (Esri Inc., Redlands, CA, USA). We conducted an accuracy assessment by generating 200 random points in each of the 4 images that made up our study area and classified the points into 1 of the 3 categories by visual assessment plus field verification (Perotto-Baldivieso et al. 2009, Mata et al. 2018). Additionally, we took 300 points in the field, classified them into 1 of the 3 categories, and compared them to the classified image. We assessed accuracy using a confusion matrix and had an overall accuracy for the classification of 90% (Congalton 1991).

Microhabitat.—We measured nest vegetation characteristics of a nest-centered point and a random point. These vegetation measurements were taken only during 2016 due to logistical constraints in 2015. Random points were chosen by generating a random compass bearing and distance between 50 m and 100 m away from the nest; this method was similar to those used in Lusk et al. (2006). Vegetation measurements took place no more than 14 days after nest completion to avoid changes in structure between nesting and sampling times. We estimated percent canopy cover of woody, grass, forb, and bare ground at each nest site and at its corresponding random location using a 1-m^2 frame centered over the nest or random point (Daubenmire 1959). Additionally, we measured distance from the nest clump to the nearest woody cover.

Aerial Surveys for Density Estimates

During December 2015 and 2016, respectively, we conducted line transect distance sampling surveys by helicopter on our 3 study sites; we followed the sampling methods and protocols described by Schnupp et al. (2013) and Rusk et al. (2007). This method of bobwhite density estimation has been shown to work well in rangelands (Rusk et al. 2007, DeMaso et al. 2010). Our survey was conducted from a 4-seat R-44 with room for a pilot and 3 observers (Rio Grande Helicopters, Laredo, TX, USA). The same 3 observers were used throughout each survey to avoid observer bias. The 2 rear observers were responsible for locating coveys on their

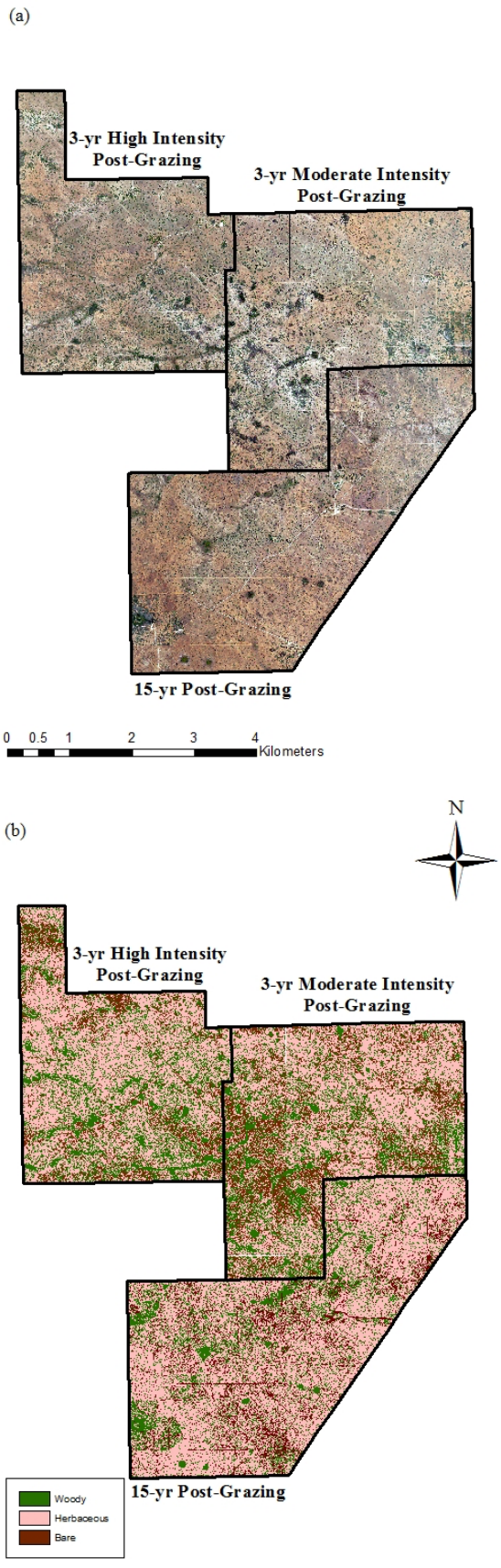

Fig. 2. Map of a) original unclassified 2014 National Agriculture Imagery Program natural color/color infrared aerial photography and b) final classified images of the study area, Jim Hogg County, Texas, USA.

sides of the helicopter while the front-seat observer located coveys in front of the helicopter. When a covey was detected, the helicopter hovered while the rear-seat observers marked the covey location with a laser rangefinder that measured distance, compass bearing, and angle of inclination from the helicopter (Trimble LaserAce 1000, Trimble Navigation Ltd., Sunnyvale, CA, USA). The laser rangefinders were linked to a Juno handheld GPS unit controlled by the front-seat observer which documented detections with covey size and GPS locations (Trimble Juno 5 series handheld, Trimble Navigation Ltd., Sunnyvale, CA, USA) (Schnupp et al. 2013).

During 2015, our survey design consisted of 23 east-west transects across the entire ranch (all 3 sites). Transects were placed 400 m apart for 50% coverage of the area with a total survey effort of 95 km and a survey time of 3.5 hours (Figure 3a). In 2016, survey coverage was increased to 100% with 42 east-west transects placed 200 m apart for a total survey effort of 194 km and survey time of 7 hours (Figure 3b). Surveys were flown at an altitude of 7–10 m and a speed of 37 km/hr (Schnupp et al. 2013). The entire ranch was flown in 1 day each year.

Statistical Analyses

Adult Breeding Season Survival.—We calculated breeding season (Apr–Aug) survival using the "known fate" platform in Program MARK (White and Burnham 1999). This method is often used with telemetry data because it assumes that resighting probability is equal to 1. We created encounter histories for each radio-marked bobwhite according to the LDLDLDLD format described in White and Burnham (1999). We coded the encounter history for each bobwhite in 1 of 3 ways: 10 means the bobwhite survived the interval, given it was alive at the start of the interval, 11 = the bobwhite died during the interval, given it was alive at the start of the interval, and 00 = the bobwhite was censored for the interval. For example, an individual with the encounter history 1010101100 was alive at the beginning of month 1, survived in months 2 and 3, and died in month 4. We built 12 candidate models in Program MARK and chose a best model based on Akaike's Information Criterion values with a correction for small sample size (AIC_c).

Nest Survival.—We used the nest survival platform in Program MARK to estimate bobwhite daily nest survival on our study areas (Mayfield 1961, 1975; Dinsmore and Dinsmore 2007). Nests found late in the incubation period due to later trapping were excluded so as to not bias these estimates (n = 2). The nesting season was defined as the day we found the first nest to the day the last successful nest hatched over the 2 nesting seasons monitored. We ran 10 candidate models using the nest survival platform in Program MARK examining whether nest survival differed by 1) site, 2) year, and 3) time. Models were ranked using AIC_c. Program MARK estimates daily nest survival; these estimates were then extrapolated to the 23-day incubation period to estimate overall probability of a nest surviving. The site model was used to generate estimates for the 3 different postgrazing sites. However, due to high model

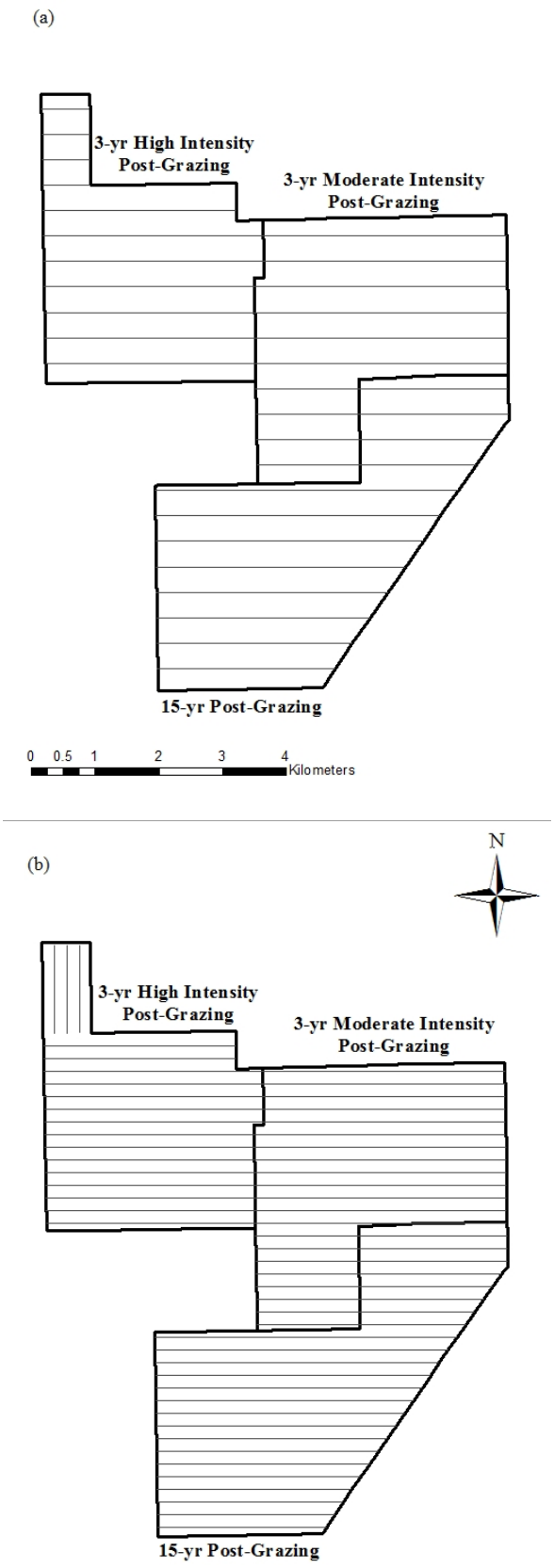

Fig. 3. Aerial survey design for northern bobwhite (*Colinus virginianus*) density estimation based on distance sampling a) during 2015 with transects placed 400 m apart and b) during 2016 with transects placed 200 m apart across the 3 postgrazing sites, Jim Hogg County, Texas, USA.

uncertainty, averaging was also used to predict nest survival on the 3 sites during the 2 years of the study. The delta method was then used to generate standard errors and confidence intervals for the model averaged estimates (Powell 2007).

Home Range.—We estimated home range size for radio-marked bobwhites with ≥20 locations based on a 95% and 50% core area using a fixed kernel home range with cross-validation in BIOTAS 2.0 (Ecological Software LLC, Hegymagas, Hungary, 2005) (Tri et al. 2014). We used the fixed kernel estimator, using least squares cross-validation to choose the smoothing parameter; this approach is assumed to provide accurate results with smaller variances compared to other animal home range estimation methods (Seaman and Powell 1996, Seaman et al. 1999). While most recommend at least 30–50 locations for the most accurate results, Haines et al. (2009) showed evidence that mean home range size and coefficients of variation leveled off at about 20 locations. Locations of bobwhite were assumed to be independent of one another since they could travel across their entire home range between each sampling event (White and Garrott 1990). We compared mean home range and core area size among the sites using an analysis of variance (alpha level of 0.05) using SPSS (version 24.0; IBM Corp., Armonk, NY, USA).

Macrohabitat.—During 2015–2016 we monitored 102 nests. In order to determine how often quail nests on the study area were in woody, herbaceous, and bare ground, bobwhite nesting locations were pooled between years, and we compared usage of the 3 classes by nesting bobwhites in proportion to their availability using a chi-square contingency analysis with a significance level of 5% (Brennan et al. 1987).

Around each nest site, we created buffers of 5 different sizes (10, 20, 30, 40, 50 m) using ArcGIS. The 5 different buffers were selected because we wanted to see how the influence of different landscape metrics might differ as distance from the nest site increased. We calculated 8 metrics of landscape structure that describe elements of woody cover for each study site and also around individual nest sites among the 3 postgrazing sites using FRAGSTATS (version 4.2; University of Massachusetts, Amherst, MA, USA). We selected 8 landscape metrics that, in our view, represent spatial elements of vegetation structure that contribute to meeting the annual cycle habitat needs of northern bobwhite in South Texas. There are undoubtedly scores of different landscape metrics that meet this criterion, but many of these metrics are difficult to understand. Thus, we selected only basic and easy-to-interpret landscape metrics known to be components of northern bobwhite habitat in rangeland environments. The selected metrics were: aggregation index (AI, %), mean patch area (AREA_MN, ha), Euclidean nearest neighbor distance distribution (ENN_MN, m), edge density (ED, m/ha), interspersion and juxtaposition index (IJI, %), patch density (PD, #/100 ha), percent of landscape (PLAND), and mean shape index distribution (SHAPE_MN) (He et al. 2000, Perotto-Baldivieso et al. 2011, Pellissier et al. 2012, Zemanova et al. 2017). We compared these metrics between the 3 postgrazing sites (at each of the 5 buffer sizes) by a PROC MIXED procedure in SAS 9.4 (SAS Institute Inc., Cary, NC, USA, 2017). For each of these analyses a variance-covariance matrix was selected using AIC_c and the distribution of residuals was then examined for normality. In order to satisfy the normality assumption, we analyzed percent of landscape, mean patch area, Euclidean nearest neighbor distance distribution, and mean shape index distribution on the log-scale and then back-transformed for final data reporting.

Microhabitat.—We compared vegetation characteristics (percent bare ground, percent forbs, percent grasses, and distance to woody vegetation) between two locations (nest sites and paired random points) in the 3 study sites. We used a linear mixed model with a fixed location effect (nest site or paired random point) and a random effect to account for variation among pairs of locations. The same analysis and model were applied to all pairs across all 3 study sites for an overall examination of characteristics between nest sites and paired random points.

Density Estimation.—We estimated density of bobwhite population on the 3 sites of interest using Program Distance version 7.0, release 1 (March 2015, https://distancesampling.org/Distance/old-versions/distance70.html). This program allows for the selection of 4 key functions (uniform, half normal, hazard, and negative exponential) and 3 different adjustment terms (cosine, simple polynomial, and hermite polynomial). The best detection function has 100% detection on the line (g (0) = 1) and decreases monotonically with good model fit and small variance (Buckland et al. 2001). Density estimates are calculated by Program Distance as,

$$\widehat{D} = \frac{n}{2\hat{\mu}L} \times E(s)$$

$$\mathrm{var}(\widehat{D}) = \widehat{D}^2 \times \{[\mathrm{CV}(n)]^2 + [\mathrm{CV}\{f(0)\}]^2\}$$

where D is density, n is the number of coveys detected and u is the estimate of effective half-width, L is the length of transects, E(s) is the average covey size, CV is the coefficient of variation, and f(0) is the probability density function of detected distance from the line, evaluated at 0 distance.

Preliminary analysis of the data involved fitting 4 initial models: half normal with no adjustment, hazard rate with no adjustment, uniform with cosine, and half normal with cosine. Using these models, we selected cut points and a truncation distance if necessary. Once cut points and a truncation distance for the data were chosen, we reevaluated the data with the previous 4 models in addition to hazard rate with simple polynomial and half normal with hermite polynomial models. We determined model fit by examining the Kolmogorov-Smirnov and Cramer-von Mises tests. We selected a best model for our data using AIC_c and goodness-of-fit tests.

Density Surface Modeling.—Development of recent spatial analysis techniques has allowed researchers to account for spatial distribution when using distance sampling to estimate abundance (Hedley and Buckland 2004, Hedley et al. 2004). The development of density surface models (DSMs) allows for improved precision of density estimates

compared to conventional distance sampling (Hedley et al. 2004). We created DSMs using both geographic information system (GIS) and the statistical package R (version 3.3.2; R Foundation for Statistical Computing, Vienna, Austria). The dataset for building the DSMs was created in GIS and R was used for model fitting, selection, and density prediction using the 'dsm' package for R (Miller et al. 2013).

Density surface models of bobwhite abundance across the surveyed areas were based on the transect lengths, width of truncation distance was specified by the detection function model, and number of detections on each study site. Because both density and environmental factors of interest can vary over this distance, transects were split into relatively small segments where density was assumed to be constant. We used recommendations from Miller et al. (2013) and divided each transect into 100-m segments, which was about twice the truncation distance from each of our conventional distance sampling analyses.

We used color infrared aerial photography of our study sites from 2014 at 1-m resolution to create an NDVI used for covariate classification. We classified this map using unsupervised classification (convergence threshold of ≥95%) in ERDAS IMAGINE 2015 to divide the landscape into 2 categories (woody and non-woody). An accuracy assessment of this classification was conducted by generating 200 random points in each image that made up our study area and classifying them into the 2 categories by visual assessment plus field verification (Perotto-Baldivieso et al. 2009, Mata et al. 2018). We used 5 metrics of woody cover, Normalized Difference Vegetation Index (NDVI) and geographic location (x,y) as the independent variables for the DSM. The 5 metrics of woody cover were: edge density (ED, m/ha), landscape shape index (LSI), mean patch area (AREA_MN, ha), patch density (PD, #/100 ha), and percent of landscape (PLAND). Accuracy was assessed using a confusion matrix and met the minimum standard of ≥85% (Congalton 1991). We used FRAGSTATS version 4.2 to analyze the 5 classification metrics using a moving-window approach using a 100-m radius based on quail movement biology as well as for fitting with segment sizes and truncation distances. We thus created a raster map for each covariate metric across the entire study area that was used to build the corresponding prediction grid of the DSM in R.

These habitat covariate data were associated with each transect segment by interpolating each raster dataset at the segment midpoint. The prediction grid template was created using a 100-m grid constant raster in GIS, clipped to the extent of the study area. We then used backwards selection to determine a best model. Covariates that were not significant, had extreme outliers, or were highly correlated (>0.8) were removed. A top model was chosen based on maximum deviance explained and best model fit.

RESULTS

Adult Breeding Season Survival

We trapped and banded 119 bobwhites and deployed 50 radio transmitters during 2015. During 2016, we trapped and banded 202 bobwhites and placed radio transmitters on 77 birds. Adult survival was most influenced by a quadratic time trend (Table 1). Bobwhites had a 0.48 ± 0.04 probability of surviving the breeding season (Apr–Aug). Monthly survival was highest in April and then decreased to a low point in June and July, with a slight improvement in August (Figure 4).

Nest Survival

During 2015, we located 52 nests: 33 on the 15-year postgrazing site and 19 on the 3-year postgrazing site. In 2016, we found 50 nests: 20 on the 15-year postgrazing site, 14 on the 3-year moderate postgrazing site, and 16 on the 3-year high

Table 1. List of all models run using the known fate platform in Program MARK to estimate northern bobwhite (*Colinus virginianus*) adult breeding season survival on the study area during 2015 and 2016 in Jim Hogg County, Texas, USA.

Model name	AIC_c	Delta AIC_c	AIC_c weight	Model likelihood	Number of parameters	Deviance
S(quadratic time trend)	361.3974	0.0000	0.71251	1.0000	3	355.6450
S(time)	363.5267	2.1293	0.24571	0.3449	5	353.3951
S(site+quadratic time trend)	367.6595	6.2621	0.03112	0.0437	9	349.2612
S(linear time trend)	372.7154	11.3180	0.00248	0.0035	2	368.6893
S(site*time+year)	373.1247	11.7273	0.00202	0.0028	15	342.1485
S(site)	373.6430	12.2456	0.00156	0.0022	3	367.5906
S(.)	373.7178	12.3204	0.00150	0.0021	1	371.7091
S(site*time)	374.6130	13.2156	0.00096	0.0013	15	343.5368
S(year)	375.0155	13.6787	0.00079	0.0011	2	370.9894
S(site+year)	375.3968	13.9994	0.00065	0.0009	4	367.3093
S(site+linear time trend)	376.0827	14.6853	0.00046	0.0006	6	363.8981
S(site*year)	377.1469	16.0195	0.00024	0.0003	5	367.2853

postgrazing site. Nest survival was most influenced by site but also by time of initiation within the season (Table 2). Overall, the 15-year postgrazing site had a higher probability of a nest surviving the 23-day incubation period at 0.61 ± 0.12 (mean nest survival + standard error) compared to a probability of 0.32 ± 0.12 and 0.33 ± 0.12 on the 3-year moderate density and 3-year high postgrazing sites respectively (Figure 5). Early (April) nests and late season nests (August) had a lower survival across all sites and years (Figures 6, 7). In 2015 the 15-year postgrazing site had a consistently higher nest survival probability than the 3-year high postgrazing site. In 2016, the 15-year postgrazing site was slightly higher than either of the 3-year postgrazing sites, which both had similar nest survival estimates.

Home Range Estimates

We estimated 50% and 95% kernel home ranges for 62 birds across each study site both years. The mean 50% core area estimate on the 15-year postgrazing site was 2.7 ± 0.3 ha (n = 29) with a range of 0.2–8 ha. The mean estimate on the 3-year moderate postgrazing site was 2.8 ± 0.5 ha (n = 10) with a range of 1–7 ha. The mean estimate on the 3-year high postgrazing site was 4 ± 0.5 ha (n = 23) with a range of 0.3–11 ha. There were no differences in 50% core area sizes between the 15-year postgrazing site and the 3-year moderate postgrazing site ($P \geq 0.93$) and the 3-year moderate postgrazing site and the 3-year high postgrazing site ($P \geq 0.13$). However, there was a significant difference in 50% core area size between the 15-year postgrazing site and the 3-year high postgrazing site ($P \geq 0.02$) (Figure 8a).

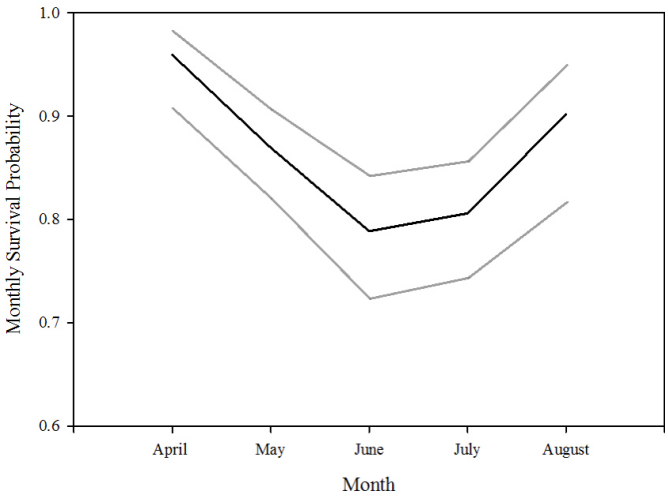

Fig. 4. Mean (dark line ± 95% confidence interval, upper and lower gray lines) estimates of adult breeding season survival (Apr–Aug) for northern bobwhite (*Colinus virginianus*) over the entire study area during 2015 and 2016, Jim Hogg County, Texas, USA.

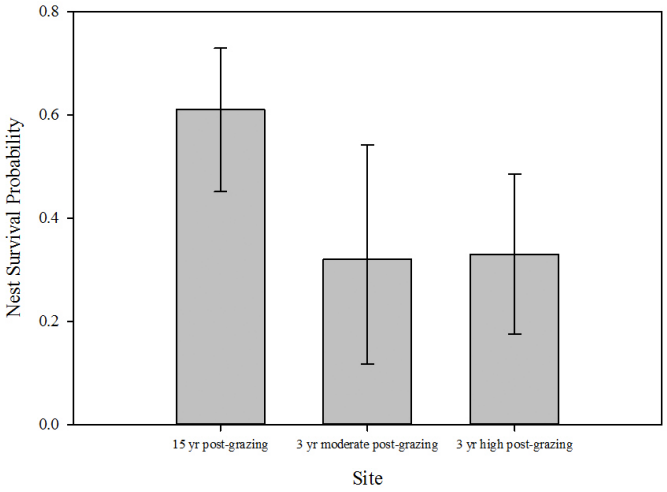

Fig. 5. Mean (±95% confidence interval) estimates of northern bobwhite (*Colinus virginianus*) nest survival across the 23-day incubation period from the S(site) model in Program MARK for the 3 postgrazing sites during 2015 and 2016 in Jim Hogg County, Texas, USA.

Table 2. List of all models run using the nest survival platform in Program MARK to estimate northern bobwhite (*Colinus virginianus*) nest survival on the study area during 2015 and 2016 in Jim Hogg County, Texas, USA.

Model name	AIC_c	Delta AIC_c	AIC_c weight	Model likelihood	Number of parameters	Deviance
S(site)	263.0957	0.0000	0.27132	1.0000	3	257.0778
S(site+quadratic time trend)	263.1746	0.0789	0.26083	0.9613	5	253.1298
S(site+linear time trend)	264.6977	1.6020	0.12179	0.4489	4	256.6679
S(site*linear time trend)	265.0895	1.9938	0.10012	0.3690	6	253.0268
S(site*year)	265.3185	2.2228	0.08929	0.3291	5	255.2738
S(year)	266.5145	3.4188	0.04910	0.1810	2	262.5055
S(.)	266.8148	3.7191	0.04226	0.1558	1	264.8118
S(site*quadratic time trend)	267.2994	4.2037	0.03316	0.1222	9	249.1648
S(linear time trend)	268.5499	5.4542	0.01775	0.0654	2	264.5410
S(quadratic time trend)	268.9724	5.8767	0.01437	0.0530	3	262.9546

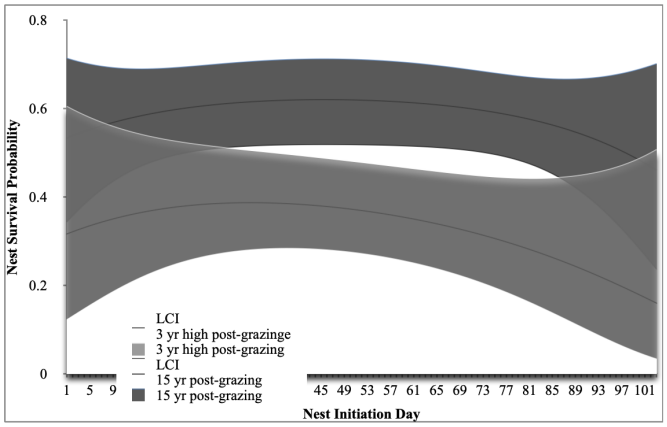

Fig. 6. Mean (±95% confidence interval) model averaged estimates of northern bobwhite (*Colinus virginianus*) nest survival during 2015 on 2 postgrazing sites, Jim Hogg County, Texas, USA.

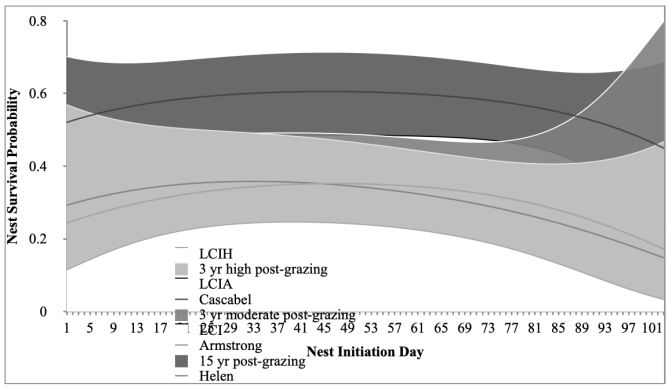

Fig. 7. Mean (±95% confidence interval) model averaged estimates of northern bobwhite (*Colinus virginianus*) nest success during 2016 on the 3 postgrazing sites, Jim Hogg County, Texas, USA .

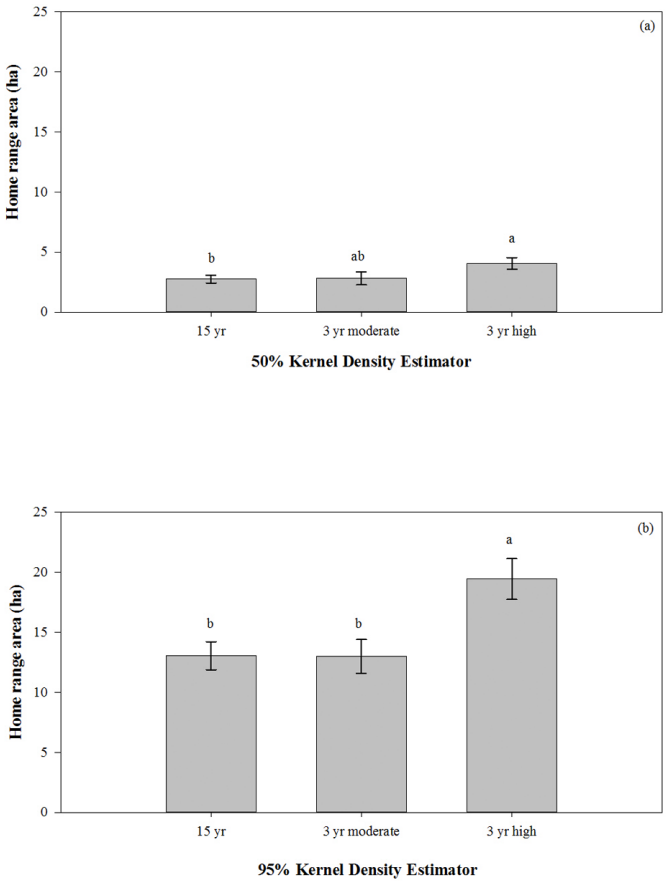

Fig. 8. Mean (±standard error) estimates of a) 50% kernel density estimator home ranges and b) 95% kernel density estimator home ranges of northern bobwhite (*Colinus virginianus*) during 2015 and 2016 on the 3 postgrazing sites, Jim Hogg County, Texas, USA. Means followed by the same letter are not significantly (P > 0.05) different.

The mean 95% kernel home range estimate on the 15-year postgrazing site was 13.0 ± 1.2 ha (n = 29) with a range of 0.5–29 ha. The mean estimate on the 3-year moderate postgrazing site was 12.9 ± 1.4 ha (n = 10) with a range of 7–21 ha. The mean estimate on the 3-year high postgrazing site was 19.4 ± 1.7 ha (n = 23) with a range of 5–41 ha. There was no difference between 95% kernel home range size on the 15-year postgrazing site and the 3-year moderate postgrazing site (P ≥ 0.98). However, there were differences between the 3-year high postgrazing site and the 15-year postgrazing site (P ≥ 0.002) and between the 3-year high postgrazing site and the 3-year moderate postgrazing site (P ≥ 0.03) (Figure 8b).

Vegetation

Macrohabitat.—In 2015 and 2016, we found 102 nests across the 3 study sites. Across the entire study area, birds used herbaceous cover for nesting in a higher proportion (%) relative to its availability (%) (Table 3). On the 15-year and 3-year moderate postgrazing sites, bobwhites used nest sites in all the vegetation cover types in proportion to their availability (Table 3). However, on the 3-year high postgrazing site we observed bobwhites using more herbaceous cover and less woody cover for nesting than expected (Table 3).

At the individual site scale, percent woody cover, edge density, and mean patch area, were lowest on the 15-year postgrazing site (Table 4). Patch density and interspersion and juxtaposition were highest on this site (Table 4). Euclidean nearest neighbor distance was similar among the 3 sites. Aggregation index and mean shape index were just slightly smaller on the 15-year postgrazing site (Table 4). Notably, the 3-year moderate postgrazing site estimates for these metrics fell between the 15-year and 3-year high postgrazing sites in all but 2 of the metrics measured.

At a smaller scale, landscape structure around nest sites differed among the 3 sites. At 10- 20-, and 30-m buffers around the nest site, percentage of woody cover was significantly higher on the 15-year postgrazing site; however, at the 40- and 50-m buffer sizes the 3-year moderate postgrazing site was not different from the 15-year postgrazing site. The 3-year moderate postgrazing site consistently had a lower

Table 3. Chi-square contingency analysis of macrohabitat use by northern bobwhite (*Colinus virginianus*) nests across 3 postgrazing sites during 2015 and 2016 in Jim Hogg County, Texas, USA.

	Number of bobwhite nests			
Study area cover type	Proportion	Observed	Expected[a]	*P*
Entire study area				
Bare ground	25.6	22	26	
Herbaceous	58.4	73	60	
Woody	16.0	7	16	<0.025
15-year postgrazing				
Bare ground	22.0	9	12	
Herbaceous	63.9	38	34	
Woody	14.1	6	7	>0.10
3-year moderate postgrazing				
Bare ground	27.2	3	4	
Herbaceous	52.1	10	7	
Woody	20.7	1	3	>0.10
3-year high postgrazing				
Bare ground	28.8	10	10	
Herbaceous	57.8	25	20	
Woody	13.5	0	5	<0.05

[a] Expected values based on proportions of available cover type

Table 4. Mean estimates of percent of landscape, patch density, edge density, mean patch area, mean shape index, Euclidean nearest neighbor distance, aggregation index, and interspersion and juxtaposition index for woody cover on the 3 postgrazing sites in Jim Hogg County, Texas, USA.

Site	Metric							
	% of woody cover	Patch density (#/100 ha)	Edge density (m/ha)	Mean patch area (ha)	Mean shape index	Euclidean nearest neighbor distance (m)	Interspersion and juxtaposition index (%)	Aggregation index (%)
15-yr postgrazing	22.0162	9849.7458	1935.3337	0.0022	1.2106	3.1991	37.2149	78.0142
3-yr moderate postgrazing	27.1804	8505.7808	2184.0097	0.0032	1.2406	3.1887	35.2341	79.9137
3-yr high postgrazing	28.7581	8958.1309	2318.0203	0.0032	1.248	3.0703	27.2789	79.8759

percentage of woody cover across all buffer sizes (Figure 9a). Woody patch density was statistically greater on the 15-year postgrazing site compared to the 2 recently grazed sites at the 10 and 20-m buffer sizes. At the 30-, 40-, and 50-m buffers the 3-year moderate postgrazing site had patch density estimates that were between the patch density estimates on the 15-year and 3-year high postgrazing sites (Figure 9b). Edge density estimates were statistically greater on the 15-year postgrazing sites across all buffer sizes. The 2 recent postgrazing sites had statistically similar estimates across all buffer sizes (Figure 9c). Mean woody patch area was very small and similar among the 3 sites at the 10-m buffer size, but began to diverge and increase with increasing buffer sizes (Figure 9d). Mean shape index was highest on the 15-year postgrazing site at the 10- and 20-m buffer sizes, but the 3-year moderate postgrazing site increased to similar estimates at the 30-, 40-, and 50-m buffer sizes (Figure 9e). Euclidean nearest neighbor distance was greatest on the 3-year high postgrazing site at the 10-m buffer size and gradually decreased as the buffer size increased (Figure 9f). Aggregation index was similar on all 3 sites at the 10-m buffer size; the 15-year and 3-year moderate postgrazing sites at the 50-m buffer size ended with a similar estimate that was significantly greater than the estimate for the 3-year high postgrazing site (Figure 9g). Finally, the 15-year postgrazing site had a significantly greater interspersion and juxtaposition index than the other sites at all 5 buffer sizes, while the 2 recent postgrazing sites had similar estimates of this metric across all buffer sizes (Figure 9h).

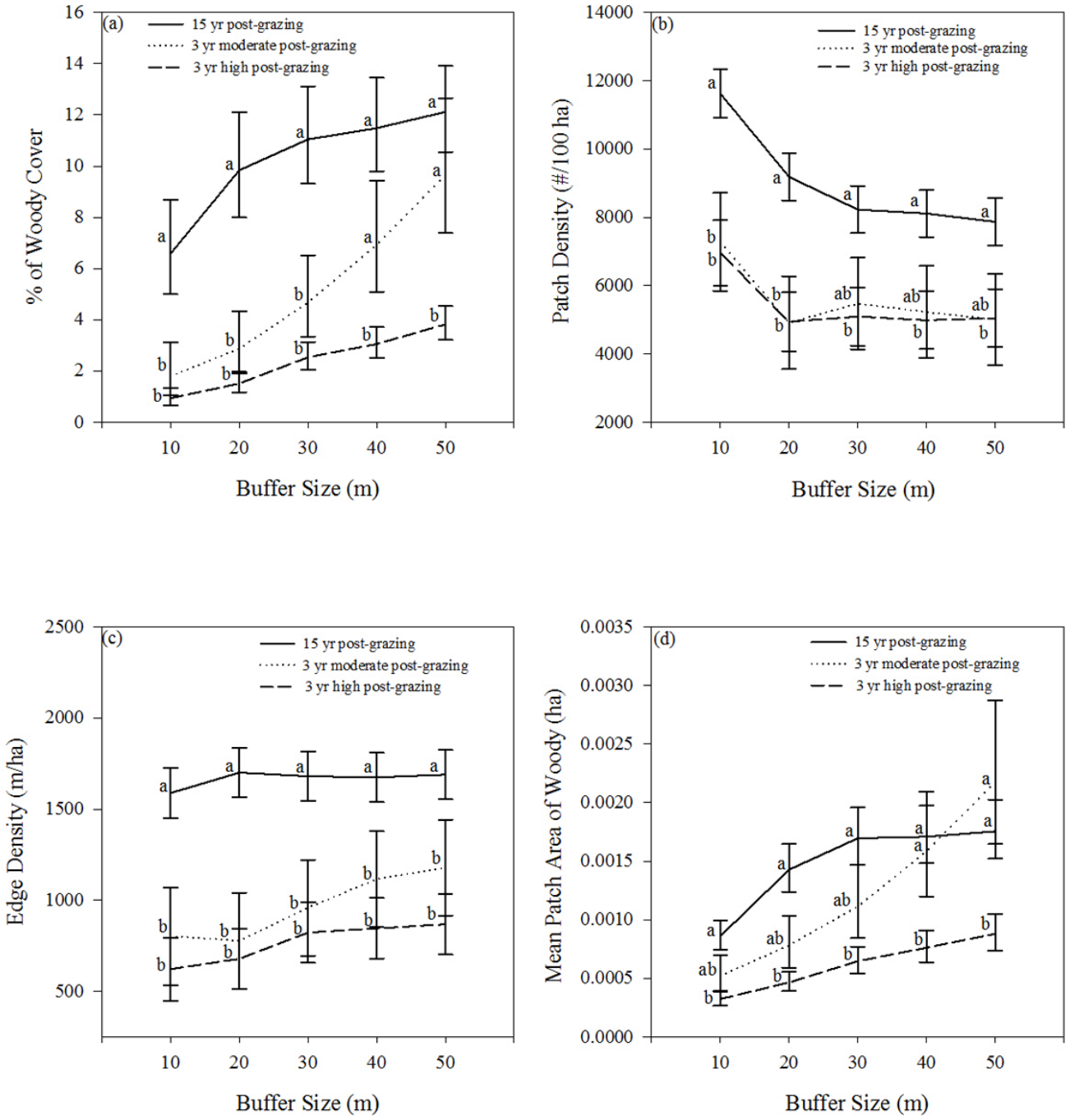

Fig. 9. Mean estimates of a) percent of landscape, b) patch density, c) edge density, d) mean patch area, e) mean shape index, f) Euclidean nearest neighbor distance, g) aggregation index, and h) interspersion and juxtaposition index for woody cover on northern bobwhite (*Colinus virginianus*) nest sites (n = 102) on the 3 postgrazing sites during 2015 and 2016 in Jim Hogg County, Texas, USA. Means followed by the same letter are not significantly (P > 0.05) different.

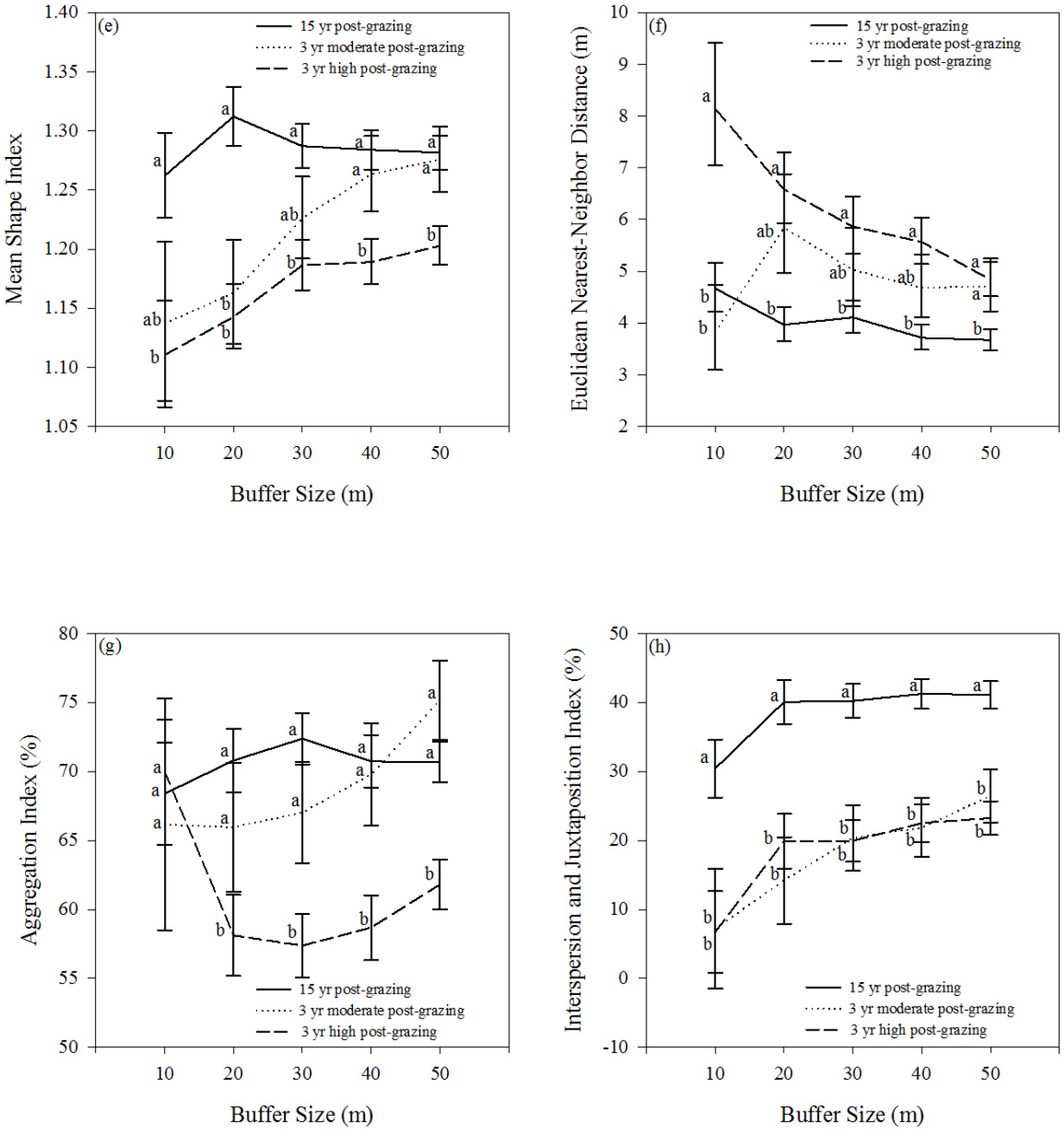

Figure 9 continued.

Microhabitat.—Across the entire study area, nest sites ($n = 50$) had 3 vegetation characteristics that were significantly different from random points (Figure 10). Nest sites had a greater percentage of woody cover and less bare ground than did random locations. At the individual site level, nest locations on the 15-year postgrazing ($n = 20$) and 3-year high postgrazing ($n = 16$) sites generally showed no significant difference in vegetation characteristics compared to random locations (Figures 11, 12, 13). However, nest sites ($n = 14$) on the 3-year moderate postgrazing site had significantly less bare ground than the paired random points (Figure 12).

Density Estimation

For the 2015 distance sampling data, we used a half-normal detection function with metrics of patch density, landscape shape index, and edge density in the density surface model to predict density (Table 5). During 2016, bobwhite density estimates increased on all sites and the best model was a half normal function with cosine adjustment plus the metrics of percent of landscape, patch density, edge density, and landscape shape index (Table 5). Bobwhite density across all 3 study sites was greater in 2016 than 2015. Density in 2015 was similar between the 15-year postgrazing site and the 3-year

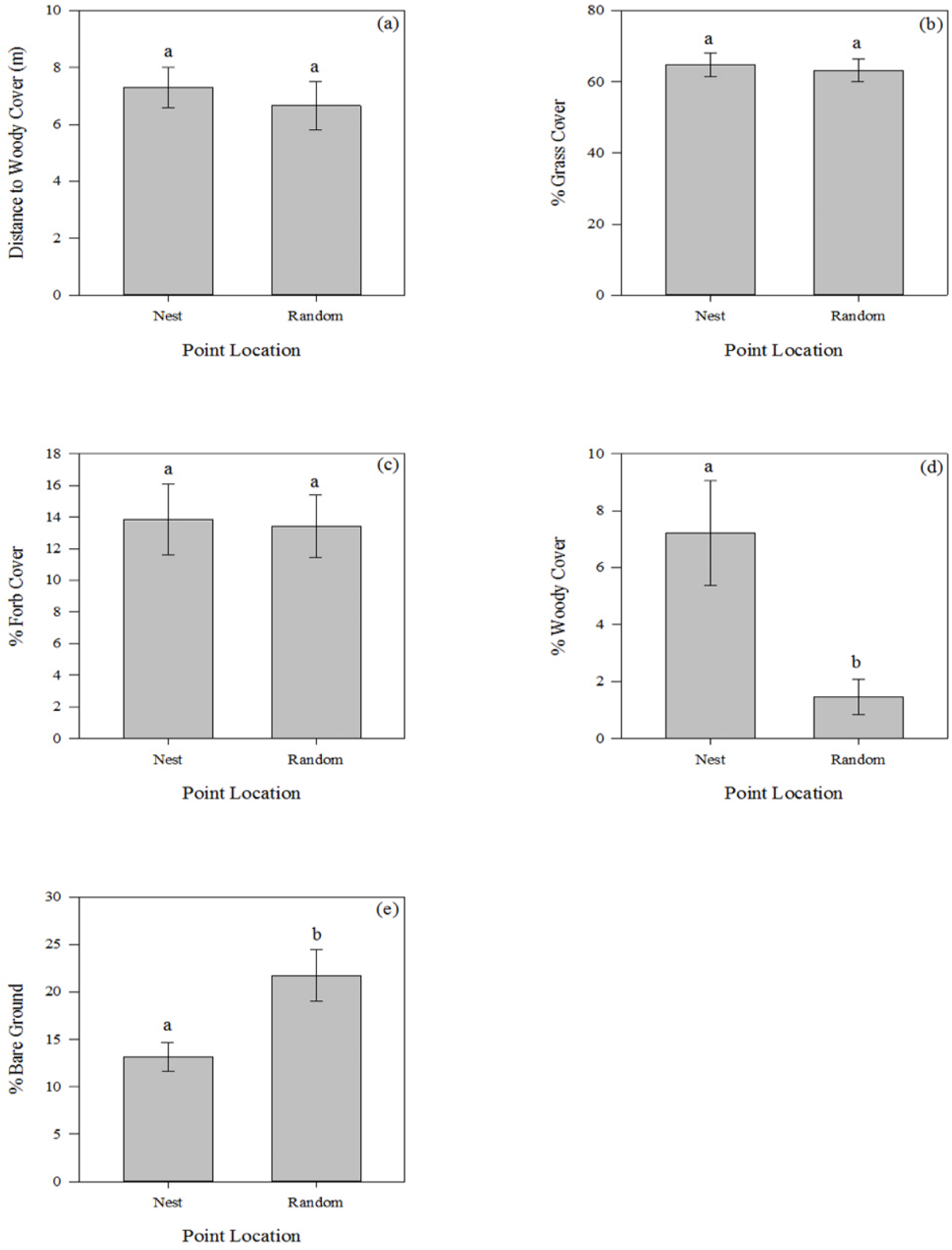

Fig. 10. Mean (±standard error) estimates of a) distance to woody cover, b) percent grass cover, c) percent forb cover, d) percent woody cover, and e) percent bare ground for northern bobwhite (*Colinus virginianus*) nest sites (n = 50) and random locations (n = 50) pooled across the 3 postgrazing sites during 2016, Jim Hogg County, Texas, USA. Means followed by the same letter are not significantly ($P > 0.05$) different.

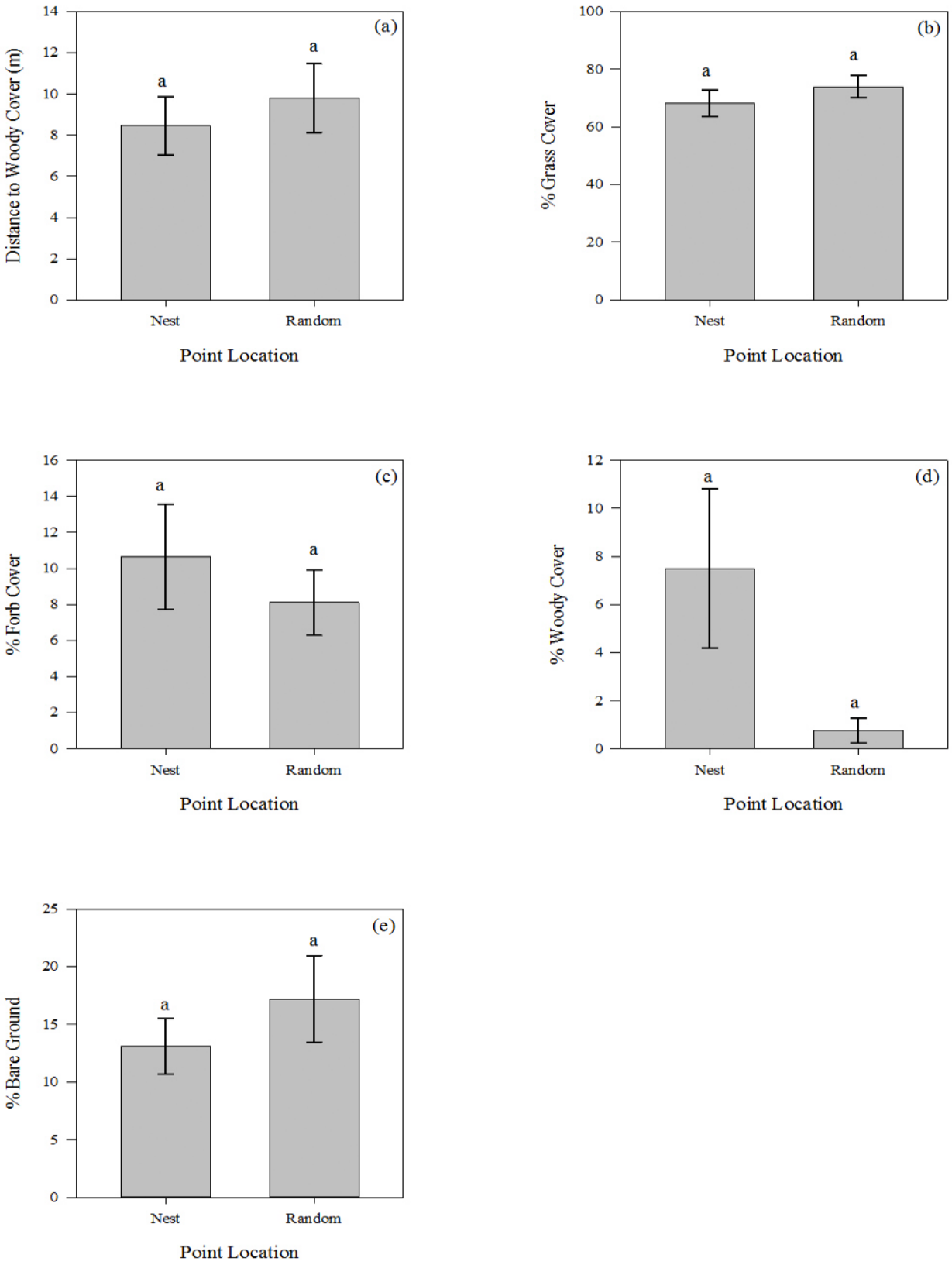

Fig. 11. Mean (±standard error) estimates of a) distance to woody cover, b) percent grass cover, c) percent forb cover, d) percent woody cover, and e) percent bare ground for northern bobwhite (*Colinus virginianus*) nest sites (n = 20) and random locations (n = 20) on the 15-year postgrazing site during 2016, Jim Hogg County, Texas, USA. Means followed by the same letter are not significantly (P > 0.05) different.

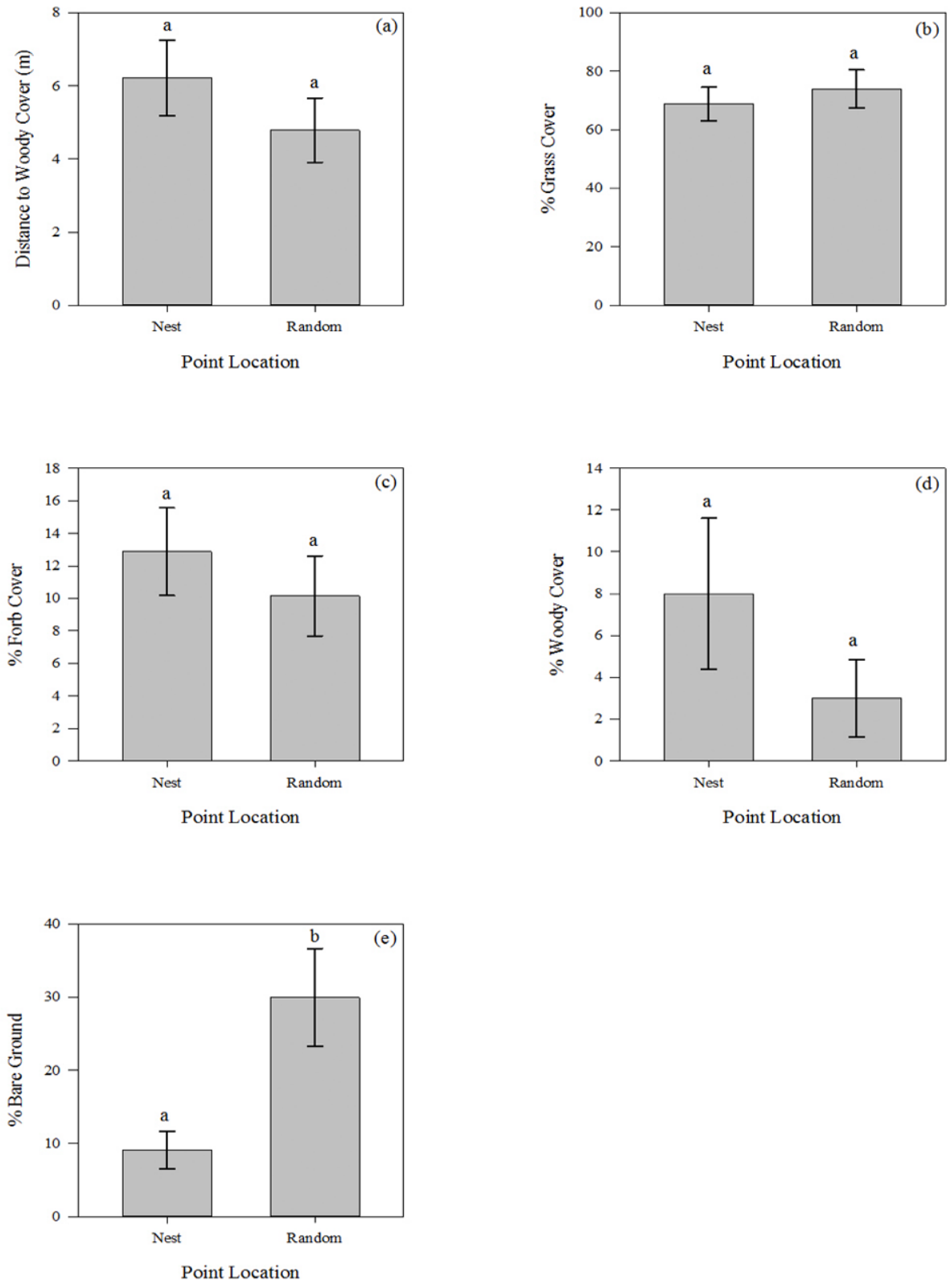

Fig. 12. Mean (±standard error) estimates of a) distance to woody cover, b) percent grass cover, c) percent forb cover, d) percent woody cover, and e) percent bare ground for northern bobwhite nest sites (n = 14) and random locations (n = 14) on the 3-year moderate postgrazing site during 2016, Jim Hogg County, Texas, USA. Means followed by the same letter are not significantly ($P > 0.05$) different.

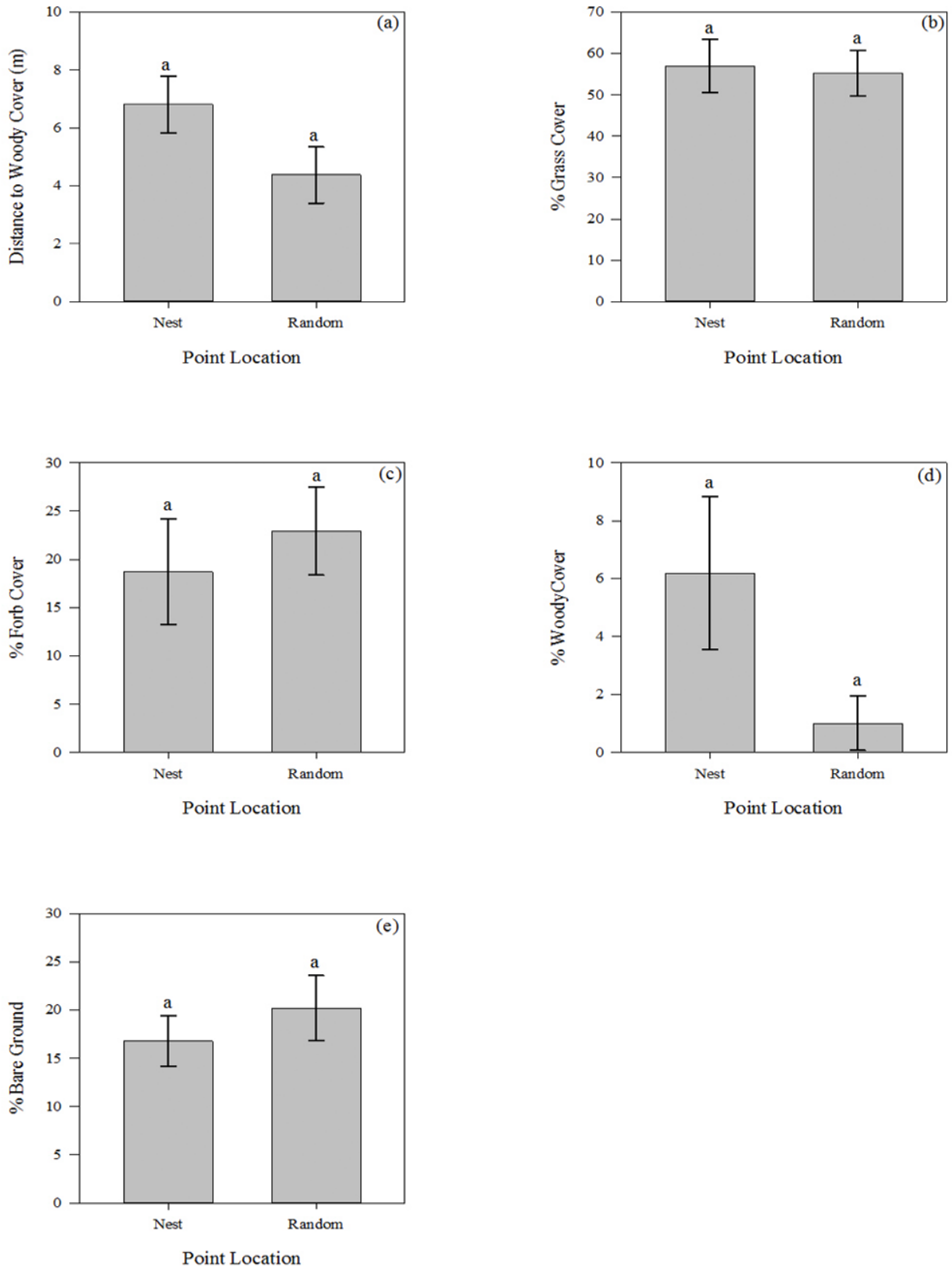

Fig. 13. Mean (±standard error) estimates of a) distance to woody cover, b) percent grass cover, c) percent forb cover, d) percent woody cover, and e) percent bare ground for northern bobwhite (*Colinus virginianus*) nest sites (n = 16) and random locations (n = 16) on the 3-year high postgrazing site during 2016, Jim Hogg County, Texas, USA. Means followed by the same letter are not significantly (P > 0.05) different.

moderate postgrazing site at 1.87 ± 0.14 birds/ha and 1.82 ± 0.14 birds/ha, but these densities were higher than the 3-year high stocking density postgrazing site, which had a density of only 0.92 ± 0.06 birds/ha (Table 6; Figure 14). During 2016, density was highest on the 15-year postgrazing site at 3.68 ± 0.25 birds/ha with the 3-year moderate postgrazing site at 2.86 ± 0.20 birds/ha and the 3-year postgrazing site once again with the lowest density at 2.01 ± 0.14 birds/ha (Table 7; Figure 15).

Table 5. Detection functions and covariates used to build density surface models for northern bobwhite (*Colinus virginianus*) in 2015 and 2016 from aerial surveys across the 3 postgrazing sites, Jim Hogg County, Texas, USA.

Survey	Detection function model	Covariates	Deviance explained
2015	Half-normal	s(x) + s(y) + s(ED) + s(LSI) + (PD)	15.1
2016	Half-normal + cosine	s(x) + s(y) + s(ED) + s(LSI) +s (PD) +s(PLAND)	9.3

Table 6. Number of transects (k), total transect length (L, km), number of covey detections (n), detection probability (p), effective strip width (ESW, m), density (D, birds/ha), coefficient of variation (CV), and 95% confidence intervals (CI[D]), from the 2015 survey on the 3 postgrazing sites, Jim Hogg County, Texas, USA.

						D		
Site	k	L	n	p	ESW	D	CV	95% CI(D)
15-yr postgrazing	12	39	74			1.87	7.45	1.62–2.16
3-yr postgrazing (moderate)	10	30	39			1.82	7.45	1.57–2.10
3-yr postgrazing (high)	11	26	22			0.92	7.45	0.79–1.06
Total	33	95	135	0.59	38.16	1.57	7.45	1.35–1.81

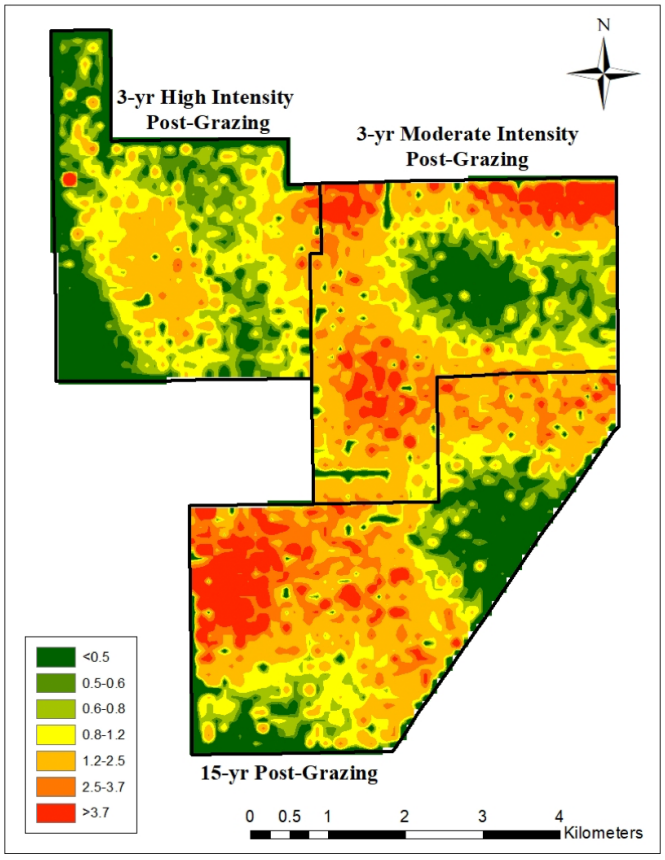

Fig. 14. Density surface model of northern bobwhite (*Colinus virginianus*) density (birds/ha) across the 3 postgrazing sites, Jim Hogg County, Texas, USA, 2015.

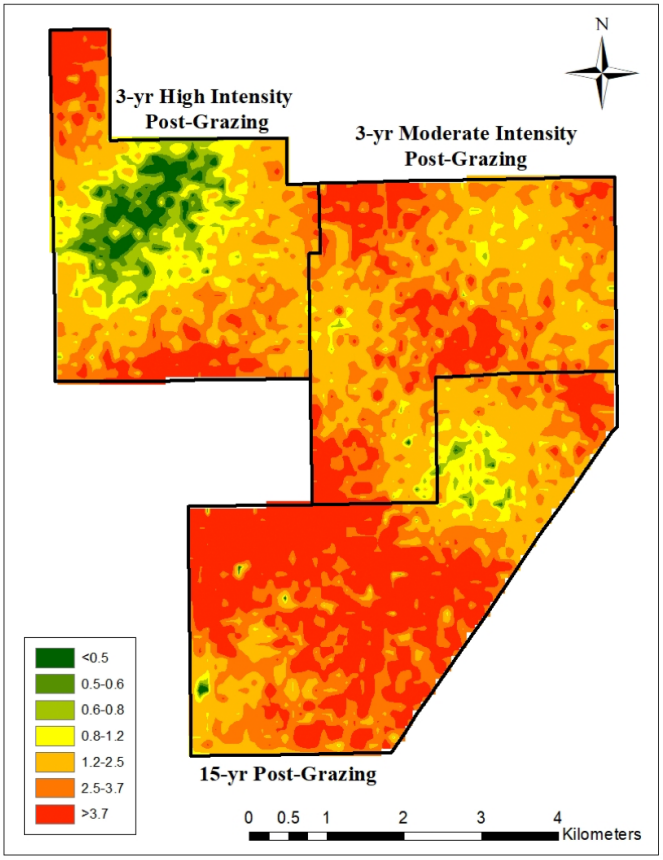

Fig. 15. Density surface model of northern bobwhite (*Colinus virginianus*) density (birds/ha) across the 3 postgrazing sites, Jim Hogg County, Texas, USA, 2016.

Table 7. Number of transects (k), total transect length (L, km), number of covey detections (n), detection probability (p), effective strip width (ESW, m), density (D, birds/ha), coefficient of variation (CV), and 95% confidence intervals (CI[D]), from the 2016 survey on the 3 postgrazing sites, Jim Hogg County, Texas, USA.

						D		
Site	k	L	n	p	ESW	D	CV	95% CI(D)
15-yr postgrazing	25	77	155			3.68	6.84	3.22–4.21
3-yr postgrazing (moderate)	21	63	90			2.86	6.84	2.50–3.27
3-yr postgrazing (high)	18	54	61			2.01	6.84	1.81–2.37
Total	64	194	306	0.42	20.829	2.91	6.84	2.54–3.32

DISCUSSION

Adult Breeding Season Survival

We predicted that there would be differences in bobwhite breeding season survival among our 3 sites. However, while breeding season survival was not different among sites or between years, it was strongly influenced by month within the breeding season. Survival was highest during the beginning of the season in April, and was lowest in June and July, with a slight increase in August. This pattern has been seen before in Kansas, where bobwhite of both sexes on cropland and rangeland areas experienced steadily decreasing survival from April through August (Taylor et al. 1999). A linear time trend in breeding season survival has also been documented in translocated bobwhite on the Rolling Plains of Texas (Downey et al. 2017). Our estimate of 0.48 ± 0.04 for surviving the breeding season was higher than other estimates in Texas and the southeastern United States (Sisson et al. 2006, Grahmann 2013, Downey et al. 2017). Month-to-month variation in thermal dynamics based on variation in operative temperatures also likely contributed to this pattern.

Nest Survival

Our nest survival estimates were influenced by both site and date of initiation within the season, with the probability of a nest surviving the 23-day incubation period peaking during the middle of the nesting season. While all our sites showed a temporal trend in nest survival, the 15-year postgrazing site survival was greater than the other 2 sites, with nearly double the probability of nest survival at the peak of the season, partially supporting our hypothesis. Bobwhite nest survival estimates in the literature vary widely (Klimstra and Roseberry 1975, Burger et al. 1995, Taylor et al. 1999, Lusk et al. 2006); our estimates were similar to estimates recently documented across South Texas (Lutz 2016). Avian nest success has been documented to improve on areas rested from grazing (Ammon and Stacey 1997). Lehmann (1984) suggested that bobwhite nest survival would increase later in the summer as there tends to be more mast and increasing alternate prey for predators. During a 4-year study in South Texas, Rader et al. (2007) also found that daily nest survival of bobwhite increased with increasing temperature. Puckett et al. (1995) documented improved bobwhite nest survival from spring to summer.

Home Range Size

Home range size was smallest on the 15-year postgrazing and 3-year moderate postgrazing sites. These results somewhat supported our hypothesis that home range size would be smallest on the 15-year postgrazing site as it had been released from grazing the longest and is exclusively managed for bobwhite. The similar home range size on the 3-year moderate postgrazing site may indicate a more recovered landscape than the 3-year high postgrazing site, which had a significantly larger home range size. Larger home range size for a particular species can be an indication of 1) less usable space per unit area, 2) or low densities of food resource, as birds may need to actively search for resources in a larger area to meet their requirements (Guthery 1997). Overall, our estimates of bobwhite home range size were similar to other studies in South Texas, which had estimates ranging from 9.97 ± 0.54 ha to 26.7 ± 1.34 ha (Haines et al. 2009, Buelow et al. 2011, Tri et al. 2014). Estimates of home range size for bobwhite varied from 3.5 ha to 282 ha across their range (Brennan et al. 2014). However, in South Texas bobwhite home range size estimates tend to be smaller than in other parts of their range. This pattern may be due to the large area of continuous bobwhite habitat in South Texas and habitat management exclusively for bobwhite in outer parts of their range, such as the southeastern coastal plain (Hernández et al. 2002, Terhune et al. 2007).

Vegetation Composition and Structure

While there were few differences in vegetation composition and structure between nests and random locations at the microhabitat scale, landscape structure around nest sites showed differences that suggest the 15-year postgrazing site may contain vegetation features that are more suitable to higher nest survival, such as higher woody edge density, patch density, and interspersion. Landscape structure, in addition to weather factors, may be an important factor in determining annual bobwhite production success. While overall percentages of woody and herbaceous vegetation types among our study sites were similar, the structure and arrangement of these cover types on the landscape is crucial. The 15-year postgrazing site

had higher woody patch density and higher interspersion and juxtaposition at the management unit scale and around nest sites compared to the more recently grazed sites.

Parent et al. (2016) noted that even in drought years, bobwhite counts were positively linked to higher shrub patch density and higher brush cover interspersion using 30-m resolution data. This lends support to our findings of greater bobwhite density on the 15-year postgrazing site as well as greater nest survival and nest sites in areas which had greater woody patch density, edge density, and interspersion of woody cover. Though bobwhites persist in a variety of brush densities, there may be an upper boundary of brush cover that limits bobwhite usable space (Guthery 1997). By examining landscape structure around nesting sites, we found that bobwhites placed their nests in areas with a lower percentage of woody cover and with smaller woody patch areas than found at the management-unit scale. The 3-year high postgrazing site in particular has a larger amount of contiguous brush growth, which could impact the amount of suitable area for nesting.

Density

Density estimates on the 3 study sites supported our hypothesis; we observed the highest bobwhite density on the 15-year postgrazing site. Bobwhite population density increased on each site between 2015 and 2016. While some of this increase was likely influenced by rainfall, the improvement may also suggest that these landscapes, especially the more recently grazed sites, are continuing to recover and thereby support more bobwhites. The greater bobwhite density on the more recovered sites in our study is consistent with other studies that examined avian response to eliminating cattle grazing. In Texas, Lusk et al. (2002) found bobwhite abundance dropped as cattle density increased. Other studies in riparian habitats saw similar trends in bird species richness and abundance when comparing recently or currently grazed sites to those rested from grazing (Taylor 1986, Dobkin et al. 1998, Krueper et al. 2003, Nelson et al. 2011, Earnst et al. 2012).

Bobwhite density has been consistently linked to rainfall (Peterson 2001), and weather patterns and their effects on the vegetation are highly correlated to quail abundance in the South Texas Plains (Bridges et al. 2001). South Texas had above-average rainfall in 2015 and 2016, which resulted in high bobwhite density on all 3 sites, especially in 2016. Differences in density among the sites may have been more significant in drier years as drought has been shown to amplify differences in bird abundance between postgrazing and currently grazed areas (Bock and Bock 1999).

Overall Population Response

Throughout our study we found evidence from bobwhite habitat and population data that supported our research hypotheses. Determining differences between or among grazing treatments on landscapes can be extremely difficult, even with long-term monitoring, due to many confounding factors such as precipitation, pasture size, and lack of replication (Mashiri et al. 2008). Response of a landscape to removal of livestock ideally needs to be monitored from the time of cattle removal and over the long term in order to account for weather patterns, especially in semiarid environments (Frank et al. 2014). When this study began, the landscape had already been rested for 3 years on the recent postgrazing sites. This, combined with the above-average rainfall during our monitoring, may have limited our ability to detect significant differences in certain metrics as the 3-year postgrazing sites may have already partially recovered. Without pretreatment and initial posttreatment data after cattle removal, we can only surmise that there may have been more stark differences in bobwhite population metrics among the 3 sites during the first few years of recovery. However, these results suggest that the 15-year postgrazing site still supports higher bobwhite density and nest survival compared to the 3-year postgrazing sites. We saw evidence that the 3-year moderate density postgrazing site may be more recovered than the 3-year high density postgrazing site; bobwhite density was still high and home range size was similar to the 15-year postgrazing site.

Historical overgrazing had led to brush encroachment on much of the South Texas landscape (Archer and Smeins 1991). However, many studies have shown that simply excluding cattle from the landscape does not necessarily halt the brush invasion that may have been set in motion by overgrazing (Chew 1982, Bock et al. 1984). While grazing removal generally improves native landscapes, it is necessary to have reasonable timeline expectations and also consider complementary management strategies to improve results (West et al. 1984).

The 15-year postgrazing site is managed for bobwhite hunting, and continuous brush management using herbicide is implemented throughout the year. This site is an example of how purposeful management in removing cattle after overgrazing along with specific brush management for bobwhite and bobwhite hunting has been successful in improving bobwhite populations. Brush management targeting the young mesquite encroachment, especially on the 3-year high postgrazing site, may be necessary for improving the landscape structure to support more abundant bobwhite populations. We hypothesized that over time bobwhite population metrics on the 3-year moderate and 3-year high postgrazing sites will continue to improve and then stabilize, at which point additional management may be necessary to increase numbers to the levels on the 15-year postgrazing site. Long-term monitoring of all 3 sites would be able to account for annual precipitation variation, and allow for intelligent management decisions. The additional use of satellite imagery and classification combined with density surface models to examine relationships between bobwhites and specific landscape metrics on the 3 sites could be used to target specific areas of the study area that may be improved by various land management techniques. While multiple interacting factors limit inferences to our study area, these results can inform managers about bobwhite preferences in postgrazing landscapes and potentially provide ideas for future restoration strategies and suggestions for purposeful

management, as well as general estimates of time to pasture recovery after cattle removal.

MANAGEMENT IMPLICATIONS

Our results support the management philosophy that reduction or removal of cattle, especially after many years of continuous grazing, may be a useful step in improving habitat for bobwhite in rangeland environments. In South Texas, managers may be able to expect bobwhite population recovery on previously moderately stocked landscapes to about 2 or more bobwhite/ha within about 3–5 years as long as adequate rainfall occurs during that time frame. In any case, it is necessary that quail managers have realistic expectations for the time to recovery after cattle grazing has been removed to improve quail habitat. It is also critical that managers understand numerous different factors that may influence the rate of quail habitat and population improvement, including rainfall patterns, previous stocking densities, range condition, and landscape structure when making decisions about cattle removal and subsequent land management actions.

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EFFECT OF PRESCRIBED FIRE AND MECHANICAL TREATMENTS ON NORTHERN BOBWHITE OCCUPANCY IN MESIC PINE FLATWOODS

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ABSTRACT

We examined whether roller-chopping, mowing, and prescribed fire used to restore groundcover in pine flatwoods habitats affected northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) occupancy. We surveyed bobwhites using repeated point counts (n = 3), April–June each year, to determine response to prescribed fire and mechanical treatments on Osceola National Forest (Osceola, 78 plots) and St. Sebastian River Preserve State Park (Sebastian, 11 plots) in Florida, USA, 2013–2019. We measured groundcover each year at randomly placed transects within 200-m radius point-count plots. To assess the importance of management covariates, we fit single season occupancy models to predict occupancy (ψ) and detection (p). Detection probability was 0.12 (standard error [SE] = 0.05) and 0.35 (SE = 0.05) on Osceola and Sebastian, respectively. Modeled occupancy on both sites was best predicted by presence of roller-chopping, years since fire, and year. Predicted occupancy was highest on plots with 1 year since fire (Osceola, 0.22 [SE = 0.10]; Sebastian, 0.67 [SE = 0.18]). Predicted occupancy was higher on roller-chopped plots (Osceola, 0.33 [SE = 0.15]; Sebastian, 0.85 [SE = 0.15]) than on mowed (Osceola, 0.08 [SE = 0.03]) or untreated plots (Osceola, 0.07 [SE = 0.03]; Sebastian, 0.38 [SE = 0.34]). Roller-chopping and fire reduced density of palmetto (*Seranoa* spp.)-shrub vegetation and increased grasses and forbs. To increase bobwhite occupancy and improve habitat suitability of degraded mesic pine flatwoods, we recommend roller-chopping and a 2-year fire frequency.

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Key words*: Colinus virginianus*, habitat, management, mowing, northern bobwhite, occupancy, pine flatwoods, prescribed fire, roller-chopping

Northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) have declined significantly in the southeastern United States, including Florida (Sauer et al. 2008). Changing land use, reduction in fire use and frequency, and habitat loss and fragmentation are thought to be responsible for observed declines in regional bobwhite populations (Brennan 1991, Brennan and Kuvlesky 2005). The decline in the use of frequent prescribed fire is likely to be largely responsible for bobwhite population declines in forest ecosystems in the southeastern United States (Brennan et al. 1998).

Pine flatwood ecosystems are the most extensive ecosystems dominated by longleaf pine (*Pinus palustris*) in Florida (Abrahamson and Hartnett 1990). These ecosystems present a significant opportunity for bobwhite conservation as millions of hectares are in public ownership and most are managed with prescribed fire. Further, restoring habitat suitability for bobwhite would be likely to benefit a suite of declining upland species, thus garnering public and agency support (Miley and Lichtler 2009, Palmer et al. 2011). However, few studies explore the effects of management in pine flatwoods and additional information is needed for bobwhite conservation in these habitats (Miley and Lichtler 2009).

Flatwoods are naturally dominated by longleaf pine or slash pine (*Pinus elliotii*) (or both), a flammable understory of saw palmetto (*Serenoa repens*) and gallberry (*Ilex glabra*), and—in good ecological condition—a high diversity of herbaceous species (Peet and Allard 1993, Platt 1999). While flatwoods were historically maintained by frequent, low intensity fires, most flatwoods in Florida currently exist in a highly degraded state due to fire suppression and reductions in fire frequency. Low fire frequency has resulted in increased height and density of shrubs, particularly saw palmetto, and subsequent declines in herbaceous groundcover (Maliakal et al. 2000). These changes threaten the integrity of pine flatwood ecosystems and

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significantly reduce their suitability for dozens of species of conservation concern, including bobwhite.

While increasing fire frequency may be a logical management prescription for restoring degraded pine flatwood groundstory communities, a return of prescribed fire alone may not result in a shift from perennial woody vegetation to a mixture of woody-herbaceous groundcover (Glitzenstein et al. 2003) more suitable for bobwhite. Application of mechanical treatments in combination with fire have been used to reduce woody groundcover, particularly in areas where high fuel loads inhibit safe prescribed fire application (Brose and Wade 2002). Roller-drum chopping (hereafter, roller-chopping) has been recommended over a single application of growing season fire when reduction in saw palmetto coverage is the objective (Willcox and Giuliano 2010). The combination of roller-chopping and fire may have longer term benefits as well. Watts et al. (2006) found that roller-chopped areas not maintained with burning had more shrubs and less herbaceous groundcover than did roller-chopped sites maintained with burning. Flat mowing is used to reduce the stature of saw palmetto but may not reduce the number of individual plants or their dominance in the groundstory. Flat mowing essentially "top-kills" perennial hardwoods and shrubs and results in increased resprouting of hardwood stems (Welch et al. 2004).

Though bobwhite historically existed at relatively high densities (Frye 1948, 1954), they currently exist in degraded pine flatwood habitats at relatively low densities (S. Brown, unpublished data), but are known to respond to management (Miley and Litchtler 2009). Comparing bird abundance and occupancy estimates over successive years and among areas associated with different management practices provides information on population trends and management effects (Ralph et al. 1995). Therefore, we monitored the response of groundcover and bobwhite occupancy on 2 public lands undergoing habitat restoration in Florida: Osceola National Forest (Osceola) and St. Sebastian River Preserve State Park (Sebastian). To do so, we assessed bobwhite occupancy over a 7-year period and related this to management as applied by the agencies. We modeled bobwhite occupancy in relation to fire use, roller-chopping, and flat mowing. We also measured groundstory condition to determine how vegetation changed following management. We expect this information to be of use to managers interested in restoration of pine flatwood habitats for bobwhite and other species of concern.

STUDY AREA

Osceola National Forest

Osceola, located in northeastern Florida, was composed of a mixture of forested wetlands and mesic pine flatwoods with sandy-acidic soils. Approximately 70% of the pine flatwoods on the Osceola was dominated by slash pine or mixed slash-longleaf pine and the remainder was longleaf pine. Dominant groundcover vegetation types included saw palmetto, gallberry, runner oak (*Quercus minima*), vaccinium (*Vaccinium* spp.), oak (*Quercus* spp.), fetterbush (*Lyonia lucida*), waxmyrtle (*Myrica cerifera*), smilax (*Smilax* spp.), wiregrass (*Aristida* spp.), and bluestem (*Andropogon* spp.). Longer fire-return intervals (4–10 years) on much of the Osceola forest has resulted in a nearly complete coverage of palmetto-shrubs in the groundcover and a decline or absence of many fire-adapted wildlife species. The U.S. Department of Agriculture Forest Service began a Collaborative Forest Landscape Restoration project in 2005 on approximately 25,000 ha of the forest to reduce wildfire threat and increase habitat quality for declining species. Management included increased prescribed fire, roller-chopping and flat-mowing of groundstory vegetation, thinning of younger slash pine stands, and planting longleaf pine.

St. Sebastian River Preserve State Park

The Sebastian study area was on a 1,070-ha portion of the northeast quadrant of the park, located in Brevard County, Florida. The mesic flatwood habitat was dominated by longleaf and slash pine and associated groundcover typical of these ecosystems. Dominant groundcover vegetation types were similar to those on the Osceola. Managers have dramatically increased the use of prescribed fire and roller-chopping over the past 15 years and Sebastian participates in the Upland Ecosystem Restoration Project (Palmer and Sisson 2017). Our study area on Sebastian was managed using frequent prescribed fire, roller-chopping, hardwood control, and some overstory pine thinning. Fires were applied on a 2-year fire frequency and burn size units ranged from approximately 100 ha to 300 ha.

METHODS

Bird Monitoring

We randomly placed 200-m radius survey plots >600 m apart along forest roads within upland habitats (78 plots on Osceola and 11 plots on Sebastian). A single trained observer surveyed bobwhite using point counts at each survey plot during April–June 2013–2019. In order to maximize detection, we visited each survey plot 3 times/year from 15 minutes before sunrise to ≤3 hours after sunrise on days with no rain and low winds. We conducted a 5-minute point count and recorded male bobwhite calls within a 200-m radius. We recorded wind and cloud cover (on the Beaufort scale), date, time, and temperature.

Management

We merged management records provided by Osceola and Sebastian with our survey plots using ArcGIS (Esri Inc., Redlands, CA, USA). To assess the effects of mechanical treatments on focal species, we created categorical variables for thinning (Thin), roller-chopping (Chop), and mowing (Mow) and classified each plot as "treated" or "untreated" in

each year. We considered a plot treated if 40% or more of a plot received a management treatment. Some mechanically treated plots were burned within the same year or in years following treatment. We calculated the years since burn by determining the number of days since the most recent burn within the plot divided by 365.

Vegetation

We collected vegetation information on 8 randomly placed 10-m transects within each 200-m radius survey plot. Transects were randomly placed at the beginning of the study to track changes over time. Vegetation surveys were conducted from April–June each year, concurrent with bird surveys. At 1-m intervals (11 locations/transect) we placed a 1.5-m pole marked with decimeter increments (modified from Mills et al. 1991) and recorded the presence of each vegetation category (palmetto, shrub, hardwood, vine, pine regeneration, grass, forb, and legume) that was within a 1-dm radius from the pole. For each transect we summed the count for each vegetation category and divided this sum by the total number of decimeters per transect to represent an average "density" for each category. We calculated the density of grass, forb, and legume as a variable (Herbaceous) and density of palmetto, shrub, hardwood, pine regeneration, and vines as a variable (Woody). We assessed each vegetation variable at 2 height levels: above 5 dm (Herbaceous >5 dm, Woody >5 dm) and below 5 dm (Herbaceous ≤5 dm, Woody ≤5 dm).

Bobwhite Occupancy

We fit the single season occupancy model (MacKenzie et al. 2002) to bobwhite presence–absence data to model occupancy (ψ) and detection (p) in relation to covariates using the *occu* function in the R 4.1.0 (www.R-project.org, accessed 5 Aug 2021) package *unmarked* 1.0.1 (Fiske and Chandler 2011). Due to differences in management intensity and management actions, we fit one set of models for Osceola and one set of models for Sebastian. Low detection of bobwhite required us to stack data from all 7 years into a single season and, therefore, we included a year covariate in all models. Year was modeled as a trend variable as we believed management would result in increasing bobwhite occupancy over time. For ease of comparisons and model convergence we standardized all continuous covariates at mean 0 unit variance.

We considered 5 potential covariates for bobwhite detection (p): date, time of day, wind, cloud cover, and temperature. We considered a quadratic term for time of day because we observed a nonlinear relationship between vocalization rate and time of day with more vocalizations in the early and late morning. To examine annual effects on p, we considered interaction terms between date and the other covariates.

We considered 3 potential management-specific explanatory variables for bobwhite occupancy (ψ): roller-chopping, flat-mowing, and years since the last burn within a plot. We did not include thinning because it was not a useful predictor based on preliminary modeling of occupancy. We used Akaike's Information Criterion (AIC) in conjunction with a manual stepwise selection process to identify the best model representing management variables and their interaction with fire. We considered models within 2 AIC units from the most parsimonious model to be plausible (Burnham and Anderson 2002) and we model averaged (Buckland et al. 1997) prediction estimates. We assessed goodness of fit of the global model using a parametric bootstrapping procedure (Dixon 2002) to compute several fit statistics (e.g., sum-of-squared errors, Pearson chi-square, and Freeman-Tukey test), which provided no evidence of lack of fit ($P > 0.323$). We used the best approximating model (lowest AIC) among all models to estimate occupancy of bobwhite. All analyses were done in R 4.1.0. All values are reported as means ±1 standard error unless noted otherwise.

Vegetation Response to Mechanical Treatments

We assessed changes in groundstory composition and structure from mowing and roller-chopping by comparing average vegetation variables prior to and after a management action. For each transect, pre- and post-densities for vegetation categories were calculated by averaging annual densities, before and after a management action was applied. We used paired t-tests to determine whether the difference between pretreatment and posttreatment averages for vegetation categories was different than zero at the 0.05 significance level.

RESULTS

Management

On Osceola, 53 of the 78 plots received a mechanical treatment: mowing occurred within 22 plots, roller-chopping occurred within 22 plots, and 9 plots received both mowing and roller-chopping. Sixty-two plots received prescribed burning during the study. The average years since fire for plots was 3.0 (range 0.0–12.3). On Sebastian, all 11 plots received roller-chopping and burning during the study. The average years since fire for plots was 0.9 (range 0.0–2.0).

Bobwhite Surveys

On Osceola, we detected 39 bobwhite during point-count surveys (n = 1,638). In 2013, we detected 4 bobwhite (0.02 quail/plot) with detections in 2/78 (2.6%) of the plots; in 2019, we detected 6 bobwhite (0.03 quail/plot) with detections in 5/78 (6.4%) of the plots (Table 1). Occupancy probability of bobwhite adjusted for detection probability indicated an increasing trend in occupancy, from 0.06 ± 0.03 in 2013 to 0.31 ± 0.18 in 2019.

On Sebastian, we detected 72 bobwhite during point-count surveys (n = 231). In 2013, we detected 17 bobwhite (0.51quail/plot) with detections in 6/11 (54.5%) of the plots; in 2019, we detected 7 bobwhite (0.21quail/plot) with detections in 6/11 (54.5%) of the plots (Table 1). Occupancy probability of bobwhite adjusted for detection probability indicated an increasing trend in occupancy, from 0.51 ± 0.33 in 2013 to 0.91 ± 0.11 in 2019.

Bobwhite Occupancy and Management

For Osceola, model selection results indicated support for 2 models based upon ΔAIC <2.0 (Table 2). The top model included roller-chopping, years since fire, and year (w = 0.66). Only parameter estimates for roller-chopping and fire frequency were significant ($P \leq 0.009$). Bobwhite occupancy was negatively related to years since fire. Predicted occupancy probability, ignoring yearly and roller-chopping effects, was greater on plots with 1 year since fire (0.22 ± 0.10**)** than on plots with 4 years since fire (0.07 ± 0.04). Bobwhite predicted occupancy was 4 times greater on roller-chopped plots (0.33 ± 0.15) than on mowed plots (0.08 ± 0.03) and 4.7 times greater than on plots that were not roller-chopped or mowed (0.07 ± 0.03; Figure 1). An additive effect between date and time of day was included in all top models, indicating detection was positively related to the day of the year and negatively related to time of day. Overall detection probability was 0.12 ± 0.05 when date and time were set to their mean values.

On Sebastian, model selection results indicated support for 2 models based on ΔAIC <2.0 (Table 3). The top model included roller-chopping, years since fire, and year (w = 0.67) and was 1.40 AICs below the second-best approximating model, which included years since fire and year. Only parameter estimates for years since fire were significant ($P \leq 0.013$).

Bobwhite predicted occupancy was highest on plots with 1 year since fire (0.67 ± 0.18) and declined after 2 years since fire (0.09 ± 0.10). Predicted occupancy was 2.2 times higher on roller-chopped plots (0.85 ± 0.15) than on untreated plots (0.38 ± 0.34; Figure 2). An additive effect between wind and year was included in all top models, indicating detection was negatively related to wind and year. Overall detection probability was 0.35 ± 0.05 when wind and year were set to their mean values.

Vegetation Response to Mechanical Treatments

On Osceola, roller-chopping significantly increased the density of herbaceous groundcover above 5 dm (t_{117} = 7.63, p < 0.001) and below 5 dm (t_{117} = 8.03, p < 0.001) and significantly decreased the density of woody groundcover above (t_{117} =−12.75, p < 0.001) and below 5 dm (t_{117} =−6.95, p < 0.001; Table 4). Mowing significantly increased the density of herbaceous groundcover below 5 dm (t124 = 4.50, p < 0.001), but not above (t_{124} = 0.51, p = 0.611), and significantly decreased the density of woody groundcover above 5 dm (t_{124} = −12.10, p < 0.001), but not below (t_{124} = −1.27, p = 0.206). Posttreatment density of herbaceous vegetation below 5 dm was two-fold greater on roller-chopped sites than mowed sites.

On Sebastian, roller-chopping significantly increased the density of herbaceous groundcover above 5 dm (t_{69} = 14.68, p < 0.001) and below 5 dm (t_{69} = 19.10, p < 0.001) and significantly decreased the density of woody groundcover above (t_{69} = −9.23, p < 0.001) and below 5 dm (t_{69} = −8.44, p < 0.001; Table 5).

Table 1. Northern bobwhite predicted occupancy probability and percentage of 200-m radius plots with a detection, by year. Data are from 78 survey plots located in Osceola National Forest, Olustee, Florida, USA and 11 survey plots located in St. Sebastian River Preserve State Park, Micco, Florida, 2013–2019.

	Survey site					
	Osceola National Forest			St. Sebastian River Preserve State Park		
Year	Detected per plot	% plots with a detection	Occupancy probability	Detected per plot	% plots with a detection	Occupancy probability
2013	0.02	2.6	0.06 ± 0.03	0.51	54.5	0.51 ± 0.33
2014	0.01	2.6	0.08 ± 0.04	0.48	63.6	0.60 ± 0.28
2015	0.03	5.1	0.10 ± 0.05	0.12	27.3	0.69 ± 0.23
2016	0.05	7.7	0.14 ± 0.07	0.27	36.4	0.76 ± 0.19
2017	0.02	6.4	0.18 ± 0.10	0.39	72.7	0.83 ± 0.16
2018	0.02	5.1	0.24 ± 0.13	0.18	54.5	0.87 ± 0.13
2019	0.03	6.4	0.31 ± 0.18	0.21	54.5	0.91 ± 0.11

Table 2. Model selection results with ΔAkaike's Information Criterion [AIC] <2.0 for northern bobwhite occupancy in relation to management covariates[a]. All models include year as a covariate. Data are from 78 survey plots located in Osceola National Forest, Olustee, Florida, USA, 2013–2019.

Occupancy (ψ)	Detection (p)	Number of parameters	AIC	ΔAIC	AIC_{wt}
Chop+YearsSinceFire	Date+Time	7	273.42	0.00	0.66
Chop+YearsSinceFire+Mow	Date+Time	8	274.84	1.42	0.32

[a] Covariates are coded as follows: Chop = roller-chopped, YearsSinceFire = years since fire, Mow = mowed.

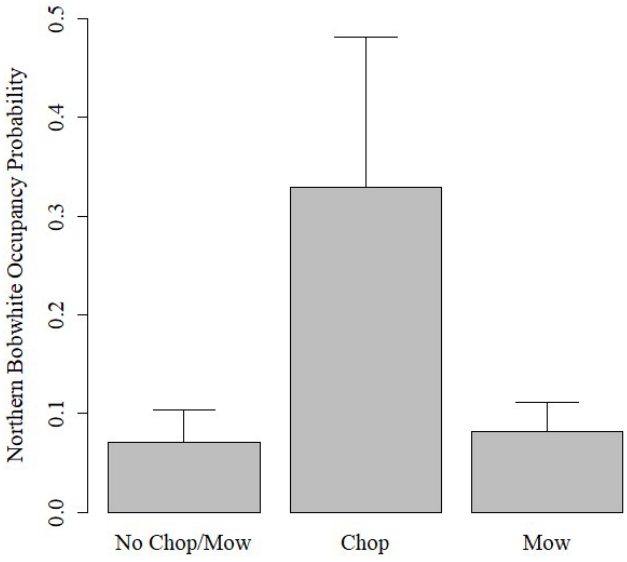

Fig. 1. Northern bobwhite occupancy probability in relation to roller-chopping and mowing on Osceola National Forest, Olustee, Florida, USA, 2013–2019. Error bars are +1 standard error.

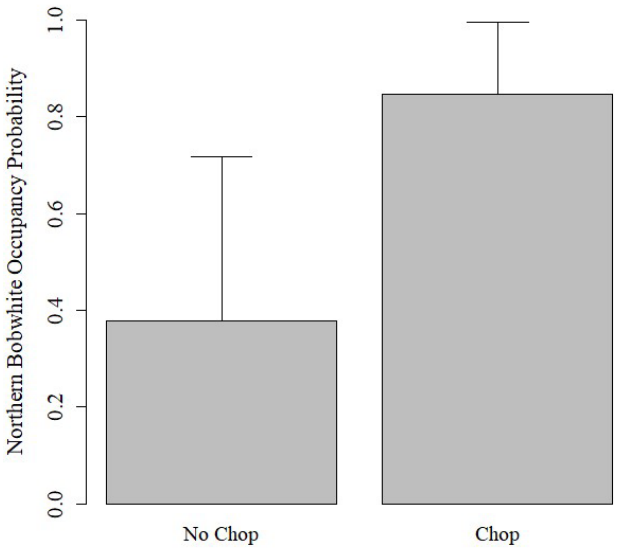

Fig. 2. Northern bobwhite occupancy probability in relation to roller-chopping on St. Sebastian River Preserve State Park, Micco, Florida, USA, 2013–2019. Error bars are +1 standard error.

Table 3. Model selection results with ΔAkaike's Information Criterion [AIC]< 2.0 for northern bobwhite occupancy in relation to management covariates[a]. All models include year as a covariate. Data are from 11 survey plots located in St. Sebastian River Preserve State Park, Micco, Florida, USA, 2013–2019.

Occupancy (ψ)	Detection (*p*)	Number of parameters	AIC	ΔAIC	AIC_{wt}
Chop+YearsSinceFire	Wind+Year	7	241.53	0.00	0.67
YearsSinceFire	Wind+Year	6	242.94	1.40	0.33

[a] Covariates are coded as follows: Chop = roller-chopped, YearsSinceFire = years since fire.

Table 4. Average density of herbaceous and woody groundcover[a] on roller-chopped and mowed plots pre-treatment ("Pre") and post-treatment ("Post") and associated p-values from paired t-tests of mean differences. Data are from 78 survey plots located in Osceola National Forest, Olustee, Florida, USA, 2013–2019.

	Treatment							
	Roller-chop				Mow			
Groundcover	Pre average	Post average	Mean of differences	p-value	Pre average	Post average	Mean of differences	p-value
Herbaceous ≤5 dm	0.272	0.460	0.189	<0.001	0.172	0.248	0.075	<0.001
Herbaceous >5 dm	0.030	0.087	0.056	<0.001	0.023	0.025	0.002	0.611
Woody ≤5 dm	1.076	0.919	-0.156	<0.001	1.101	1.079	-0.022	0.206
Woody >5 dm	0.374	0.176	-0.197	<0.001	0.456	0.221	-0.234	<0.001

[a] Groundcover is described by the following: herbaceous = grass, forb, legume; woody = palmetto, shrub, hardwood, pine regeneration, vine.

Table 5. Average density of herbaceous and woody groundcover[a] on roller-chopped plots both pre-treatment ("Pre") and post-treatment ("Post") and associated p-values from paired t-tests of mean differences. Data are from 11 survey plots located in St. Sebastian River Preserve State Park, Micco, Florida, USA, 2013–2019.

Groundcover	Pre average	Post average	Mean of differences	p-value
Herbaceous ≤5 dm	0.855	1.161	0.306	<0.001
Herbaceous >5 dm	0.060	0.241	0.181	<0.001
Woody ≤5 dm	0.638	0.444	-0.193	<0.001
Woody >5 dm	0.111	0.025	-0.086	<0.001

[a] Groundcover is described by the following: herbaceous = grass, forb, legume; woody = palmetto, shrub, hardwood, pine regeneration, vine.

DISCUSSION

Bobwhite occupancy declined with time since fire, indicating that the effects of fire on habitat suitability were temporary. Similar to our study, Miley and Lichtler (2009) found that bobwhite were more abundant in pine flatwoods burned within 1 year and abundance declined in areas >2 years since fire. Other studies have documented the importance of frequent fire to bobwhite habitat suitability (Stoddard 1931, Brennan et al. 1998, Palmer and Sisson 2017, Rosche et al. 2019, Weber et al. 2022, this volume).

Fire frequency has long-term effects that drive pine forest community structure and composition (Glitzenstein et al. 2003, 2012; Rother et al. 2020). In fire-suppressed pine flatwoods, or those with longer fire rotations, groundstory communities become dominated by saw palmetto and shrubs (Glitzenstein et al. 2003) and applying frequent fire may not reduce their dominance. A long-term study on Osceola determined that annual burns, spanning several decades, did not produce herbaceous-dominated groundcover and only slightly reduced the dominance of saw palmetto (Glitzenstein et al. 2003). Therefore, fire alone may not be a viable management technique for improving bobwhite habitat in degraded habitats.

Roller-chopping reduces dominance of saw palmetto in the groundstory and releases grasses and forbs because it kills the roots of saw palmetto (Hendricks 1983, Willcox and Giulano 2010). Conversely, mowing essentially mimics fire by top-killing individual plants that quickly resprout without a change in species composition (Welch et al. 2004, Menges et al. 2020). On Osceola, where both mowing and roller-chopping occurred, mowing reduced the stature of hardwoods and saw palmetto, but only modestly increased grasses and forbs in comparison to roller-chopping. We believe the positive response of bobwhite to roller-chopping was due to the large changes in habitat structure and composition that it caused; mowing did not elicit a bobwhite response because it did not adequately reduce saw palmetto dominance. Our results indicate that mowing is not an effective, long-term treatment for increasing bobwhite habitat in fire-suppressed pine flatwoods.

Though roller-chopping shifted the plant community and improved bobwhite habitat suitability, the effects of roller-chopping were temporary without the application of frequent fire. We observed increased density of saw palmetto on roller-chopped plots that did not receive adequate fire. Application of roller-chopping requires frequent fire to sustain herbaceous groundcover (Brose and Wade 2002, Watts and Tanner 2004, Watts et al. 2006, Willcox and Giuliano 2010). Watts et al. (2006) observed effects of roller-chopping and burning and found that sites roller-chopped and burned maintained higher forb richness and higher density of grasses even 12–13 years post-treatment. Therefore, long-term frequently applied fire is needed to sustain benefits accrued from roller-chopping degraded flatwood habitats.

Increased management activities improved habitat and resulted in a modest increase in bobwhite occupancy on both our study sites. However, bobwhite occupancy was lower on Osceola than Sebastian. Fire frequency on Osceola averaged nearly 5 years (compared to every 2 years on Sebastian), which resulted in large areas of palmetto-shrub dominance in the groundstory. In addition, less roller-chopping per plot occurred on Osceola than on Sebastian. Finally, the spatial extent and distribution of management on Osceola was determined by an ecological index model, resulting in patches of suitable habitat (this may change with continued management), whereas management on Sebastian concentrated on a focal area, which resulted in more contiguous habitat. We believe the lack of contiguous habitat on Osceola reduced the effectiveness of management actions for eliciting a bobwhite population response (Dunning et al. 1995, Fies et al. 2002, Cox and Kesler 2012).

While bobwhite numbers on Osceola were limited by the extent and distribution of suitable habitats, suitable habitat on Sebastian covered most of the area. However, the number of bobwhites on Sebastian plateaued at a relatively low level (<1 bobwhite detected/plot), while sympatric species, such as Bachman's sparrow (*Peucaea aestivalis*), increased in abundance each year (S. Brown, unpublished data). Bobwhite numbers on Sebastian appeared to be lower than other sites with high fire frequency in central Florida studies (Miley and Lichtler 2009, Johnson et al. 2014). We believe the plateau in bobwhite numbers may be associated with the size and season of fires used on Sebastian. Objectives for management of Sebastian were implemented to benefit a suite of fire-adapted species and therefore fire management was not optimized for bobwhite. Prescribed fires at Sebastian shifted in season over the course of our study from January–May to April–June. Fires occurring in April–June coincide with peak nesting season in central Florida and we suspect that these fires may have impacted nesting success and brood survival, potentially impacting population growth (Kamps et al. 2017). In addition, fires were relatively large in size. The combination of high fire frequency

applied during peak nesting season at larger scales (larger than recommended for bobwhite), likely limited the positive response of the population (Weber et al. 2022, this volume).

MANAGEMENT IMPLICATIONS

Roller-chopping followed by fire is an effective technique to increase bobwhite occupancy in degraded mesic pine flatwoods. We suggest that management actions should be directed toward maintaining current areas of high-quality habitat with frequent fire (≤2-year fire rotation) and treating highly degraded areas with roller-chopping followed by fire. We do not recommend the use of mowing on saw palmetto-shrub communities for improving bobwhite habitat suitability. Though mowing may have utility in reducing fuel loads to facilitate burning, roller-chopping has the added benefit of increasing habitat suitability and occupancy of bobwhite. When possible, managers should apply these techniques on large continuous areas to improve bobwhite response.

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BOBWHITE RESPONSE TO CATTLE GRAZING IN SOUTH TEXAS

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ABSTRACT

Range management practices to improve habitat for wildlife by reducing brush and increasing herbaceous plants, coupled with reduced stocking rates, can lead to dense stands of dominant grasses, such as four-flower trichloris (*Trichloris pluriflora*). This monoculture of trichloris creates dense vegetation unsuitable for northern bobwhite (*Colinus virginianus*; hereafter, bobwhite), reduces plant species diversity, and alters ecosystem functions. The objectives of this study are to 1) evaluate the effects of a proper cattle grazing regime to improve bobwhite habitat and 2) develop a management guide documenting how cattle grazing can be used as a tool to reduce the density and cover of dominant grasses and thereby allow higher plant species richness. The study is taking place in Duval County, Texas, USA, between 2 pastures with a combined area of 2,500 ha. One pasture serves as the control (1,337 ha) while the other (1,109 ha) is grazed to maintain a stubble height of 30–40 cm. We placed 10 grazing exclosures and 10 25-m transects within each treatment to determine botanical composition and cover. Double sampling is conducted monthly to determine forage standing crop. Forage standing crop, plant species richness, total ground cover, and forage utilization will be estimated. We hypothesize that 1) the grazed pasture will contain more bobwhites than the nongrazed pasture, 2) plant species richness will be greater in the grazed pasture, and 3) grazing will reduce the cover of trichloris. In 2020, plant species richness varied among sampling periods and was recorded as 7.5 species/transect and 4.8 species/transect higher in the nongrazed control compared to the grazed pasture in June and August, respectively. After the end of the first year of grazing, however, there was no statistical difference in plant species richness between the 2 pastures, a result that does not coincide with our second hypothesis. Litter cover did not vary among sampling periods in the nongrazed pasture but changed in the grazed pasture. Litter cover was 9.4%, 14.3%, 14.6%, and 8.9% higher in the grazed pasture than in the nongrazed pasture in May, August, September, and December 2020, respectively. Bare ground cover changed throughout sampling periods in the nongrazed and grazed pastures. Bare ground cover was 22%, 18%, and 22% higher in the grazed pasture than in the nongrazed pasture in May, September, and December 2020, respectively. Trichloris cover did not change throughout the sampling period in the grazed pasture but varied in the nongrazed pasture. Trichloris cover was 31%, 20%, 37.5%, and 35.3% higher in the nongrazed pasture than in the grazed pasture in May, August, September, and December 2020, respectively; these results support our third hypothesis. We began the cattle grazing in May 2020 with a herd of 228 mother cows placed in the grazing treatment. After 109 days of grazing, the pasture reached the target stubble height and the herd was removed. In 2021 we began grazing in June with a herd of 337 stocker calves. Vegetation growth outpaced what the calves could eat, so we removed them after 56 days and added 300 bred cows. These mother cows grazed for another 96 days until the current utilization rate was

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met. We completed aerial surveys for both 2020 and 2021, and the results indicate that bobwhite density on the grazed pasture was about 80% higher in 2020 and 25% higher in 2021 compared to the nongrazed pasture. These findings are consistent with our first hypothesis. In theory, by reducing the trichloris cover and increasing bare ground, we are creating more usable space for bobwhites; consequently, we are recording more bobwhites in the grazed pasture. The results are preliminary, but our study has the potential to shed light on bobwhite responses to proper cattle grazing and in turn to inform decisions about managing bobwhite habitat across South Texas.

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Key words: *Colinus virginianus*, four-flower trichloris, grazing, habitat management, livestock, northern bobwhite, *Trichloris pluriflora*

NORTHERN BOBWHITE AND PRESCRIBED FIRE: A REVIEW AND SYNTHESIS

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ABSTRACT

Our understanding of the relationship between northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) and fire began with Herbert Stoddard's work in the early 20th century. Research on the topic has continued, but our application of fire is deeply rooted in Stoddard's work, even as it has become evident that fire regimes must be adapted to variable environmental conditions that are evolving with a changing landscape and climate. A comprehensive review and synthesis of the literature on this topic would help formalize research advancements since Stoddard and identify knowledge gaps for future research. Results from experiments suggest fire creates favorable local habitat conditions for bobwhite such as plant composition, bare ground, and plant structure. Frequent prescribed fire is closely tied to where bobwhite populations are at their greatest (e.g., Red Hills region of Georgia and Florida, USA). However, an empirical gap exists between patch-level conditions and the bobwhite-landscape ecology interface. For example, it is well established that a 2-year fire return interval in pine savanna ecosystems with fertile soil is best for bobwhite. But causal evidence is limited for areas of different soil types, precipitation, and past land use across the bobwhite range. We review the extant literature describing prescribed fire use for bobwhite management, focusing on documented effects of fire on life-history characteristics of bobwhite under different environmental conditions. Habitat outcomes of fire management depend on fire frequency, seasonality, scale, and interaction with other management, and different strategies should be employed depending on the environment and desired effects. Adaptive management strategies will be necessary to address the challenges of rising temperatures associated with a changing climate, which are likely to alter the conditions under which burns occur and increase the difficulty of meeting basic burn criteria. Positive public attitudes toward prescribed fire will be key to developing a policy and management framework that supports efficient prescribed fire application. Our review elucidates range-wide processes and patterns to better inform the site-specific application of fire.

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Key words: climate change, *Colinus virginianus*, Great Plains, habitat management, life history, northern bobwhite, pine savanna, policy

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The northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) has declined significantly throughout its range since at least the 1960s (Pardieck et al. 2020) and has likely declined in parts of its range since well before then (Stoddard 1931). Habitat loss and fragmentation associated with changes in land use, including plant succession, urbanization, and a shift toward agricultural and silvicultural practices that maximize commodity yield, have likely been the main drivers of this decline (Brennan 1991, Hernández et al. 2013). General bobwhite habitat requirements have been known for almost a century, and the use of fire has been well established as a tool to create and maintain a plant community favorable to bobwhite that includes a mixture of bare ground and grass, forb, and shrub cover (Stoddard 1931, Brennan et al. 1998, Cox and Widener 2008). Inconsistent and inappropriate application of prescribed fire, however, has hindered its efficacy in reversing bobwhite declines, making it paramount to build a common understanding of the relationship between bobwhite and prescribed fire throughout its range.

Bobwhite evolved in a pyrogenic ecosystem (Stoddard 1931). Prior to European settlement, lightning ignited fires across the bobwhite range as dry fuels accumulated or during periods of drought (Reid et al. 2010), maintaining grassland communities against encroaching woody species (Komarek 1965). Native American tribes used fire extensively to create landscapes for resource production, composing a mosaic of vegetation types and patches with different times since fire (Buckner 1989, DeVivo 1991, Pyne et al. 1996). Historical fire return intervals throughout much of the bobwhite range remained relatively frequent (i.e., 2–6 years; Guyette et al. 2012) until the early 1900s. It was then that government agencies attempted to ban fire use for forest protection and pine regeneration in the southeastern United States, while also suppressing fire in the Great Plains to limit risks to increasing human settlement. Moreover, increased grazing pressures that reduced fuel loads became common in the Great Plains (Fuhlendorf and Engle 2001), and decreased fire frequencies followed shifts in grazing management (Van Auken 2009). The reductions in burning in the early 20th century created conditions unsuitable for bobwhite, as the lack of fire or other disturbance allowed vegetation communities to shift to forest, resulting in a loss of food resources and cover and contributing to bobwhite declines (Brennan 1991). It was not until the 1940s and 1950s that prescribed burning for fuel reduction gained general acceptance (Pyne 1982). Since then, prescribed fire has been a common management strategy to promote bobwhite populations. However, there exists uncertainty among managers as to the optimal implementation of prescribed fire parameters across the bobwhite range.

Fire provides a multitude of benefits to bobwhite, most importantly creating habitat conditions that promote bobwhite food abundance and availability (Brennan et al. 2000), provide cover and diverse vegetation structure (Brennan et al. 1998), and increase ease of mobility (Carver et al. 2000, Cram et al. 2002). As a facultative grassland species that requires herbaceous vegetation with shrub components, bobwhite depend upon intermittent disturbance to prevent encroachment of trees that outcompete annual and perennial herbaceous plants. Historically, periodic, low-intensity fire was the primary disturbing force across the bobwhite range (Pyne 1982). Fire reduces litter and can prevent canopy closure or excessive woody plant encroachment (Fuhlendorf and Engle 2001, Vander Yacht et al. 2017, Varner 2018) and is necessary to maintain open-canopy forest types in eastern forested systems and herbaceous components in rangelands of the Great Plains.

Prescribed fire frequency, timing, and size are all known to be important parameters affecting bobwhite habitat quality (Wellendorf and Palmer 2009, Kroeger et al. 2020). Fire frequency affects the heterogeneity of vegetation structure and composition and the degree to which woody plants may encroach on and shade herbaceous vegetation beneficial to bobwhite (Stoddard 1931, Brockway and Lewis 1997, Fuhlendorf and Engle 2001). In pine ecosystems, frequent fire (occurring every 1–2 years) promotes environments dominated by grasses and forbs (Streng et al. 1996, Glitzenstein et al. 2012), providing important nesting and brood cover for bobwhite (Brooke et al. 2017). Less frequent fire (occurring every 3–5 years) promotes a greater abundance of woody plants (Streng et al. 1996, Glitzenstein et al. 2012), which can provide escape cover (Cram et al. 2002, Brooke et al. 2017, Rosche 2018). The time at which prescribed fire occurs during the year relates to plant phenology and potentially fire intensity, thereby differentially affecting plant community composition and subsequently bobwhite habitat. Dormant-season burning tends to promote and maintain low woody cover, while growing-season fire tends to reduce woody species and stimulate diversity of the herbaceous understory (Boyer 1993, Drewa et al. 2002, Knapp et al. 2009). Burn size affects the degree of patch interspersion, and thus the distance bobwhite must travel to access different food and cover sources, and patch edge-to-interior ratios, which may influence predation dynamics (Wellendorf and Palmer 2009, Kamps et al. 2017, McGrath et al. 2017).

The effects of burn parameters on bobwhite are further complicated by the fact that bobwhite resource selection varies with life stage and spatial scale (McGrath et al. 2017). Some fire regimes will produce better food resources for chicks, whereas others may produce better cover for nesting. This important nuance helps us understand how bobwhite optimize resource selection when acquiring food and avoiding predators.

Prescribed fire alone may not be sufficient to achieve substantial long-term shifts in vegetation composition and structure. However, the effects of prescribed fire can be augmented or enhanced with complementary management actions. Grazing, herbicide, mechanical vegetation treatment, and other management tactics can all influence the impact of prescribed burning on bobwhite habitat. Managers must consider the frequency, timing, and type of application of each of these management strategies. However, there is limited cohesive information available on how different management strategies interact with prescribed burning to alter vegetation patterns in bobwhite habitat.

In addition to balancing fire frequency, timing, size, and interacting effects with other management strategies, managers must contend with effects of environmental conditions on fire impacts. For example, a fire return interval that is appropriate for mesic areas may be too frequent for xeric sites (Hardy 2003, Pausas and Keeley 2014, Rosche et al. 2019), and fire frequencies that produce herbaceous-dominated communities in Ultisol flatwoods have been shown to have little effect on shrub cover in Spodosol flatwoods (Glitzenstein et al. 2003). Appropriate fire regimes will thus vary regionally but have the objective of creating a mixture of herbaceous and woody cover, while limiting the woody stratum to avoid shading the understory (Rosche et al. 2019).

Despite the relatively common use of prescribed fire, overall efforts to reverse bobwhite declines have had limited success, although there have been isolated examples of bobwhite recovery through exceptional management, including appropriate use of prescribed fire (Sisson et al. 2012). Moreover, in much of the Great Plains, fire has been viewed as a tool rather than an ecological process (Fuhlendorf and Engle 2001). This approach has often led to homogenization of fire regimes (i.e., early intensive stocking of cattle) that reduces variation in fire frequency, fire extent, and fire severity, resulting in decreased habitat for bobwhite. Prescribed fire management may be operating at scales too large or too small relative to habitat patch size or too frequent or infrequent to alter plant communities optimally for bobwhite (Williams et al. 2004, Bowling et al. 2014). Furthermore, there are few cohesive recommendations on how fire management should vary according to regional environmental conditions and to meet the needs of bobwhite across their life cycle and spatial scales. We reviewed and synthesized the literature on how fire frequency, timing, size, and interactions with other management strategies influence bobwhite ecology and provide management recommendations for these parameters under differing environmental conditions.

METHODS

We sought and reviewed relevant studies using web search engines (e.g., Google Scholar) and targeted search terms (e.g., "bobwhite," "fire," "prescribed burn," "habitat management,") and reviewed studies cited in these papers. We also used our knowledge of the extant literature to augment the web search engines (e.g., recent theses and dissertations). We reviewed direct and indirect relationships between prescribed fire and bobwhite and provided generalized conclusions and recommendations for managers based on our findings. We categorized impacts according to 4 burn parameters that managers have most control over: fire frequency, fire timing, burn size, and interaction with other types of management. Understanding how these parameters affect bobwhite demographics and life history will allow bobwhite managers to make prescribed burning decisions that better meet their objectives. We reviewed the potential effects of climate change on managers' ability to conduct prescribed burns and the human dimensions influencing fire policy and public perception. Finally, we identified opportunities for future research and challenges facing prescribed fire use for bobwhite recovery.

RESULTS

Influence of Prescribed Fire on Bobwhite

Fire frequency in mesic environments.—Effects of fire frequency on bobwhite ecology vary with region and site productivity. Studies occurring in different regions, with different soil conditions, and targeting different bobwhite life stages have reported differing bobwhite habitat use and abundance patterns related to time since fire (Table 1). On private property in Georgetown County, South Carolina, USA, McGrath et al. (2017) found that bobwhite selected for areas with longer fire return intervals during winter (1 Dec–1 Mar) than during the breeding season (1 May–1 Oct; Table 1). Nonbrooding birds may prefer more cover as they search for nest sites, as nest sites are typically within areas of greater cover compared to the surrounding area (Lusk et al. 2006). McGrath et al. (2017) suggested that a 2-year fire return interval may provide a good balance for the cover-food resource optimization problem by promoting concealing vegetation for nests while still allowing ease of mobility and decreased visual obstruction for predator avoidance. This is consistent with findings from Dougherty and Baker counties, Georgia, USA that prescribed burning creates suitable cover conditions for nesting 1 and 2 years after fire (Simpson 1972). Similarly, at Avon Park Air Force Range in south-central Florida, USA, where primary plant communities include pine flatwoods, wet and dry prairies, and pine plantations, Miley and Lichtler (2009) reported that bobwhite abundance increased on sites that received a burn the previous year but decreased after 2 years post-burn (Table 1).

The dominant vegetation at a site influences habitat outcomes of prescribed fire frequency. Kroeger et al. (2020) suggest that the discrepancy between their findings of bobwhite selection for areas 1 year since fire and the findings of Cram et al. (2002) of selection for areas 3 years since fire (Table 1) is likely due to the dominance of different grasses. Wiregrass (*Aristida* spp.) in the Sandhills region of North Carolina, USA becomes matted to the point of restricting movement as time passes since last burn, whereas bluestems (*Andropogon* and *Schizachyrium* spp.) in Arkansas, USA remain upright after senescence and provide cover for multiple dormant seasons. Frequent burning in highly-productive mesic sites is likely necessary to keep diverse ground cover intact and viable, reduce woody stem density, and maintain bare ground (Moore 1972, Lewis and Harshbarger 1986, Hermann et al. 1998).

Frequent fire alone is enough to sustain shortleaf pine (*Pinus echinata*) and loblolly pine (*P. taeda*) woodland communities (Robertson et al. 2021). In these systems,

Table 1. Time since fire for which northern bobwhite (*Colinus virginianus*) show highest habitat use or abundance.

Study	Location	Parameter studied	Time since fire with greatest positive effect
Carroll et al. 2017a	Great Plains (OK)	Habitat use	No effect
Cram et al. 2002	Ouachita Mountains (AR)	Relative abundance	3 growing seasons
Kroeger et al. 2020	Sandhills (NC)	Nonbreeding habitat use	1 growing season or ≥3 growing seasons (if recent fire occurred in dormant season)
McGrath et al. 2017	Coastal Plain (SC)	Winter habitat use	2–3 years
McGrath et al. 2017	Coastal Plain (SC)	Breeding habitat use	1–2 years
Miley and Lichtler 2009	Coastal Plain (FL)	Abundance	1–2 years
Rosche 2018	Sandhills (NC)	Breeding habitat use	2 years
Rosche et al. 2019	Sandhills (NC)	Breeding habitat use	1–2 years
Sinnott et al. 2021	Central Plains (MO)	Brood habitat use	<2 years

fire return intervals of 1–2 years are likely necessary to maintain a fire-vegetation feedback loop, in which frequent fire promotes vegetation that creates more flammable fuels, namely pine litter and grasses (Beckage et al. 2009, Varner 2018, Robertson et al. 2019). However, loblolly-shortleaf pine communities may eventually transition to hardwood forest with fire return intervals >2–3 years (Matusick et al. 2020, Robertson et al. 2021). Under these longer return intervals, pine regeneration declines, likely because of excessive competition with other woody vegetation (Yocom 1972). The ensuing loss of flammable pine needle fuels would be expected to break the fire-vegetation feedback loop and allow for hardwood encroachment. Thus, under longer fire return intervals, these plant communities may transition to ones dominated by hardwoods or woody surface vegetation, which are inadequate for bobwhite (Brennan et al. 1998, Palmer and Sisson 2017, Robertson et al. 2021).

Fire frequency in xeric and semiarid environments.— Fire management should be adapted to site productivity and ultimate climatic conditions. Fire return intervals appropriate for mesic sites may be too frequent for xeric sites. Rosche (2018) found that bobwhite in the Sandhills region selected areas primarily 2 years after fire for nesting (Table 1). Thus, shortening fire return intervals to less than 3 years could increase the proportion of bobwhite nests exposed to fire and reduce nesting cover. At the microsite scale, bobwhite strongly select for areas with greater woody understory cover (Rosche et al. 2019, Kroeger et al. 2020). A 2- to 3-year fire return interval may be optimal for maintaining herbaceous groundcover, but it is too frequent to allow sufficient development of woody understory cover for bobwhite on unproductive sites (Kroeger et al. 2020).

Bobwhite response to prescribed fire varies along a gradient of soil productivity. In semiarid rangelands, bobwhite were found to have higher densities with early successional stages on more productive sites, whereas density was not affected by successional stage on less productive sites (Spears et al. 1993). Long et al. (2014) detected higher relative abundance of bobwhite in unburned patches compared to 2-year and 4-year time-since-fire patches in a semiarid shortgrass prairie ecosystem in the panhandle of Texas, USA. Bobwhite should be considered a mid- to late successional species on less productive sites, and thus, fire management should be less aggressive in these areas (Spears et al. 1993).

In a sand shinnery oak (*Quercus havardii*) community in western Oklahoma, USA, prescribed fire applied across large portions of the landscape appeared to have minimal effect on bobwhite space use (Carroll et al. 2017*a*) and nest survival (Carroll et al. 2017*b*). Individuals were neither relatively attracted to nor repelled by different time-since-fire treatments, and there was no difference in spring dispersal movements among these treatments. These observations were similar to those of Ransom and Schulz (2007), who found little effect of fire on bobwhite density in Texas. However, Carroll et al. (2017*a*) reported that bobwhite coveys using burn treatments of 25–36 months post fire, which coincides with the time necessary for shinnery oak to recover to prefire structure (McIlvain 1954, Harrell et al. 2001), did exhibit smaller home range sizes compared to coveys using burn treatments of shorter or longer fire return intervals. Moreover, bobwhite exhibited reproductive plasticity in this system relative to time since fire. Nesting individuals would vary the dominant nesting substrate used depending on a patch's time since fire. In areas burned more recently (0–12 months since fire), nests were primarily located in shrubs, while a shift to herbaceous substrate occurred as time since fire increased (>36 months since fire). Though this shift in nesting substrate occurred due to changes in fire frequency, nest survival remained consistent across different time-since-fire patches (Carroll et al. 2017*b*). Overall, fire frequency may not have strong effects on bobwhite demographics in shinnery oak communities that exhibit rapid resprouting and structural recovery following fire.

Similarly, sand sagebrush (*Artemisia filifolia*) communities function as important areas for bobwhite in western rangelands (Tanner et al. 2015). This species has also been shown to exhibit rapid resprouting and structural recovery following fire. Plant height, canopy area, and canopy volume will return to unburned structural conditions 4 years post-fire, while plant

density remains the same 0.5–5 years post-fire compared to unburned patches (Winter et al. 2011).

These relationships between fire and vegetation response may not be consistent across the western fringe of the bobwhite range, where different types of vegetation may dominate. For example, lotebush (*Ziziphus obtusifolia*) is the primary source of fall, winter, and spring cover for bobwhite in the Rolling Plains region of West Texas (Renwald et al. 1978). However, once burned, lotebush may take 6–10 years to again become useful to bobwhite (Renwald et al. 1978). Thus, a frequent fire return interval in this region would be likely to eliminate important cover unless species like lotebush are protected from fire. However, direct management implications from other studies on bobwhite responses to prescribed fire in Oklahoma and Texas have not been definitive (Baumgartner 1946, Wilson and Crawford 1979, Carter et al. 2002, Ransom and Schulz 2007), and this area warrants further research.

Managers have virtually no control over soil moisture and water availability, yet these factors regularly influence the frequency of prescribed burning, especially on western rangelands. Successful burning depends on appropriate soil moisture conditions pre-burn and post-burn, and a lack of suitable conditions can restrict the burn window or eliminate it altogether. Damp soil is critical for protecting tree roots and microbes (Wade and Lundsford 1990). Burning under adequate soil moisture conditions may reduce damage to favorable plants for bobwhite, such as lotebush in the Rolling Plains of Texas (Renwald et al. 1978), or more effectively remove undesirable invasive plants, such as smooth brome (*Bromus inermis*; Blankespoor and Larson 1994). Managers seeking to reduce fire severity must also consider hydrologic conditions, as increased soil moisture has been shown to decrease heat transfer to soils (Badía et al. 2017).

Fire timing.—Here, we refer to "fire timing" as the period within the year that prescribed fire occurs. "Dormant season" refers to the period in which most plants are dormant, and "growing season" refers to the period during which most plants are actively growing. The timing of these seasons varies regionally. Lightning-ignited fires in the southeastern United States were historically common throughout the summer and peaked during May at the transition point between the dry spring and wet summer, when lightning incidence was at its highest (Knapp et al. 2009). Dormant-season fires were also common, likely the result of burning by Native Americans and early European colonists (Stambaugh et al. 2017). Prescribed burns in the Southeast on lands managed for bobwhite overwhelmingly occur during late dormant season or early growing season to avoid direct impacts on nesting birds, particularly bobwhite, and other wildlife (Knapp et al. 2009, Nowell et al. 2018). However, prescribed burns in the growing season (late spring and early summer) have increased in popularity as research has emerged demonstrating that this coincides with the historical period of lightning-ignited fire (Cox and Widener 2008). Fire timing may present unique challenges to managers, as the ability to burn depends on fuel loads and weather conditions. Managers of shortleaf pine stands in Arkansas, for example, must contend with higher amounts of live fuels, lower amounts of fine (1 hour) fuels, lower total fuel loads, higher temperatures, and more unpredictable rainfall in the growing season compared to the dormant season (Sparks et al. 2002).

The primary differences in ecological effects of fire season are related to differences in fuel load, and thus fire intensity, and differences in plant phenology or growth stage at the time of fire (Knapp et al. 2009). In general, early growing-season burns tend to favor an understory with greater cover of grasses and forbs, whereas dormant-season burns favor sprouting of woody stems and shrubs (Boyer 1993, Brockway and Lewis 1997, Drewa et al. 2002, Knapp et al. 2009, Robertson and Hmielowski 2014). Studies at the Tall Timbers Research Station in Tallahassee, Florida, have found only subtle population-level effects of dormant-season versus growing-season burns on bobwhite (Brennan et al. 1998, 2000; Carver et al. 2000), but study authors acknowledge that much additional research is needed to fully understand long-term effects (Brennan et al. 2000). Fire timing in the context of wildlife management is certainly worth consideration as it affects bobwhite food resources, cover, and nesting success.

The timing of prescribed fire directly affects vegetation important to bobwhite for food provision. Brennan et al. (2000) found that sites burned in the growing season (May–Jun) produced more ragweed (*Ambrosia* spp.) and panicgrass (*Panicum* and *Dichanthelium* spp.), whereas sites burned during the dormant season (Feb–Mar) produced more legumes and oak (*Quercus* spp.) sprouts. Both ragweeds and panicgrasses are thought to be valuable plants for bobwhite, providing desirable food and structure for overhead cover (Korschgen 1948, Hurst 1972, Robel et al. 1979, Peters et al. 2015). Legumes, on the other hand, may provide enhanced forage quality over grasses due to their superior mix of essential amino acids (Peoples et al. 1994). Growing-season fire additionally produces greater insect prey abundance during brood-rearing months (Brennan et al. 2000). Availability of insects as a food resource is critical for bobwhite chick growth and survival (Nestler et al. 1942, Hurst 1972).

Fire timing also affects the availability of different components of cover for bobwhite. Dormant-season burns promote woody understory growth important for bobwhite cover. In the Sandhills region of North Carolina, Kroeger et al. (2020) found that bobwhite selected upland areas ≥3 growing seasons since fire if the recent fire occurred in the dormant season. Rosche et al. (2019) found that bobwhite selected for areas burned in the dormant season of the same year but avoided areas burned in the current growing season, likely because of a lack of woody understory important for escape, nesting, and thermal cover. This is congruent with the additional finding of Kroeger et al. (2020) that bobwhite selected upland areas 1 growing season since fire regardless of burn season. On oldfields in East Tennessee, USA, dormant-season fire increased coverage of native warm-season grass and decreased coverage of grass undesirable for bobwhite (Gruchy and Harper 2014), consistent with other studies conducted in the South

(Whitehead and McConnell 1980, Manley 1994). In central Florida, Miley and Lichtler (2009) reported marginally higher bobwhite abundance following dormant season burns than growing season burns. However, other studies report that early growing-season fires are more effective than dormant-season fire in promoting native grass and forb growth and creating bare ground to allow for effective bobwhite movement (Waldrop et al. 1987, Streng et al. 1993, Glitzenstein et al. 1995). Growing-season fires can also maintain desirable vegetation structure as much as 6 months longer than dormant season fires (Cox and Widener 2008).

In southern Texas where invasive grasses dominate many rangelands (Wied et al. 2020) indicative of bobwhite habitat, species such as buffelgrass (*Cenchrus ciliaris*) respond positively to dormant-season prescribed fires (Kuvlesky et al. 2002, Tjelmeland et al. 2008). Such herbaceous invasive species' responses to prescribed fire can reduce bobwhite habitat and present a novel challenge for managers when implementing prescribed fire management in semiarid rangelands within the bobwhite distribution. In cases such as these, additional management strategies are necessary to revegetate infested rangelands with native vegetation. Sequentially applying herbicide, prescribed fire, and reseeding with native plants has been shown to increase productivity on range sites (Masters and Nissen 1998). Fire timing is still critical in this integrative management approach. Fire should be applied when the undesirable plants are in their vegetative stage of development and are more vulnerable to fire and native vegetation is dormant.

There is some risk of nest destruction during growing-season fires. The specific month during which burning occurs is important because bobwhite nesting varies significantly across the growing season. On Fort Bragg in North Carolina, Rosche (2018) documented 2 nests (6.7%) burned by prescribed fire during June and July. Twenty-three documented nests (77%) were located within units that were burned at least 2 years prior, putting them at greater risk of being destroyed by prescribed fire occurring on a return interval shorter than 3 years. The risk of nest destruction by fire was approximately proportional to the percentage of study area burned during the nesting season. Similarly, Martin (2010) found that dormant-season fires had positive effects on nest survival compared to growing-season fires, which resulted in direct nest losses. Fires conducted during the growing season may also reduce the area of available nesting habitat and increase predator search efficiency. Interestingly, both dormant season and growing season fires produced better outcomes on nest survival than no fire. Rosche et al. (2021), on the other hand, found that early growing-season (Apr–May) prescribed fire posed relatively low risk to bobwhite nests on Fort Bragg. In their study, most nests were in 2-year-old rough not scheduled to be burned on a predominantly 3-year fire return interval, and thus were not at risk of destruction from prescribed burning. A more frequent fire return interval would be likely to put nests at greater risk of destruction in this area. However, the authors note that nest site selection in relation to time since fire varies with soil productivity. For example, a 2-year fire return interval would pose less risk to bobwhite in areas with high soil productivity, where bobwhite commonly nest in 0- or 1-year time-since fire areas (Simpson 1972). Other studies have shown few strong effects of fire timing on direct mortality, breeding success, or survival of birds (Engstrom et al. 1996, Cox and Widener 2008, Carroll et al. 2017*b*). As managers experiment with varying seasonality of burning, future research should evaluate direct and indirect effects on bobwhite habitat suitability.

Burn size.—The size of a prescribed burn influences bobwhite ecology through its effects on total area of a landscape burned, the ratio of burn edge to interior, which decreases as burn size increases, and the amount of resource interspersion, which also decreases as burn size increases. Wellendorf and Palmer (2009) reported that when comparing burn sizes of approximately 2.25 ha and 8 ha, smaller fires were associated with higher nest production, greater bobwhite autumn density, and lower risk of mortality in some years but not in others. Similarly, Martin (2010) found that for experimental burn sizes of 10 ha, 20 ha, and 40 ha, bobwhite densities were consistently greatest on plots with smaller fires. Martin (2010) proposed that foraging bobwhite may have greater difficulty escaping from avian predators on larger burn patches where postfire cover is sparse. Furthermore, the smallest fire size treatment in the study produced more chicks per hen than the 2 larger treatments.

In line with these two studies, McGrath et al. (2017) found selection patterns for smaller burn sizes. For the burn sizes observed in their study, odds of use for nonbrooding bobwhite increased linearly by 1.8 times for every 15.7-ha reduction in burn size (95% credible interval [CrI] = 1.7–1.9). Brooding birds also selected for areas with decreasing burn sizes at the second-order scale. However, at the third-order scale, brooding birds showed the highest selection for mid-range burn sizes (~79 ha). The authors suggest that as burn size increases, bobwhite food availability may increase while ability to avoid predators may decrease. Their findings could support the notion that bobwhite optimize habitat selection based on predator avoidance and food availability.

Larger burn sizes (>80 ha) appear to have mixed effects on bobwhite. Comparing average burn sizes of 85.87 ha and 1220.10 ha on a property consisting mostly of prairie and pine flatwoods, Kamps et al. (2017) found that apparent chick survival was positively correlated with amount of home range burned during the previous dormant season. Burned area also had an indirect positive effect on chick growth by reducing home range size. The authors attributed these findings to greater invertebrate abundance in areas with larger burns, but they did not measure invertebrate abundance. However, there may be tradeoffs between chick survival and adult survival. Kamps (2015) reported that as fire size increased, larger portions of individual bobwhite home ranges were burned, leading to increased movement and a reduction in adult survival. Miley and Lichtler (2009) found that bobwhite abundance increased more after larger fires (where at least

40% of an area was burned) than smaller fires. However, they did not investigate the effects of differing burn patch sizes for a consistent proportion of area burned. Further research should quantify how variable burn sizes affect bobwhite movement, food availability, and predation at different scales to better understand if and how these factors drive differences in bobwhite demographics and habitat selection patterns. The ratio of burn size to overall amount of habitat should also be investigated. We hypothesize that optimal individual fire sizes for bobwhite should be scaled to overall habitat amount. Quantifying the scalar function is an opportunity for future research.

Bobwhite response to different burn sizes is likely to vary regionally and by dominant vegetation type. In a sand shinnery oak community in western Oklahoma, landscape-scale fire had limited effects on short-term bobwhite movement and space use (Carroll et al. 2017*a*). Moreover, in a sand sagebrush community in western Oklahoma, bobwhite density was not shown to be different in pastures (406–848 ha) managed with patch-burn grazing compared to unburned, seasonal grazing (Holcomb et al. 2014). Similarly, burn sizes ranging from 57.1–109.7 ha had limited effects on bobwhite covey space use within the Rolling Plains of Texas, if residual woody plant species (primarily lotebush) remained present within the burn patches (Renwald et al. 1978). However, when coupled with grazing practices (i.e., pyric herbivory), positive responses in bobwhite densities have been shown to occur with burns ranging from 0.1–3.9 ha in size within semiarid rangelands, likely due to increases in vegetation heterogeneity (Grahmann et al. 2018). Rangelands within the western portion of the bobwhite distribution evolved with fire as an ecological process to maintain certain stable states and vegetation communities (Boyd and Bidwell 2001, Fuhlendorf and Engle 2001). Even within the context of extreme values of fire patch size in these rangelands (e.g., the East Amarillo Complex Wildfire [~367,000 ha]), there was little evidence to suggest any demographic response to this large fire patch size, and space use changed only marginally (Warren 2014). In general, it is likely that behavioral plasticity allows bobwhite to adapt to changing habitat conditions related to fire events, even across a wide range of fire patch sizes in western rangelands (Carroll et al. 2017*b*)

It is important to note that practical resource constraints may limit the flexibility managers have in applying fine-scale prescribed fire. For example, the average prescribed burn size on public lands from observations in the Federal Wildland Fire Occurrence database (Goodman 2016) is 226 ha (standard deviation = 839 ha; Mason and Lashley 2021), meaning many burns occur on a scale significantly larger than that investigated by most of the studies discussed in this review. Practitioners are limited by equipment, time, and personnel, and thus may be forced to burn at the largest, most efficient scales possible, and to burn adjacent blocks concurrently (Mason and Lashley 2021). While managers with ample resources often burn at much smaller scales on private lands where quail is a priority, more research is warranted to assist public land managers and others in finding ways to cost effectively apply prescribed fire at finer scales appropriate for bobwhite.

Interaction of prescribed fire and other management.—Prescribed burning has interacting effects with other management strategies on bobwhite ecology. When used appropriately, herbicide application, grazing, mechanical vegetation treatment, and reseeding have the potential to enhance or complement the effects of prescribed burning on bobwhite habitat. On native grassland and intensively managed sites in southwestern Missouri, USA, for instance, bobwhite showed stronger selection for sites that were grazed and burned within 2 years relative to sites that were only grazed or only burned (Sinnott et al. 2021). Coupling grazing and burning promotes greater heterogeneity of vegetation composition and structure on grasslands. A shifting mosaic emerges as more intensive grazing occurs on certain patches of a burned area, and new burns further change the landscape (Fuhlendorf and Engle 2004, Veen et al. 2008, Grahmann et al. 2018). Sinnott et al. (2021) proposed that these heterogeneous, diverse prairie plant communities facilitate brood use through their provisioning of adequate cover, bare ground, and abundant invertebrates, which benefit juvenile foraging, growth, mobility, and survival (Hurst 1972, Taylor et al. 1999, Kamps et al. 2017). Grazing under appropriate stocking densities in conjunction with prescribed burning may also be used to effectively manage monotypic nonnative grasslands for bobwhite in semiarid environments by maintaining pressure on aggressively growing plants like bunchgrasses (e.g., *Cenchrus ciliaris*; Grahmann et al. 2018).

Although frequent prescribed burning alone may be sufficient to sustain shortleaf and loblolly pine communities (Robertson et al. 2021), additional management strategies are often necessary to maintain open-canopy forests to compensate for external constraints on the timing and frequency of prescribed fire and land use histories (Bragg et al. 2020). These strategies include timber management (Mitchell et al. 2006), mechanical and chemical treatment of understory vegetation (Welch et al. 2004, Burke et al. 2008), or planting and fertilizing native species (Knapp et al. 2011). Timber density may vary significantly even under consistent fire applications, and this variation has a relatively large effect on bobwhite abundance (Little et al. 2009). Therefore, reducing canopy coverage of timber and frequent prescribed fire may both be necessary to maintain or restore bobwhite populations.

In areas of severe hardwood encroachment, a one-time application of herbicide in conjunction with post-spray burning may be the most effective means of restoring suitable bobwhite habitat, as hardwoods recover quickly via root or collar sprouting after mechanical treatment alone (Welch et al. 2004, Burke et al. 2008). However, the choice of when to burn post-spray should be carefully considered because burning too soon may limit fuels and make pine regeneration difficult to control.

In western rangelands where invasive grasses are of particular concern, herbicide and reseeding may be used in

conjunction with fire to reduce the dominance of invasive plants. Application of herbicide followed by prescribed burning and seeding with warm-season grasses has been shown to reduce biomass of invasive grasses such as smooth brome and leafy spurge (*Euphorbia esula*) while increasing grass species richness, relative to no treatment (Masters and Nissen 1998, Link et al. 2017). Applying glyphosate before burning and seeding was significantly more effective at reducing smooth brome biomass than burning and seeding alone (Link et al. 2017). Overall, the effects of prescribed fire may be augmented, enhanced, or suppressed in conjunction with other management strategies, and the full range of management tools should be considered to meet objectives.

Implications of Global Climate Change on Bobwhite Management and Fire

Historically, variation in weather and climate have impacted bobwhite and other wildlife in several ways. Weather cycles and their effects on bobwhite have been studied and are known to vary regionally (Lusk et al. 2001). In the southwestern portion of the bobwhite range, for example, alternating wet and dry year cycles associated with the El Niño Southern Oscillation (ENSO) and dynamic fuel loads account for the bulk of interannual variability in the amount of area burned (Ryan et al. 2013). In the Southeast, however, where fuels are abundant, fire plays a major role in maintaining vegetation conditions conducive to bobwhite, but changes in fire extent and wildfire risk are also linked to the ENSO cycle (Brenner 1991, Chiodi et al. 2018). During La Niña years, the Southeast experiences reduced precipitation, which can increase fire risk, whereas El Niño years typically bring above-average precipitation and a reduced fire risk. This, in turn, impacts the interaction of vegetation conditions, predator-prey dynamics, and management prescriptions. Despite long-term management under these stochastic weather conditions, climate change presents added challenges to resource management due to its directionality and potential to influence the extent, duration, and intensity of weather patterns (Kupfer et al. 2020). Climate change is generally expected to create warmer, drier conditions in the west-southwest portion of the bobwhite range (Guyette et al. 2014), resulting in increased droughts. Meanwhile, warmer, wetter conditions are expected in parts of the Southeast (Guyette et al. 2014), resulting in more intense weather events (e.g., hurricanes, rainfall). These challenges hit at the heart of fire application and bobwhite management in multiple ways.

Investigations conducted by the Intergovernmental Panel on Climate Change (IPCC 2021) suggest that a heightened integration of climate change adaptation strategies into resource management is warranted for preserving ecosystem integrity and conserving species. Given that bobwhite are so tightly linked to fire, the need to assess the role that climate change might have on their future conservation and management is apparent. We lack an understanding of the inherent risk and extent of potential impacts of climate change on bobwhite. As such, we must be intentional in our approach to research into fire effects on vegetation and bobwhite germane to climate change as well as be prescriptive and objective-oriented in our approach to management. At this point we know some of the ways that climate change will influence bobwhite as it relates to changing fire conditions.

Ecosystem function is influenced by the intersection of climate, management timing, and vegetation response. The role of fire in shaping vegetation is critical, yet regionally variable and contingent on edaphic conditions and precipitation. Given that prescribed burns require the proper alignment of time, resources, and suitable weather conditions, changing climate will unequivocally alter the effectiveness of fire and fuel management; accordingly, we must adapt how we manage fire and fuels (Kupfer et al. 2020, Gao et al. 2021).

The application of prescribed fire in the future does not come without challenges. Escalating temperatures will change fire regimes and our application of controlled burns as lower soil and fuel moisture will result in longer fire seasons and increased fire risk (Mitchell et al. 2014, Kupfer et al. 2020, Gao et al. 2021). Kupfer et al. (2020) contended that the practical constraints of rising temperatures on prescribed burning activity present a significant challenge and suggested that meeting basic burn criteria will become increasingly difficult over time. Furthermore, the warmer conditions are expected to increase wildfire frequency, intensity, and extent throughout much of the landscape (Price and Rind 1994, Gillett et al. 2006, Gao et al. 2021), presenting an additional challenge to prescribed fire activity. Moreover, increases in unprecedented droughts are projected over the next century within the American Southwest and central Great Plains (Cook et al. 2015). Wildfire activity is generally expected to increase in response to changing temperature and precipitation patterns within the bobwhite distribution, though this pattern will vary across the distribution (Liu et al. 2013, Guyette et al. 2014). Variability in drought conditions is also predicted to increase in North America (Cook et al. 2019). Decreases in fuel loads due to drought conditions can occur (Brown et al. 2005), making implementation of prescribed fire difficult in already semiarid systems. Moreover, within the southern Great Plains, wildfire activity is greatest after average or above-average precipitation conditions followed by drought conditions (Scasta et al. 2016), illustrating the challenges that drought variability may create for fire management.

Given the less desirable and less predictable weather conditions associated with climate change, land managers are projected to have fewer opportunities to conduct prescribed burns in the United States. For instance, recent research indicates that in some areas of the Southeast, fewer than 10–15% of summer days will remain viable for conducting prescribed burns by the end of the century under the most severe climate change projections (Kupfer et al. 2020). Those remaining available burn days in the growing season are expected to be more variable and less predictable, making it more difficult for resource managers to prepare and plan (Kupfer et al. 2020). As the likelihood of severe droughts amplifies wildfire occurrence and simultaneously restricts

burning opportunities, we can expect heightened public apprehension about prescribed fire and increased scrutiny for degradation of air quality when burns are conducted.

Despite the unknowns surrounding climate change effects, applying an adaptive management approach to changing fire regimes will help reduce ecosystem vulnerabilities and promote desirable conditions for bobwhite (Millar et al. 2007, Joyce et al. 2009). Taking advantage of prescribed fire in conjunction with other management practices (e.g., supplemental feeding, predator control) may buffer bobwhite populations during poor years and harsh conditions (e.g., inclement weather) and overcome shortfalls in prescribed fire application due to changing fire conditions from year to year. As the climate in the bobwhite range changes, research that captures how extremes influence fire application, habitat responses, and bobwhite life history should be prioritized.

Human Dimensions of Prescribed Fire

Continued use of prescribed fire in bobwhite management is contingent on public policies and regulations across the bobwhite range. Most of the states encompassing the bobwhite range have substantial prescribed fire programs, supported by state policies that encourage prescribed fire via reducing liability for burners, "Right to Farm" legislation supporting prescribed burning as a land use right, and state and federal programs that aid landowners (Brennan et al. 1998, Burger et al. 2006, Ryan et al. 2013). Challenges remain for the continued use of prescribed fire, however. Social acceptance for prescribed fire is surprisingly strong (studies report >79% public acceptance across the United States; McCaffrey 2006, Polo et al. 2020). This acceptance varies across the bobwhite range, with high acceptance in many rural communities near prescribed burns where habitat is also most prioritized. Escaped prescribed fires, smoke incidents in cities and on major highways, and greenhouse gas regulations all have the potential to reduce public support and erode state and federal protections. The engagement of bobwhite advocacy and management groups offers some promise to maintain support for prescribed fire.

Prescribed burn associations (PBAs) are increasing throughout much of the bobwhite's western distribution in the southern Great Plains and are crucial to providing information about prescribed fire and facilitating prescribed burning activity on private rangelands (Toledo et al. 2014). Lack of training and lack of equipment are 2 common reasons why private landowners in western rangelands decide not to use prescribed fire as a management tool (Polo et al. 2020). The local land managers and private landowners who make up the PBAs work together to promote and provide support for local prescribed fire activity and offer a unique social construct for continuing prescribed fire practices in parts of the bobwhite distribution. An example, the Edwards Plateau Prescribed Burn Association in Texas, which started in 1997, now has >300 members and works on >150,000 ha as of 2015 (Twidwell et al. 2013). Belonging to a PBA is a strong predictor of whether a landowner has an increased probability of using prescribed fire in these rangelands (Stroman et al. 2020). These associations will continue to be an important catalyst for implementation of prescribed fire in the western portion of the bobwhite distribution.

Challenges and Research Needs

Further research is needed to comprehensively understand the effects of prescribed fire on bobwhite ecology and how these effects vary across the bobwhite range (Table 2). Almost no research has been done outside of the historical longleaf pine (*Pinus palustris*) range or the rangelands of the Great Plains. The ideal fire return interval will vary by region, and more research is needed to understand what interval is best for what area. Similarly, it is unclear how fire timing should vary across the bobwhite range. More research is also needed to better understand the effects of different burn sizes at different management scales on bobwhite demographics. Researchers should quantify how burn size at different scales affects invertebrate prey abundance and predation risk, but more importantly, how fire size, timing, and frequency interact to affect bobwhite demography.

Rising temperatures associated with climate change may pose practical constraints on fire activities. Adaptive management strategies will be needed to prepare for a future in which meeting basic burn criteria becomes increasingly difficult, especially during the growing season (Kupfer et al. 2020). Moreover, research on the effects of prescribed fire on thermal landscapes is largely lacking (Elmore et al. 2017). As discussed earlier, fire alters the vegetation structure and composition within a patch, which in turn will alter the thermal landscape (Anthony et al. 2020, Londe et al. 2020) and may reduce thermal refuges under changing climate scenarios. Linking climate-change induced effects on bobwhite life history to challenges and restrictions on prescribed fire will be critical to long-term conservation of bobwhite populations.

Finally, necessary policy changes to allow for efficient and

Table 2. Research needs for northern bobwhite *(Colinus virginianus)* in relation to prescribed fire.

Research question or project
A manipulative experiment to address range-wide variation in fire frequency, fire season, and burn timing. Ideally, the experiment would explore the interactive effects of each factor.
What are the impacts of exotic and invasive plants on fire management for bobwhite?
How does prescribed fire interact with other disturbances and land uses such as grazing?
How does the future climate-constrained burn window affect plant communities and bobwhite demography?
What are the tradeoffs among fire surrogates such as mechanical treatments, herbicides, and grazing for bobwhite habitat demography?
What are the direct and indirect effects of prescribed fire on the spatial and population ecology of the masked bobwhite (*Colinus virginianus ridgwayi*), and how can these relationships help guide future recovery plans?

appropriate fire management must be identified. Prescribed fire is a necessary element to bobwhite management and a tremendous diversity of other animals and plants within the bobwhite distribution (Brennan et al. 1998, Engstrom and Palmer 2005). Prescribed fire policies and regulations are state based, so the diversity of challenges within the native bobwhite range will be great. Restrictions on burning near the wildland-urban interface and in areas with limited prescribed fire windows will be a major challenge in long-term conservation efforts (Ryan et al. 2013). Looking beyond overcoming burn restrictions, there exists an emerging opportunity to increase prescribed fire through new state and federal policies which will increase funding for prescribed fire, fire training, and fire education as well as mechanical treatments to mitigate wildfire risks. Given the importance of fire to bobwhite, policy synthesis and additional research are urgently needed to ensure that conservation of species is included in fire policy outcomes.

To overcome uncertainty surrounding prescribed burning, developing invigorated decision-support tools that allow for better prediction of smoke transport and ensuring safety should be prioritized (Hiers et al. 2020). Moreover, prescribed burn associations offer an important platform for working collectively to provide support for prescribed fire implementation (Toledo et al. 2014, Polo et al. 2020). Last, engagement between wildlife biologists and fire managers with state and federal regulators should be emphasized to better integrate the latest science with pragmatic application of fire.

MANAGEMENT IMPLICATIONS

Prescribed fire managers charged with considering bobwhite objectives have several critical variables to consider when planning burns—fire frequency, fire timing, burn size, and interactions with other management—in addition to the essential safety precautions. Our implications assume bobwhite are the primary objective while recognizing that other objectives and constraints exist. Principally, the ideal fire regime to maximize bobwhite populations maintains a plant community dominated by forbs (>50%), moderate grass cover (25–50%), 15–30% shrub cover, and minimal litter on the ground. Thus, managers must balance burning frequently enough to create and maintain the aforementioned plant community without removing so much cover as to negatively affect survival. Local conditions should dictate the optimal fire frequency, timing, and scale; however, we offer some best management practices to achieve suitable bobwhite habitat. A 2-year fire return interval is ideal on mesic sites in temperate climate zones, especially in the presence of aggressive tree species such as sweetgum (*Liquidambar styraciflua*); otherwise, a midstory develops that rapidly reduces bobwhite habitat. On sandhill sites or other xeric environments that lack a strong invasive tree component, an average return interval of 3 years, with some areas allowed to go 4–5 years between burns to allow for development of shrub cover, may create favorable conditions. In semiarid or arid environments, even longer fire return intervals may be warranted to allow important native food and cover plants to recover. In the maintenance phase of management (i.e., bobwhite population meeting target density), prescribed fire should occur during the late dormant through the early growing season. Pulses in predatory hawk populations during migration should be a consideration for burn timing (Rectenwald et al. 2021). We recommend altering the seasonality of burns across years for a given burn unit and spatially among burn units within years to minimize the homogenization of vegetation. During restoration, burning outside this window to reduce fuels and kill hardwoods is acceptable. Outside of western rangelands where fire size has limited effects on bobwhite, individual fire sizes should be the smallest possible given operational constraints. The composition of the landscape should be a mosaic of recent burns and less recent burns such that any given point on the landscape is proximal to multiple seral stages. Other management strategies (e.g., herbicide, grazing, mechanical treatment, reseeding) should be integrated with fire management when appropriate to achieve desired vegetation outcomes.

Climate change will affect bobwhite and other wildlife. Learning to adapt to this new reality, mitigating risks associated with wildfires, and overcoming impediments to implementation of prescribed burns will require intentional, decisive action from policy makers and resource managers. Operationally, the main threat to prescribed fire use for bobwhite is the shrinking burn window. Thus, we recommend establishing habitat cooperatives among well-managed private and public lands to maintain or increase burned area in the face of climate change.

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NORTHERN BOBWHITE RESPONSE TO CONTROL OF RED IMPORTED FIRE ANTS IN THE GULF COAST PRAIRIE OF TEXAS

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ABSTRACT

The population decline of northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) on the Texas Gulf Coast Prairie, USA is largely attributed to habitat loss. However, red imported fire ants (*Solenopsis invicta*) occur throughout the region and are considered a possible contributing factor to the bobwhite decline. The objectives of our study were to determine the influence of red imported fire ants on bobwhites by comparing bobwhite nest success, survival, and density between sites treated with fire ant bait (treatment) and reference (control) sites. Our study was conducted on 3 private ranches in Goliad and Refugio counties, Texas. Each ranch contained 2 paired experimental units that consisted of a treatment and control site (500 ha each). The treatment sites received an aerial application of fire ant bait (Extinguish® Plus) during April 2018, whereas the control sites were not treated. We estimated mound density by counting fire ant mounds using distance sampling. We used radio-telemetry to monitor bobwhite nest success and survival, and we estimated bobwhite densities using distance sampling via helicopter surveys. Fire ant mound density decreased through time on both treatment and control sites. However, fire ant mound density was lower on treatment sites than control sites, indicating the insecticide was effective at decreasing fire ant mound density. Bobwhite survival, nest success, and density did not statistically differ between control and treated sites either pre-treatment (2017) or post-treatment (2018), but survival and nest success metrics were numerically higher in treated units. Bobwhite survival remained relatively stable in the treatment units 4 weeks after application but decreased in the control units. Following treatment, apparent nest success in the treated units increased by 37.4% while nest success in the control units decreased by 35.2%. Bobwhite populations were low in this ecoregion, which influenced our ability to trap and monitor many bobwhites or monitor many nests. In addition, it may be possible that repeated, annual treatments for fire ants are necessary for a benefit to accrue and be observed in bobwhites. Our results indicate that there may be potential benefits to bobwhites from fire ant reduction that deserve further research attention.

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The northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) is an important gamebird that has declined throughout its geographic distribution (Brennan 1991). Bobwhites are a significant economic and recreational species for hunting, birding, and photography (Johnson et al. 2012). Over the last 30 years, bobwhite populations have exhibited a steady decline, which is of particular concern to property owners, land managers, and sportspeople (Brennan 1991, Johnson et al. 2012). Although bobwhite populations in some regions of Texas, USA generally are considered relatively stable (Brennan 2007), the Gulf Coast Prairies and Marshes (hereafter, Gulf Coast Prairie) is an ecoregion of Texas (Gould 1969) where bobwhite populations have experienced population declines (Perez 2007).

There are 2 leading hypotheses concerning why bobwhites have declined in the Gulf Coast Prairie: habitat loss, and impacts from the nonnative red imported fire ant (*Solenopsis invicta*; hereafter, fire ant). Most ecologists and managers agree that the most significant reason for the decline of bobwhites has been the loss, degradation, and fragmentation of their habitat (Perez 2007, Hernández et al. 2013). In the Gulf Coast Prairie, 3.6 million ha have been lost to development from presettlement times to 1999, while the remaining land has succumbed to increasingly intensified agriculture and nonnative plant invasions (Lehmann 1941, Allain et al. 1999). Although habitat loss may be the ultimate factor, it is possible that invasion by fire ants could be a contributing factor in the population declines given that this ant is widespread throughout the region and known to cause bobwhite mortality (Allen et al. 1993, 1995, 2000).

Fire ants were accidentally introduced from South America to Mobile, Alabama, USA in the 1930s and have successfully invaded one-quarter of the U.S. mainland (Vinson and Sorenson 1986). When fire ants invade an area, these ants have the potential to cause both direct and indirect impacts on avian species (Allen et al. 1994, 1995). For example, depredation by fire ants can be a source of direct nest loss for ground- and shrub-nesting birds (Mueller et al. 1999, Allen et al. 2004). Nests are especially vulnerable to fire ants when chicks start to pip out of their shells (Johnson 1961, Mitchell 1989). If chicks are not stung to the point of mortality, fire ants can affect body mass and overall health of the bird. Giuliano et al. (1996) documented that chick body mass was negatively affected when the birds were exposed to 200 ants for 60 seconds. Mueller et al. (1999) linked increased fire ant activity in the nest to decreased probability of bobwhite chick survival to 21 days. In addition, several studies have documented adult bobwhite disturbance (e.g., ant bites) and mortality as a result of fire ants (Travis 1938, Johnson 1961, Dewberry 1962).

Fire ants also can have indirect effects on bobwhites (Vinson 2013). Both bobwhites and fire ants consume insects as a food source throughout the year, and insects are especially critical food items during the first few weeks of life for gamebirds (Jones 1963, Hurst 1972, Rumble et al. 1988, Savory 1989, Hagen et al. 2005). Several studies have demonstrated the ability of fire ants to displace and outcompete other invertebrates (Glancey et al. 1976, Hooper 1976, Burns and Melancon 1977, Morril 1978, Lopez 1982, Summerlin et al. 1984, Vinson and Scarborough 1991, Porter 1992). Porter and Savignano (1990) documented that native ant species richness was 70% lower and total number of native individuals declined by 90% in fire ant infested areas. Morrow et al. (2015) suggested that the reduction of invertebrate abundance by fire ants negatively affected brood survival of Attwater's prairie-chickens (*Tympanuchus cupido attwateri*), an endangered galliform species whose chicks have similar food habits to those of bobwhite chicks (TPWD 2017*a*). They reported that Attwater's prairie-chicken broods located in areas with higher invertebrate abundance had a greater probability of survival than broods located in areas with lower invertebrate abundance. Probability of brood survival was >2 times higher for broods that spent all of their time in fields treated for fire ants compared to those that spent no time in these areas (Morrow et al. 2015).

Research on the effects of fire ants on bobwhite populations is ambiguous. For example, Allen et al. (2000, 2004) documented that bobwhite abundance decreased following fire ant invasion into an area although these results may have been confounded by the study area habitat, which was dominated by bermudagrass (*Cynodon dactylon*). Johnson (1961) suggested that fire ants did not affect bobwhite production. Brennan et al. (1991) documented a 10-fold increase in bobwhite coveys found per day following 13 years of habitat management on a study site in Mississippi, USA, even though fire ant mound density was high (200/ha). This finding suggests that even in areas infested with fire ants, bobwhite populations can persist and have the potential to increase if habitat is managed.

Despite the number of studies that have been conducted attempting to link declines of upland gamebirds with fire ants, the impact that fire ants can have on galliform populations remains uncertain. There are 2 potential reasons for this. First, studies have occurred during different seasons and employed different methodologies, which may explain why studies fail to yield comparable results (Travis 1938, Johnson 1961, Dewberry 1962, Mitchell 1989, Allen et al. 1995, Giuliano et al. 1996, Pedersen et al. 1996, Mueller et al. 1999, Allen et al. 2000, Morrow et al. 2015). Another reason could be that the effects of fire ants on bobwhites could differ by scale of observation. For example, at the individual (point-of-use or point-in-time) scale, bobwhites (especially chicks) may be negatively affected, particularly when in close proximity to fire ants (Mueller et al. 1999). At the population (pasturewide) scale, however, the negative effects experienced by individuals may be canceled given the compensatory nature of this *r*-selected species. Such scale-dependent phenomena (i.e., detrimental effects at the individual scale but neutral effects at the population scale) have been documented regarding bobwhite survival and nest success. For example, depredation is the primary cause of nest failure for bobwhites (Stoddard 1931, Newton 1998, Rollins and Carroll 2001) and a major source of mortality at all life stages for bobwhites (Rollins and

Carroll 2001). However, several studies indicate that predator control to increase bobwhite populations has had little to no population effect (Beasom 1974, Guthery and Beasom 1977, Lehmann 1984, Palmer et al. 2005, Rader et al. 2007, Ellis-Felege et al. 2012). One reason why bobwhite populations are able to persist despite such high mortality is their tendency to renest, which increases the likelihood of nest success (Hernández and Peterson 2007). Another reason may be the compensatory nature of mortality in bobwhites. Guthery (2002) suggested that reducing one source of mortality was likely to increase the probability of another, resulting in the cumulative effect of predators even when the depredation sources change spatially and temporally. Thus, although reducing predator numbers could increase survival of a nest or individual, it does not appear to translate into a population-level effect. This same phenomenon also could apply to the relationship between fire ants and bobwhites. Other studies have not examined the effects on bobwhites at both the point-of-use and pasture scales. There is continued controversy among scientists as to whether fire ants are the ultimate cause of the bobwhite decline, particularly in the Gulf Coast Prairie.

The objectives of our study were to 1) determine the effect of fire ant density on nest success and bobwhite survival (point-of-use scale) and 2) document changes in bobwhite density following application of an aerially applied insecticide to reduce fire ant densities (pasture scale). Both sets of results were examined as a test for scale-dependent effects of fire ants on bobwhites. We hypothesized that 1) fire ants would negatively affect nest success and bobwhite survival because fire ants can invade bobwhite nests and cause direct mortality of adults and 2) aerially applied insecticide would reduce fire ant densities, but bobwhite densities would remain unaffected because of the compensatory nature of mortality factors in bobwhite populations.

STUDY AREA

Our study was conducted on 3 spatially independent (≥ 11 km apart) privately owned ranches in the Refugio-Goliad Prairie of southeastern Texas. The Refugio-Goliad Prairie complex was the largest parcel (approximately 105,000 ha) of native midgrass/tallgrass prairie remaining along the coast of the Gulf of Mexico. This area was located in the Gulf Coast Prairies and Marshes ecoregion (TPWD 2017*b*). The ecoregion was nearly level (0–5% slopes: NRCS 2017*a*) and experienced mild winter temperatures (mean: 14º C) and hotter and humid summer temperatures (mean: 28.8º C). Annual rainfall averaged 88.7 cm (Goliad County, 1912–2010; WRCC 2017) and occurred in a bimodal pattern, peaking in April–May and September–October. Historically, this region was maintained by frequent, anthropogenic and natural fires that rendered it nearly devoid of woody vegetation (with the exception of bisecting water courses and mottes). Vast areas were dominated by midgrasses and tallgrasses existing in a matrix of mima and pimple mounds and prairie potholes on Vertisol clays. Eolian sand hills and marshes, with their own unique vegetation assemblages, also dotted the landscape (TPWD 2017*c*). In this system, Attwater's prairie-chicken and other prairie-obligate and facultative wildlife species thrived (Morrow et al. 1996). However, beginning about 200 years ago, coinciding with settlement by Europeans, this landscape began to change as row-crop farming, overgrazing by livestock, and the suppression of grassland fires altered its vegetation composition (NRCS 2017*a*). Today, much of the Gulf Coast Prairies ecoregion is considerably more wooded, farmed, or overgrazed by cattle (or combination thereof). In contrast to the general condition of the ecoregion, our study ranches still contain parcels of native grassland.

Ranch 1 (3,240 ha) was located in southwestern Goliad County, Texas (N28º31'4.2" W97º30'46.0"; Figure 1). Our study areas on this ranch were dominated by Weesatche sandy clay loam and Goliad sandy clay loam soils, which support clay loam ecological sites (NRCS n.d.). This ranch was dominated by mid-grass and tallgrass herbaceous species, intermixed with frequent post oak (*Quercus stellata*) and live oak (*Q. virginiana*), and various Tamaulipan shrubs. Primary land management activities included the feeding and harvest of white-tailed deer (*Odocoileus virginianus*) and bobwhite, brush management via roller-drum chopper and prescribed fire, and conservative grazing by cattle (5.66 ha/animal unit rotated every 35–40 days).

Ranch 2 (10,117 ha) was located in northern Refugio County, Texas (N28°26'31.7" W97°09'54.3"; Figure 1). Our study areas on this ranch were dominated by Victoria clay and pockets of unclassified sandy soil supporting the blackland ecological site (NRCS 2017*b*). These areas were dominated by mid-grass and tallgrass herbaceous species, intermixed with honey mesquite (*Prosopis glandulosa*) and huisache (*Acacia farnesiana*). Primary land management activities included conservative grazing by cattle (6 ha/animal unit rotated every 30–40 days), the spraying of mesquite and huisache

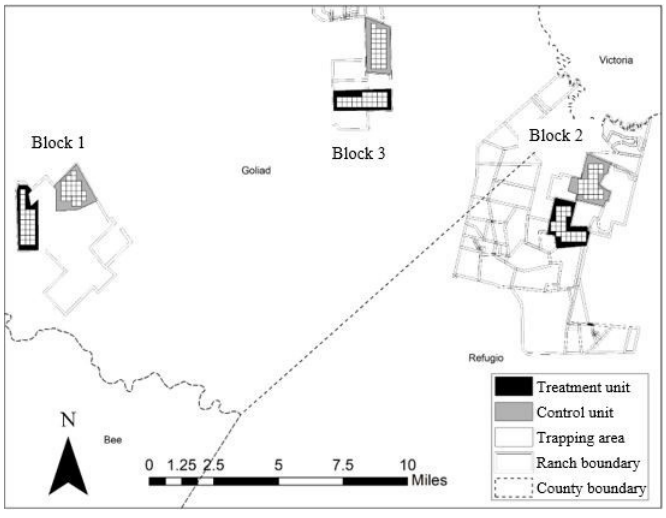

Fig. 1. Locations of ranches (blocks), experimental units, and internal 10-ha sampling cells, Goliad and Refugio counties, Texas, USA, 2017–2018.

via fixed-winged aircraft and individual plant treatments using GrazonNext® (51.06% 2,4-D triisopropanolamine salt; Corteva Agrisciences™), Tordon™ (20.9% 2,4-D and 5.4% picloram; Corteva Agrisciences), Grazon P+D® (39.6% 2,4-D triisopropanolamine salt and 10.2% picloram; Corteva Agrisciences), MSM 60™ (60% metsulfuron methyl; Alligare, LLC, Opelika, AL, USA), triclopyr, and Sendero™ (30.82% monoethanolamine salt; Corteva Agrisciences) herbicide, and wildlife harvest of bobwhite, white-tailed deer, and wild turkey (*Meleagris gallopavo*).

Ranch 3 (1,780 ha) was located in southern Goliad County, Texas (N 28°35'50.5" W 97°17'04.0"; Figure 1). Our study areas on this ranch were dominated by Greta fine sandy loam, Wyick fine sandy loam, and Vidauri fine sandy loam soils, which support claypan prairie, clay loam, and blackland ecological sites (NRCS n.d.). This ranch was almost exclusively open midgrass prairie (<5% woody cover) with only 6 small mottes (<6 ha in size) of coastal live oak (a distinctly more rhizomatous form of *Quercus virginianus*) scattered about the property. Primary land management activities included conservative grazing by cattle (10.07 ha/animal unit rotated every 30–40 days), relatively frequent prescribed fire (5-year return interval on average), weed spraying in strips using 2, 4-D (2,4-Dichlorophenoxyacetic acid), and brush control using spot application of herbicides such as GrazonNext.

Woody vegetation communities differed on the 3 ranches. Ranch 3 contained the least amount of woody cover, and habitat represented treeless midgrass prairie. Ranch 2 contained greater amounts of woody cover than ranch 3 and represented midgrass/tallgrass/mesquite/huisache savanna. Ranch 1 contained the highest woody cover of the 3 ranches and habitat generally represented mid-grass/tallgrass/post oak savanna.

Herbaceous vegetation communities on all 3 ranches were similar and represented by native, coastal midgrass and tallgrass prairie species. Specifically, these communities were dominated by little bluestem (*Schizachyrium scoparium*), brownseed paspalum (*Paspalum plicatulum*), rosettegrasses (*Dichanthelium* spp.), plains lovegrass (*Eragrostis intermedia*), longtom paspalum (*Paspalum lividum*), longspike threeawn (*Aristida longispica*), yellow indiangrass (*Sorghastrum nutans*), big bluestem (*Andropogon gerardii*), wooly croton (*Croton capitatus*), western ragweed (*Ambrosia psilostachya*), eastern dewberry (*Rubus trivialis*), spike rushes (*Elocharis* spp.), and a gallery of various other grasses, forbs, sedges, and rushes (Gould 1969, NRCS 2017*b*). To a lesser degree, each ranch had monotypic pockets of noxious nonnative grasses such as bahiagrass (*Paspalum notatum*), bermudagrass (*Cynodon dactylon*), Kleberg bluestem (*Dichanthium annulatum*), and Angleton bluestem (*Dichanthium aristatum*). Scientific plant names are standardized according to the U.S. Department of Agriculture's PLANTS Database (NRCS 2017*b*).

Hurricane Harvey was a destructive weather event that passed over all 3 of our study areas on 25 August 2017, delivering maximum sustained winds between 177–209 km/hr and rainfall exceeding 40 cm (NOAA 2017).

METHODS

Experimental Design

Our study design was a repeated measures, randomized complete block design where ranches served as the blocking factor and 2 experimental units (500 ha each) occurred within each block (Figure 1). We designated ranch 1 as block 1, ranch 2 as block 2, and ranch 3 as block 3 (Figure 1). We had 6 experimental units (3 ranches × 2 experimental units/block). The experimental units within a given block were nearly identical in vegetation composition and received the same management. Experimental units on block 1 represented midgrass-tallgrass/post oak savanna, block 2 represented midgrass/tallgrass/mesquite/huisache savanna, and block 3 represented treeless midgrass prairie. These plant communities were selected in order to encompass the greatest amount of variation in communities represented in this region. Fire ants were found in all pastures.

The repeated measures component of our study involved a pretreatment and posttreatment period. The first year of our study (Mar 2017–Mar 2018) served as the pretreatment period. After this period, we randomly chose experimental units on blocks 1 and 2 to receive a treatment of Extinguish® Plus (0.25% methoprene and 0.36% hydramethylnon; Central Garden and Pet, Walnut Creek, CA, USA). Extinguish Plus is a bait that contains an insect growth regulator specific to ants and a slow-acting insecticide (TAMU 2017). These chemicals disrupt the production of energy in the insect's cells, affecting the queen ant's reproduction. The bait is gathered by foragers and shared among the colony, ultimately leading to the demise of the colony. There are few risks to other ant species during application because fire ants are more dominant and aggressive at retrieving the bait before other species (Barr et al. 2005, Knutson and Campos 2008). The ranch manager for block 3 had already aerially applied Extinguish Plus at the recommended label rate of 1.7 kg product/ha to a 1,619-ha portion of the property (6 April 2016), a year prior to the start of our study (March 2017). Thus, we could not collect any true pretreatment data nor randomly assign treatments on block 3. For block 3, we randomly designated a treatment site (500 ha) within the already treated area and randomly selected an untreated unit (500 ha) to serve as the experimental control. The insecticide was applied to the treatment units of all 3 blocks via a fixed-winged aircraft at the recommended label rate of 1.7 kg/ha to designated treatment experimental units during 5–6 April 2018. Thus, block 3 had 2 treatment applications: April 2016 and April 2018. Treatment on block 1 was applied from approximately 0900–1300 under cloudy conditions and there was moderate rainfall starting around 1300. Treatment was applied to block 2 on April 6 approximately 0900–1300 under sunny, clear conditions. Treatment on block 3 was applied approximately 1400–1800 under cloudy conditions, but there was no precipitation during or after treatment. Experimental units within each block where insecticide was not applied served as experimental controls.

We chose the March–April time for insecticide application because this has been recommended as the best time of application based on preliminary data collected by the Attwater Prairie Chicken National Wildlife Refuge (M. Morrow, Attwater Prairie Chicken National Wildlife Refuge, personal communication). The 6 months following treatment application served as our posttreatment period (15 Mar 2018–31 Aug 2018). We documented fire ant density and bobwhite demographics during the breeding season on each experimental unit during pretreatment (15 Mar 2017–31 Aug 2017) and posttreatment (15 Mar 2018–31 Aug 2018). We monitored bobwhite response at 2 spatial scales: individual bobwhites (point-of-use) and population density (pasture scale).

Fire Ant Abundance

Point-of-use scale.—We collected data on fire ant abundance at bird locations, at nest locations, and at paired random points. Because of time constraints, we obtained fire ant abundance only at a subsample of bird locations, but we were able to obtain fire ant abundance at all nests. For bird locations, we randomly selected twice per week 4 bobwhites in each of the 6 experimental units to sample (6 experimental units × 4 randomly selected hens/unit × 2 days/week = 48 points sampled weekly). When a randomly selected bird was located, we placed a marking flag in the exact location where the bird was observed so the point could be sampled the following day. If 2 randomly selected birds were found at identical locations, we randomly selected another bird location to sample. We also established paired, random points for bird locations and nests by randomly selecting a direction and distance between 20–50 m from the original location (i.e., bird location or nest; Collins et al. 2009).

At each sample point (i.e., bird location, nest, or random point), we sampled fire ant density using the point center quarter method (Cottam and Curtis 1949, 1956). We delineated the area surrounding a sample point into 4 quarters using the 4 cardinal directions as delineations and the sample point as the center. We measured the distance to the nearest active fire ant mound (up to 10 m) in each quarter and calculated the mean distance. We documented measurements to active mounds only. We confirmed mounds to be active by poking a hole into the center of the mound, waiting a moment, and observing fire ants escaping. We then used this information to calculate fire ant mound density at the bird location as per Cottam and Curtis (1956) using the equation:

$$\text{Mound density} = \frac{1}{(\text{Mean distance to nearest mound})^2}$$

We used the known-fate and nest survival platforms in Program MARK, version 6.2 to model the influence of fire ants on bobwhite survival and nest success (White and Garrot 1990, White and Burnham 1999).

Pasture scale.—We quantified fire ant abundance on each experimental unit during pretreatment (Sep 2017) and posttreatment (Sep 2018) using 2 methods: 1) distance sampling to estimate density of fire ant mounds (Burnham et al. 1980, Buckland et al. 2004), and 2) baited cup method to estimate relative abundance of foragers (Porter and Tschunkel 1987, Mueller et al. 1999).

For distance sampling, we established 10 100-m transects in each experimental unit. The starting points and orientation of the transects were randomly chosen within the experimental unit boundaries using ArcGIS 10.3 (Esri Inc., Redlands, CA, USA). We walked transects during 0800–1800 and measured the perpendicular distance (0.1-m increments) to each fire ant mound detected using a Nikon® ProStaff® 3i laser range finder (Nikon Instruments, Melville, NY, USA). We did not leave the transect line in order to avoid finding other mounds that would not have been detected otherwise. Thus, we could not determine whether fire ant mounds were active. In our study area, we rarely observed mounds that were inactive, so we assumed all mounds to be active if visually detected. We walked all transects in one experimental unit before moving on to the next, and all experimental units were sampled within a 7-day period. We sampled the same transects during pretreatment (May and Sep 2017) and posttreatment (May and Sep 2018).

We calculated fire ant mound densities for each experimental unit using Program DISTANCE (Thomas et al. 2010). Assumptions of distance sampling include the following: 1) animals were distributed independently of the transect, 2) pertinent objects on the line were detected with 100% certainty, 3) points did not move before detection, 4) points did not move once located, 5) distances were measured accurately, and 6) each sighting was independent of one another (Burnham et al. 1980, Buckland et al. 2004). To determine the effectiveness of the insecticide, we compared fire ant density between treatment and control sites by block during pretreatment and posttreatment using 95% confidence intervals (CIs). We also pooled data across blocks 1 and 2 (the two blocks with true pretreatment and posttreatment data) and compared fire ant density between treatment and control sites using 95% CIs.

We used the baited cup method (Porter and Tschunkel 1987, Mueller et al. 1999) to estimate the relative abundance of foragers during pretreatment (Sep 2017) and posttreatment (Sep 2018). To designate sampling sites, we created a grid (10-ha cells) in the internal 250-ha area of each 500-ha experimental unit using the fishnet tool in ArcGIS 10.3. This process resulted in 25 grid cells in each experimental unit, of which we randomly selected 10 for sampling using their centroid as the sampling point. At each sampling point, we placed 1 30-ml plastic cup baited with a 0.5-g piece of hot dog on its side following the general protocol of Mueller et al. (1999). After 30 minutes, we securely capped the cup and placed it in a freezer at -20º C. Once the cup was frozen, we counted the number of fire ants in each cup (Mueller et al. 1999). Surveys were conducted only during periods of maximum fire ant foraging (22–32º C; Porter and Tschinkel 1987), and all sampling points in an experimental unit were completed within a 3-hour period before moving on to the next experimental unit. We used the same points for sampling during both pretreatment and posttreatment.

We compared relative abundance of foragers between treatment and control sites by block during pretreatment and posttreatment using analysis of variance (ANOVA). As was

the case for prior analyses, we pooled data across blocks 1 and 2—the two blocks with true pretreatment and posttreatment data—and compared relative abundance of foragers between treatment and control sites using a repeated measures ANOVA. We determined statistical significance using an alpha level of $P \leq 0.05$. We report all findings as mean ± standard error unless otherwise noted.

BOBWHITE DEMOGRAPHY

Survival.—We monitored survival of bobwhites using radio-telemetry during the breeding seasons (Apr–Aug 2017 and 2018). To designate trap sites, we created a grid (10-ha cells) in the internal 250-ha area of each 500-ha experimental unit using the fishnet tool in ArcGIS 10.3. One funnel-style trap was placed in the centroid of each grid cell in order to ensure equal trapping effort across each experimental unit. We placed traps along roadways (in order to check all traps within a 3-hour session) and under dense-canopied shrubs to reduce risk of predation and sun exposure (Stoddard 1931). Traps in open prairie or in areas lacking woody cover were covered with limbs of woody plants and other natural vegetation. Each trap site was prebaited with 1.5 L of milo (*Sorghum bicolor*) every 4 days, 12 days before trapping commenced. We set traps before sunrise, checked traps every 3 hours during the day, and closed the traps before twilight (Abbott et al. 2005). Upon capture of each bird, we documented its mass, age (hatch year or after hatch year), and sex. We banded all birds using size 7 aluminum bands (Rosene 1969), and bobwhite hens weighing ≥150 g were fitted with a 6-g necklace-style very high frequency radio-transmitter (American Wildlife Enterprises, Monticello, FL, USA). The radio-transmitters operated at frequencies 150.000–151.999 MHz. We collared only 3 hens/trap/covey to maintain even sampling distribution of bobwhites throughout the experimental units. Our goal was to maintain at least 15 birds in each experimental unit (6 experimental units × 15 hens/unit = 90 hens) throughout the nesting season (Apr–Aug 2017 and 2018).

We located bobwhites via homing 2–3 days/week during 15 March–31 August 2017 and 2018. We alternated days in which birds were located. Tracking times were stratified across 4 time periods (sunrise–0900, 0901–1200, 1201–1500, and 1501–sunset) to collect an equal number of locations for every radio-marked bird during each time period throughout the field season. We recorded bobwhite locations using a Trimble® Juno™ Global Positioning System (GPS) unit (Trimble Navigation Ltd., Sunnyvale, CA, USA). At each bird location, we recorded the date, time, physical location, association with other birds, and number of chicks in the group. If a bobwhite traveled outside of the ranch boundary, we made every effort to obtain access to the property to continue collecting data. If the bird was not located, it was used in analyses until the date it went missing, at which point it was censored. When a mortality signal was detected, we immediately located the transmitter and classified the suspected cause of death as 1) avian predation (skeleton intact, curled antenna, stripped tendons), 2) mammalian predation (feathers only, bite marks on transmitter), 3) snake predation (in a snake or its feces), 4) unknown (carcass intact), or 5) other reasons (Carter et al. 2002). Trapping, handling, and general research were conducted under the Texas A&M University-Kingsville Institutional Animal Care and Use Protocol #1384.

We estimated survival of radio-marked bobwhites during the breeding season (15 Mar–31 Aug 2017 and 2018) using the Kaplan-Meier estimator and staggered-entry approach (Kaplan and Meier 1958, Pollock et al. 1989). It is possible that the stress of handling and marking bobwhites may influence survival probabilities, so some studies have removed from analysis birds that survived ≤7 days (Pollock et al. 1989) or ≤14 days (Cox et al. 2004). Our study had a low sample size of bobwhites, so to keep as many birds as possible for analysis, we assumed that trapping, handling, and radio-collaring did not affect bobwhite survival. We removed from analysis only bobwhites which did not survive from the initial trapping day to the first tracking day. Birds that went missing were kept in the analysis through the last known day of survival, after which point, they were censored. Because block 3 did not have a true pretreatment data collection period, we excluded it from the Kaplan-Meier survival analyses. In addition, because of low sample sizes resulting from low bobwhite abundance in the ecoregion, we had to pool radio-marked bobwhites across blocks 1 and 2 by treatment. We compared survival curves between treatment and control during pretreatment and posttreatment for the full bobwhite breeding season (Mar–Aug) using a log-rank Chi-squared test (Pollock et al. 1989). Because the treatment takes up to 4 weeks to reach full efficacy (TAMU 2017), we also compared bobwhite survival starting 4 weeks after treatment with survival from the same pretreatment timeframe (5 May–31 Aug).

We modeled the influence of fire ants and other covariates on bobwhite survival using the known-fate platform in Program MARK, version 6.2 (White and Garrot 1990, White and Burnham 1999). This type of analysis is similar to a regression framework; thus, we used radio-marked bobwhites from all blocks for this analysis given that each bobwhite had an encounter history (i.e., "response variable") and corresponding estimates of fire ant abundance and other covariates of interest (i.e., "predictor variables"). We developed an encounter history for each bird using a 7-day interval. We modeled bobwhite survival based on time trend, age, sex, year, nearest fire ant mound, and fire ant mound density. For a given bird, we averaged nearest fire ant mound and fire ant mound density across its sampled locations. We developed 12 *a priori* models for evaluation (Table 1) and selected the best model using Akaike's Information Criterion corrected for small sample size (AIC_c) and Akaike weights (w_i) (Burnham and Anderson 2002).

Reproduction.—We considered radio-marked bobwhites to be nesting when we documented an individual in the same location for ≥2 consecutive tracking days. We obtained GPS locations of every nest location using a Trimble Juno and placed flagging tape 10 m from the nest in the 4 cardinal directions

Table 1. List of 12 *a priori* models used to evaluate the influence of time, demographic, and red imported fire ant (*Solenopsis invicta*) covariates on survival of radio-marked northern bobwhites (*Colinus virginianus*), Goliad and Refugio counties, Texas, USA, April–August 2017 and April–August 2018.

Hypothesis category		
model no.	Model	Explanation
Null		
1	S(.)	No effect of any covariate
Demographic		
2	S(Trend)	Survival varies by week
3	S(Age)	Survival varies by age
4	S(Sex)	Survival varies by sex
5	S(Year)	Survival varies between years
6	S(Age + Sex + Year)	Survival varies by age, sex, and year
Fire ant		
7	S(Nearest mound)	Survival varies by nearest fire ant mound
8	S(Mound density)	Survival varies by fire ant density
9	S(Nearest mound + Mound density)	Survival varies by nearest fire ant mound and fire ant density
Demographic and fire ant effects		
10	S(Age + Nearest mound + Mound density)	Survival varies by age, nearest fire ant mound, and fire ant density
11	S(Sex + Nearest mound + Mound density)	Survival varies by sex, nearest fire ant mound, and fire ant density
12	S(Year + Nearest mound + Mound density)	Survival varies by year, nearest fire ant mound, and fire ant density

surrounding the nest (i.e., flagged shrubs formed a "cross" with the nest in the center). We monitored each nest ≥10 m away every other day until nest fate was determined. Hens were not flushed from their nests. If the signal strength was strong towards nest location, we assumed that the hen was still incubating. The first time the incubating hen was away from the nest, we visually confirmed the nest, documented clutch size, and recorded more precise GPS coordinates. We classified nests as 1) successful (≥1 egg hatched), 2) depredated (eggs missing, eggs crushed, or surrounding vegetation trampled, or combination thereof), 3) abandoned (eggs present but hen off nest ≥7 days), or 4) other (Terhune et al. 2006, Scott et al. 2012).

We compared apparent nest success between control and treatment units during pretreatment and posttreatment using Fisher's exact test (Zar 1999) in SAS 9.2 (SAS Institute Inc., Cary, NC, USA). As was the case for survival, we analyzed only blocks 1 and 2 in this type of analysis (because these blocks possessed true pretreatment and posttreatment data) and pooled across blocks by treatment due to low sample sizes.

We modeled the influence of 5 covariates (trend, age, year, distance to nearest mound, and mound density) on nest survival using the nest survival platform in Program MARK, version 6.2. This software uses a maximum-likelihood estimator (MLE) with a logit link function to provide estimates of survival probability based on the mean and variance of the daily survival rate as influenced by covariates in a given model. The model assumed that daily survival rate was the same for all nests on all dates and for all nest ages and that nest fates were independently and identically distributed within a sample (Johnson 1979, Bart and Robson 1982). We created an encounter history for each nest based on the day the nest was found, the last day the nest was known to be alive, the last day the nest was checked, and the fate of the nest (successful or failed). We standardized the nesting-season days using day 1 as the date the first nest was detected for each year. We developed 10 *a priori* models (Table 2) and selected the best model based on AIC_c and w_i (Burnham and Anderson 2002).

Bobwhite density.—We measured bobwhite density using helicopter surveys with a distance-sampling framework during December 2017 and December 2018 following the general protocol of Rusk et al. (2007), Schnupp et al. (2013), and Edwards (2019). We recorded data on bobwhite detections using the Modified System for Electronic Surveys (MSES) as defined by Schnupp et al. (2013) and modified by Edwards (2019). The equipment consisted of a MDL LaserAce 300™ laser range finder (Measurement Devices Ltd., Aberdeen, Scotland, UK), 2 Ironix DuoTouch™ tablets (General Dynamics, St. Petersburg, FL) equipped with ArcPad 7 (Esri Inc., Redlands, CA), a Raven Cruizer™ guidance and differential GPS (Raven Industries, Sioux Falls, SD, USA), and 2 17-key keypads (Edwards 2019).

We established linear transects (n = 6–20/experimental unit), spaced 200 m apart within each experimental unit, using the fishnet tool in ArcGIS 10.3. Transects were oriented either east-west or north-south to allow flexibility in flight direction on the day of survey depending on the prevailing winds. Surveys were conducted during daylight hours (0800–1800) using a Robinson R44 helicopter (Robinson Helicopter Co.,

Table 2. List of 10 *a priori* models to evaluate the influence of time, demographic, and red imported fire ant (*Solenopsis invicta*) covariates on nest survival of radio-marked northern bobwhites (*Colinus virginianus*), Goliad and Refugio counties, Texas, USA, April–August 2017 and April–August 2018.

Hypothesis category		
model no.	Model	Explanation
Null		
1	S(.)	No effect of any covariate
Demographic		
2	S(Trend)	Survival varies by day
3	S(Age)	Survival varies by age
4	S(Year)	Survival varies between years
5	S(Age + Year)	Survival varies by age and year
Fire ant		
6	S(Nearest mound)	Survival varies by nearest fire ant mound
7	S(Mound density)	Survival varies by fire ant density
8	S(Nearest mound + Mound density)	Survival varies by nearest fire ant mound and fire ant density
Demographic and fire ant effects		
9	S(Age + Nearest mound + Mound density)	Survival varies by age, nearest fire ant mound, and fire ant density
10	S(Year + Nearest mound + Mound density)	Survival varies by year, nearest fire ant mound, and fire ant density

Torrance, CA) and were flown at an average air speed of 23–40 km/hr and average height of 8–11 m. Surveys were conducted using 4 observers: the pilot, 1 front-seat observer, and 2 back-seat observers. The pilot and the front-seat observer surveyed the 90° area in the front of the helicopter, which encompassed 45° on each side of the transect line (Edwards 2019). Once bobwhites were detected, the pilot would bring the helicopter to a hover while the observer recorded covey size and obtained a GPS location of the detection using MSES. After a covey flushed, the birds scattered and if they flew near an adjacent transect, we made note of the location to avoid double counting.

We attempted to calculate bobwhite density for each experimental unit using Program DISTANCE, but we did not have enough quail detections to obtain reliable estimates. Thus, we instead calculated relative abundance (number of bobwhites/km) to estimate bobwhite abundance pooled across blocks 1 and 2 by treatment. We compared bobwhite abundance between treatments using a generalized linear model with repeated measures (PROC GLM; SAS 9.2). We also conducted simple linear regression to evaluate at the pasture scale the relationship between bobwhite relative abundance and fire ant mound density.

RESULTS

Fire Ant Abundance

Pasture scale.—In general, fire ant mound density decreased through time on both treatment and control sites on all blocks (Figure 2). However, 95% CIs of fire ant mound density did not overlap between treatment and control sites during posttreatment in block 2 (May and Sep sampling) or block 3 (May sampling), indicating that the insecticide was effective at decreasing fire ant mound density in these blocks (Table 3). For data pooled across blocks 1 and 2, we observed the same general trend of decreasing fire ant mound density through time on both treatment and control sites (Figure 3). Regarding these pooled data, the 95% CI of fire ant mound density for the pooled dataset did not overlap between treatment and control sites during the last survey of the posttreatment period (Sep sampling), again indicating that the insecticide was effective at decreasing fire ant mound density (Table 3).

Fire ant forager abundance increased in both units of block 2 regardless of treatment but decreased to 0 foragers in the treatment units of blocks 1 and 3 (Table 4). Of the 3 blocks, only block 1 exhibited a statistical difference in forager abundance between control (n = 770 foragers) and treatment (n = 0 foragers, P = 0.05) following insecticide application (Figure 4). For pooled data across blocks 1 and 2, we observed a trend of increasing fire ant abundance through time regardless of treatment (Figure 5). However, for the pooled data, we documented no difference in fire ant forager abundance between control (n = 1,235 foragers) and treatment (n = 1,044 foragers; P = 0.76) following insecticide application (Figure 5).

Bobwhite Demography

Survival.—We captured and radio-marked 93 bobwhites in 2017 and 100 bobwhites in 2018. We were able to use survival information from 83 bobwhites in 2017 and 81

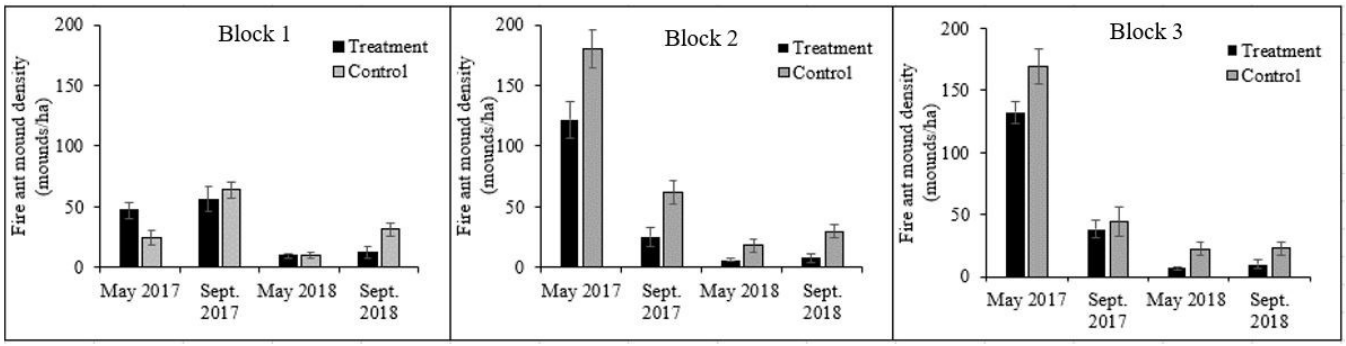

Fig. 2. Red imported fire ant (*Solenopsis invicta*) densities (mounds/ha) ($\hat{D}$ ± 95% CI) of treatment and control units estimated using distance sampling before and after application of Extinguish® Plus (5–6 Apr 2018) for block 1, block 2, and block 3 in Goliad and Refugio counties, Texas, USA. Block 3 was treated with the insecticide during April 2016 and April 2018; thus, fire ant mound density is after treatment for both years.

Table 3. Red imported fire ant (*Solenopsis invicta*) densities (mounds/ha), sample sizes, 95% confidence intervals (CIs), and coefficient of variation (CV; %) of treatment and control units estimated using distance sampling before and after application of Extinguish® Plus (5–6 Apr 2018) for blocks 1, 2, 3 and blocks 1 and 2 pooled in Goliad and Refugio counties, Texas, USA. Block 3 was treated with the insecticide during April 2016 and April 2018; thus, fire ant mound density is after treatment for both years.

Block	Date	Unit	n	$\hat{D}$ [a]	95% CI Lower	95% CI Upper	% CV
1	May 2017	Treatment	78	46.951	34.519	63.860	14.38
		Control	63	24.370	13.995	42.435	25.17
	Sep 2017	Treatment	49	56.084	38.192	82.358	18.57
		Control	50	64.171	51.785	79.519	10.56
	May 2018	Treatment	46	9.723	6.731	14.045	16.51
		Control	31	10.123	5.485	18.684	28.4
	Sep 2018	Treatment	12	12.250	5.765	26.033	37.28
		Control	38	31.589	22.257	44.835	17.46
2	May 2017	Treatment	159	121.620	93.222	158.660	12.64
		Control	217	179.880	149.820	215.970	8.91
	Sep 2017	Treatment	16	25.351	12.961	49.583	31.07
		Control	33	61.969	44.423	89.444	16.28
	May 2018	Treatment	18	5.891	3.599	9.642	22.61
		Control	22	18.212	10.123	32.765	29.18
	Sep 2018	Treatment	11	7.515	2.775	20.353	50.37
		Control	36	29.607	20.499	42.762	18.38
3	May 2017	Treatment	194	132.510	115.140	152.510	6.89
		Control	226	169.080	142.290	200.920	8.38
	Sep 2017	Treatment	30	38.373	26.955	54.628	17.49
		Control	47	44.176	24.340	80.151	27.18
	May 2018	Treatment	26	6.549	3.676	11.668	26.23
		Control	29	22.316	14.263	34.915	22.18
	Sep 2018	Treatment	17	10.000	4.705	21.254	37.72
		Control	31	22.490	13.988	36.157	23.29
1 and 2 pooled	May 2017	Treatment	237	88.69	69.39	113.35	11.91
		Control	280	86.40	63.58	117.43	14.77
	Sep 2017	Treatment	65	40.10	27.11	59.32	19.27
		Control	83	60.90	50.15	73.94	9.63
	May 2018	Treatment	64	12.88	9.13	18.17	16.63
		Control	53	10.97	7.49	16.08	18.60
	Sep 2018	Treatment	23	9.94	5.48	18.04	30.14
		Control	74	31.19	24.32	40.00	12.56

[a] $\hat{D}$: Density

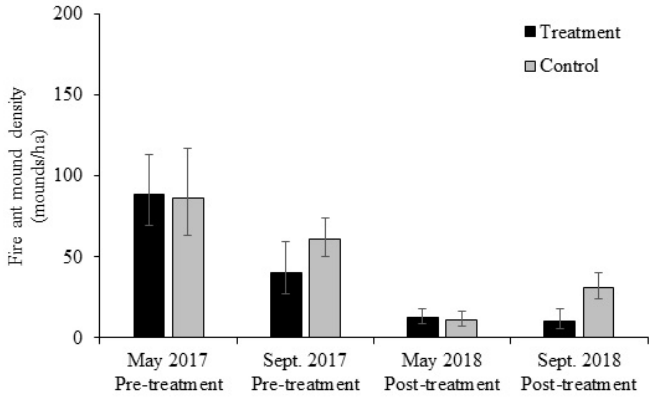

Fig. 3. Red imported fire ant (*Solenopsis invicta*) densities (mounds/ha) ($\hat{D}$ ± 95% confidence interval) of treatment and control units estimated using distance sampling before and after application of Extinguish® Plus (5–6 Apr 2018) for blocks 1 and 2 pooled in Goliad and Refugio counties, Texas, USA, 2017–2018.

Table 4. Red imported fire ant (*Solenopsis invicta*) forager abundance and standard errors (SE) of bait cup traps in treatment and control units before and after application of Extinguish® Plus (5–6 Apr 2018) for blocks 1, 2, 3 and blocks 1 and 2 pooled in Goliad and Refugio counties, Texas, USA. Block 3 was treated with the insecticide during April 2016 and April 2018; thus, fire ant mound density is after treatment for both years.

Block	Date	Unit	Forager abundance	SE	P
1	Sep 2017	Treatment	291	34.37	0.712
		Control	231	37.09	
	Sep 2018	Treatment	0	0.00	0.047
		Control	770	114.32	
2	Sep 2017	Treatment	140	20.03	0.266
		Control	270	29.68	
	Sep 2018	Treatment	1044	112.60	0.227
		Control	465	93.51	
3	Sep 2017	Treatment	205	25.75	0.272
		Control	90	19.17	
	Sep 2018	Treatment	0	0.00	0.087
		Control	283	49.44	
1 and 2 pooled	Sep 2017	Treatment	431	28.45	0.720
		Control	501	32.75	
	Sep 2018	Treatment	1044	94.20	0.761
		Control	1235	102.85	

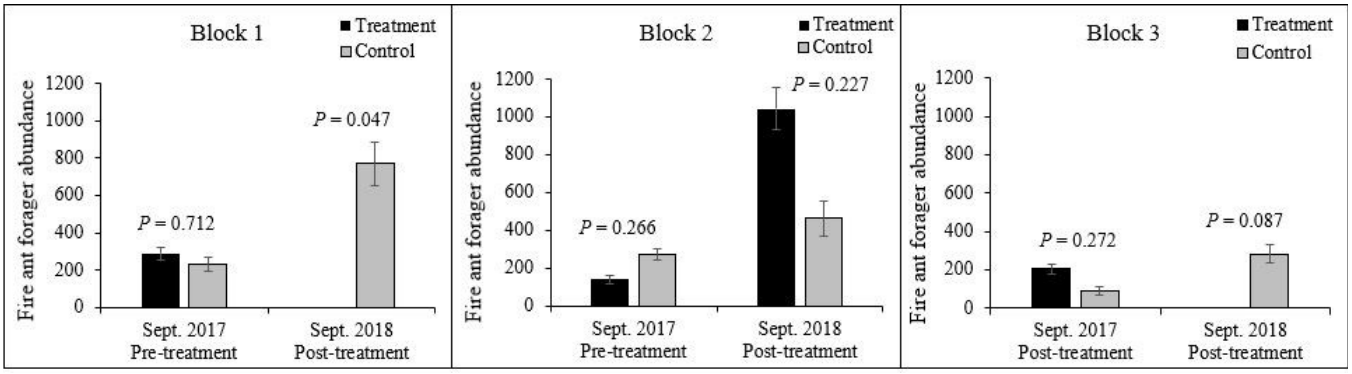

Fig. 4. Red imported fire ant (*Solenopsis invicta*) forager abundance and standard errors of treatment and control units before and after application of Extinguish® Plus (5–6 Apr 2018) for block 1, block 2, and block 3, Goliad and Refugio counties, Texas, USA, September 2017 and September 2018. Block 3 was treated with the insecticide during April 2016 and April 2018; thus, fire ant forager abundance is after treatment for both years.

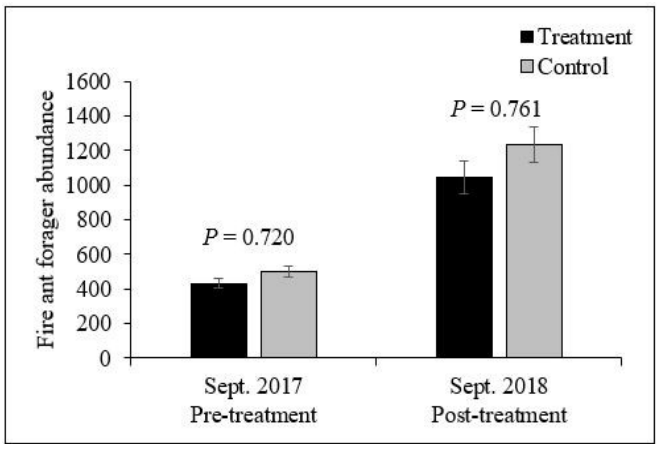

Fig. 5. Red imported fire ant (*Solenopsis invicta*) forager abundance and standard errors of treatment and control units before and after application of Extinguish® Plus (5–6 Apr 2018) for blocks 1 and 2 pooled, Goliad and Refugio counties, Texas, USA, September 2017 and 2018.

bobwhites in 2018. There was no difference in seasonal bobwhite survival between control (0.12 ± 0.02; n = 45 bobwhites) and treatment (0.16 ± 0.02; n = 38 bobwhites) during the pretreatment period (P = 0.91) (Figure 6). We also documented no difference in bobwhite survival between control (0.33 ± 0.02; n = 52) and treatment (0.46 ± 0.01; n = 29) during posttreatment (P = 0.21) during the full breeding season (15 March–31 Aug; Figure 6). Bobwhite survival was lower in the control (0.50 ± 0.01) than the treatment (0.69 ± 0.01) beginning 4 weeks after treatment took full effect until the end of the bobwhite breeding season (5 May–31 Aug 2018), but this difference was not significant (P = 0.14). However, there was more of a divergence in bobwhite survival between the control and treatment units 4 weeks following treatment application compared to pretreatment, which provides evidence for biological significance. Predation accounted for most mortalities in 2017 (59%; n = 49 total mortalities) and 2018 (70%; n = 58 total mortalities). We did not document any confirmed mortalities caused by fire ants.

Regarding evaluation of the influence of covariates on bobwhite survival, we were able to use 72 bobwhites for analyses from 2017 and 50 bobwhites from 2018. Of the 12 *a priori* models evaluated, the most parsimonious model

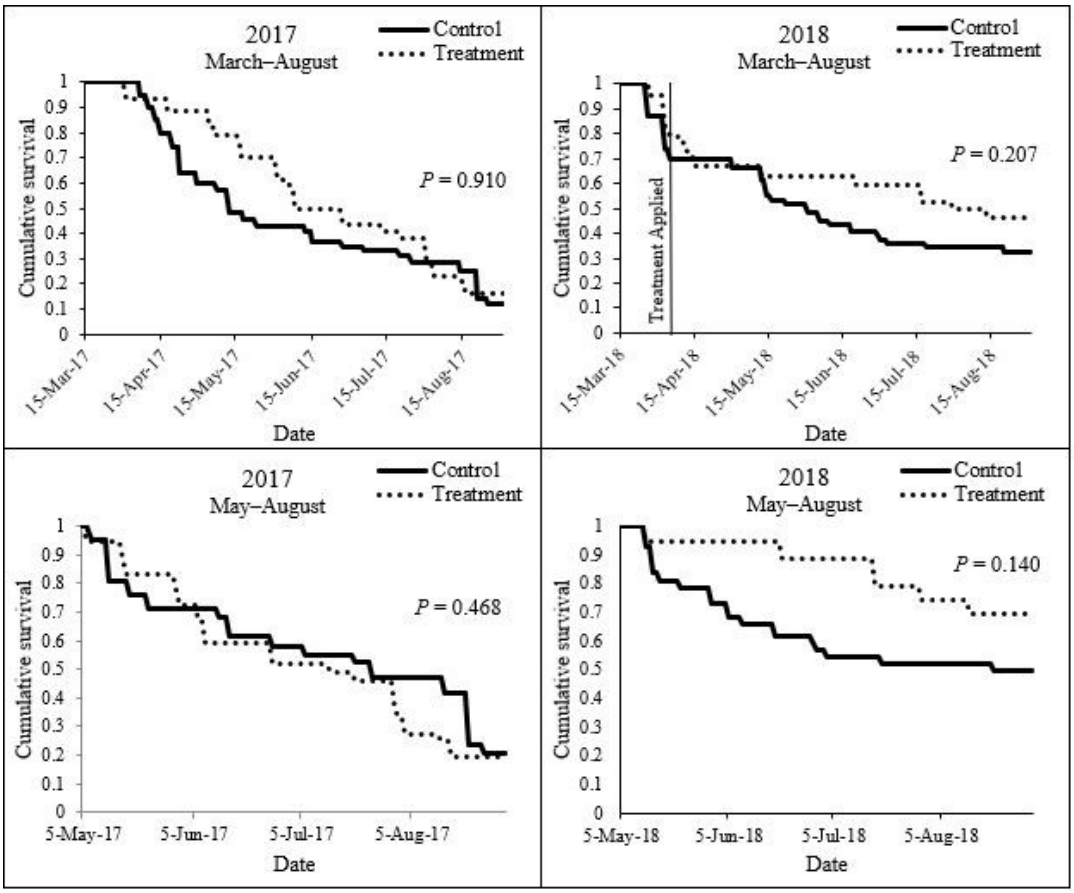

Fig. 6. Survival curves of radio-marked bobwhites (*Colinus virginianus*) before and after application of Extinguish® Plus (5–6 Apr 2018) during full breeding season (15 Mar–31 Aug) and starting 4 weeks after treatment (5 May–31 Aug), Goliad and Refugio Counties, Texas, USA, 2017–2018. Data were pooled across blocks 1 and 2 by treatment.

was the null model (Table 5). There were 9 other competing models (i.e., within 2Δ AIC_cs); however, the CIs of the beta estimates for these competing models overlapped zero, indicating they contained uninformative parameters. For example, the second-best model included an additive effect of fire ant mound density (β = 0.204, 95% CI = -0.087 to 0.494) and nearest fire ant mound (β = 0.231, 95% CI = -0.068 to 0.530), but both betas for these parameters included 0. In addition, the Akaike model weights for the top 4 models were similar (0.10–0.12), indicating no strong statistical support for any particular model (Table 5). Collectively, this information suggests that none of the competing models was superior to the null model, thereby indicating that none of the covariates (trend, age, sex, year, nearest mound and mound density) that we measured in our study influenced adult survival of our radio-collared bobwhites (Table 5).

Reproduction.—We found 26 bobwhite nests in 2017 and 25 bobwhite nests in 2018. We documented no statistical difference in apparent nest success between control (58.3%; n = 12 nests) and treatment (18.2%; n = 11 nests) during pretreatment (P = 0.09; Figure 7). We also documented no statistical difference in apparent nest success between control (23.1%; n = 13 nests) and treatment (55.6%; n = 9 nests) during posttreatment (P = 0.19; Figure 7). However, following treatment, apparent nest success in the treated units increased by 37.4% while nest success in the control units decreased by 35.2%. This result provides evidence that even though we did not detect a significant difference between the treated and controlled areas, the treatment may have been effective at improving nest success.

We observed a similar finding regarding clutch size. We documented no difference in clutch size between control (11.4 ± 3.3 eggs, n = 10 nests) and treatment (13.0 ± 2.2 eggs, n = 7 nests) during pretreatment (P = 0.28; Table 6), nor a difference in clutch size between control (11.1 ± 3.3 eggs, n = 12 nests) and treatment (12.4 ± 2.8 eggs, n = 9 nests) during posttreatment (P = 0.38; Table 6).

Of the 10 *a priori* models evaluating the influence of covariates on bobwhite nest survival, the most parsimonious model was the null model (Table 7). There were 4 other competing models (i.e., within 2Δ AIC_cs); however, the CIs for these competing models overlapped zero, indicating they contained uninformative parameters. For example, the second-best model included an additive effect of time trend (β = -0.008, 95% CI = -0.0238 to 0.008), but the beta estimate included 0. In addition, the Akaike model weights for the top 5 models after the null model were similar (0.10–0.17), indicating no strong support for any particular model (Table 7). Collectively, this information suggests that none of the competing models was superior to the null model, thereby indicating none of the covariates (trend, nearest mound, year, mound density, and age) influenced adult survival of our radio-collared bobwhite nest survival (Table 7).

Bobwhite density.—We could not obtain reliable estimates of bobwhite density using distance sampling because of low detections (n = 2–14 covey detections/experimental unit in 2017 and n = 0–5 covey detections/experimental unit in 2018). Thus, we compared relative bobwhite abundance (no. individuals/km) between treatments across time. There was no difference between treatment type ($F_{1, 5}$ = 0.15, P = 0.74), year ($F_{1, 5}$ = 1.03, P = 0.60), or treatment × year ($F_{1, 5}$ = 1.35, P = 0.37). Although the lack of treatment × year interaction permitted pooling across time, we compared the treatment and control units by year to evaluate potential differences

Table 5. Model selection results of analysis evaluating factors affecting breeding season (Apr–Aug) survival of radio-marked northern bobwhites (*Colinus virginianus*) in Goliad and Refugio counties, Texas, USA, 2017–2018.

Rank	Model	K [a]	AIC_c [b]	ΔAIC_c [c]	w [d]
1	S(.)	1	585.6297	0.000	0.1501
2	S(Mound density + Nearest mound)	3	586.0509	0.421	0.1216
3	S(Year)	2	586.1589	0.529	0.1152
4	S(Mound density)	2	586.3527	0.723	0.1046
5	S(Nearest mound)	2	586.4300	0.800	0.1006
6	S(Sex)	2	586.7268	1.097	0.0867
7	S(Year + Mound density + Nearest mound)	4	586.8613	1.232	0.0811
8	S(Sex + Mound density + Nearest mound)	4	587.2241	1.594	0.0677
9	S(Age)	2	587.6326	2.003	0.0552
10	S(Time Trend)	19	587.8838	2.254	0.0486
11	S(Age + Mound density + Nearest mound)	4	588.0194	2.390	0.0455
12	S(Year + Age + Sex)	4	589.3758	3.746	0.0231

[a] K: number of parameters.
[b] AIC_c: Akaike's Information Criterion corrected for small sample size.
[c] ΔAIC_c: difference between a model and the best performing model.
[d] w: Akaike model weight.

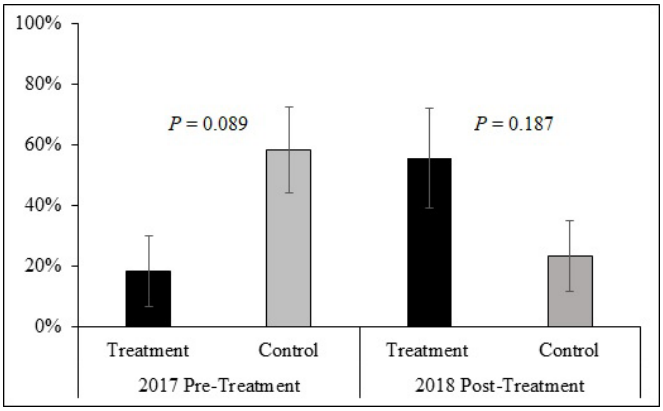

Fig. 7. Comparison of apparent nest success of northern bobwhite (*Colinus virginianus*) between treatment and control units before and after application of Extinguish® Plus (5–6 Apr 2018) in Goliad and Refugio counties, Texas, USA, December 2017 and December 2018. Data were pooled across blocks 1 and 2 by treatment.

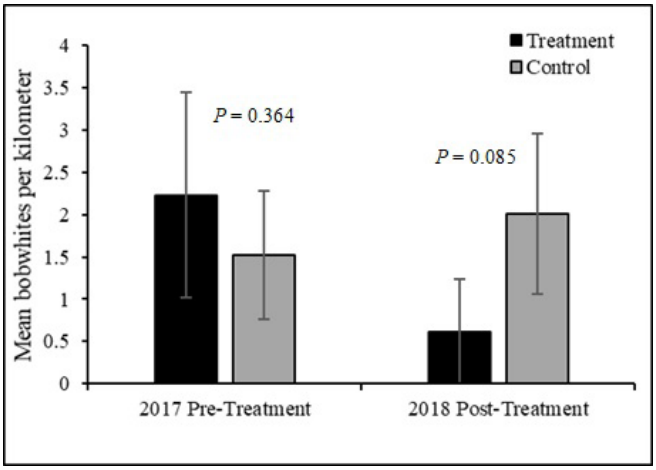

Fig. 8. Relative abundance (mean ± standard error; bobwhites/km) of northern bobwhites (*Colinus virginianus*) at treatment and control units of blocks 1 and 2 pooled before and after application of Extinguish® Plus (5–6 Apr 2018) in Goliad and Refugio counties, Texas, USA, December 2017 and December 2018.

Table 6. Mean clutch size of northern bobwhite (*Colinus virginianus*) before (2017) and after (2018) application of Extinguish® Plus (5–6 Apr 2018) in 2 sites (blocks 1 and 2), Goliad and Refugio counties, Texas, USA, 2017-2018. Block 3 was treated with the insecticide during April 2016 and April 2018; thus, mean clutch size is after treatment for both years.

	2017						
	Control			Treatment			
Site	*n*	Mean clutch size	SE	*n*	Mean clutch size	SE	*P*-value
Block 1	8	11.75	1.28	5	13.2	0.86	0.43
Block 2	2	10	1	2	12.5	2.5	0.45
Block 3	0			1	11		
Pooled (blocks 1 and 2)	10	11.4	1.05	7	13	0.82	0.28
Total (blocks 1, 2, and 3)	10	11.4	1.05	8	12.75	0.75	0.33
	2018						
	Control			Treatment			
Site	*n*	Mean clutch size	SE	*n*	Mean clutch size	SE	*P*-value
Block 1	5	11.8	1.66	4	13.25	1.31	0.53
Block 2	7	10.57	1.23	4	11.5	1.55	0.66
Block 3	0			1	15		
Pooled (blocks 1 and 2)	12	11.08	0.96	8	12.38	1	0.38
Total (blocks 1, 2, and 3)	12	11.08	0.96	9	12.67	0.93	0.26

specifically during the pretreatment and posttreatment periods. We documented no difference between the control (1.5 ± 0.8 bobwhites/km) and treatment (0.6 ± 0.6 bobwhites/km) units during pretreatment ($P = 0.36$; Figure 8). Similarly, we documented no difference between the control (2.0 ± 1.0 bobwhites/km) and treatment (0.6 ± 0.6 bobwhites/km) units during posttreatment ($P = 0.09$; Figure 8). This suggests that statistically, the insecticide treatment and year did not alter bobwhite population at the pasture scale during our study. Last, we did not document a linear relationship between pasturewide fire ant mound density and bobwhite relative abundance during either 2017 ($P = 0.44$) or 2018 ($P = 0.30$; Figure 9).

DISCUSSION

Overall, statistically, we did not document negative effects of fire ants on bobwhites at either the point-of-use or pasture scale. Our hypothesis that fire ants would negatively affect nest success and bobwhite survival was not statistically supported, but nest success and survival were both numerically higher in treated areas. Our hypothesis that the aerially applied

Table 7. Model selection results of analysis evaluating factors affecting breeding season (Apr–Aug) nest survival of radio-marked northern bobwhite (*Colinus virginianus*) in Goliad and Refugio counties, Texas, USA, 2017–2018.

Rank	Model	K [a]	AIC_c [b]	ΔAIC_c [c]	*w* [d]
1	S(.)	1	214.8018	0.000	0.2833
2	S(Trend)	2	215.8013	1.000	0.1719
3	S(Nearest Mound)	2	216.7076	1.906	0.1092
4	S(Year)	2	216.7085	1.907	0.1092
5	S(Density)	2	216.7697	1.968	0.1059
6	S(Age)	2	216.8099	2.008	0.1038
7	S(Mound Density + Nearest Mound)	3	218.5380	3.736	0.0437
8	S(Year + Age)	3	218.7115	3.910	0.0401
9	S(Year + Mound Density + Nearest Mound)	4	220.4378	5.636	0.0169
10	S(Age + Mound Density + Nearest Mound)	4	220.5478	5.746	0.0160

[a] K: number of parameters.
[b] AIC_c: Akaike's Information Criterion corrected for small sample size.
[c] ΔAIC_c: difference between a model and the best performing model.
[d] *w*: Akaike model weight.

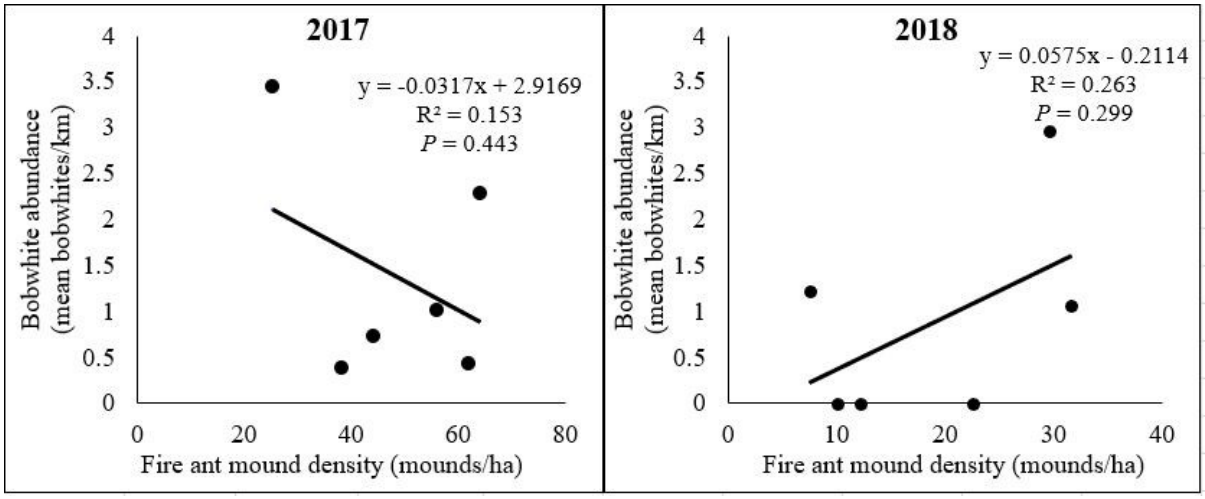

Fig. 9. Northern bobwhite (*Colinus virginianus*) relative abundance (bobwhites/km) as a function of red imported fire ant (*Solenopsis invicta*) mound density (mounds/ha) in Goliad and Refugio counties, Texas, USA, December 2017 and December 2018.

insecticide would reduce fire ant densities, but that bobwhite densities would remain unaffected, was partially supported. We did find evidence that the insecticide application reduced fire ant mound densities and forager abundances, but results were not consistent across blocks. In addition, bobwhite relative abundance was similar between control and treatment sites despite a potential reduction in fire ants. Overall, our study yielded small sample sizes which contributed to very low power in the statistical tests. Given the low power, it was unlikely for us to statistically show a difference if one existed.

Fire Ant Abundance

Pasture scale.—In general, we observed a decreasing trend in fire ant mound density. This finding is consistent with the Extinguish Plus user guide, which documented fewer active mounds in treated plots compared to untreated control plots (Central Life Sciences 2019). However, the effectiveness of the insecticide varied among blocks, which could be related to environmental conditions following insecticide application. It is recommended that the fire ant treatment be applied during times of no precipitation or dew for at least 8 hours so that the granules do not wash away or stick to the wet vegetation, making them impossible for the ants to pick up. In our study, there was brief, heavy rainfall directly following application

of the treatment in block 1. This rainfall led to poor conditions and may have influenced the efficacy of treatment. However, in block 1, we still documented reduced mound density. One restriction of our methodology was that observers could not leave the pasturewide transects to verify whether mounds were active; instead, mounds were assumed active if detected. We assumed that due to weather and rainfall in the area the mounds would disintegrate quickly, but that is not always the case and we did not test this assumption. This restriction in methodology also may have obscured results. However, even though we may have included inactive mounds in our mound density analysis, we still documented a decrease in mound density after treatment.

Regarding overall fire ant forager abundance, in general, there was only a statistical difference in fire ant forager abundance between the control and treatment units on block 1. However, forager abundance decreased to 0 on both blocks 1 and 3, which indicates biological significance of the treatment efficacy. It is unknown why forager abundance decreased on 2 blocks but increased on 1 block after treatment. Forager abundance decreased on block 1, which may have received a compromised treatment due to rainfall, but foragers increased on block 2, which received an ideal treatment with respect to rainfall. Therefore, it is unclear whether these differences in fire ant abundances are a product of the fire ant treatment or other causes. We placed only 1 bait cup per sample cell (10 ha each), which may have been an inadequate sampling effort and could explain the difference between mound densities and foraging ants relative to treatment efficacy. It is also possible that our study areas contained polygyne populations of fire ants, that is, in which a single mound harbored multiple queens instead of a single queen. When polygene populations exist, forager densities are higher and more difficult to effectively treat (Porter et al. 1991). The presence of polygene populations may explain why we did not document decreased forager abundances on all sites. We did not take exact weather measurements at each block during treatment and were unable to gather information in our study areas afterwards. Taking weather measurements at application sites during treatment is something to consider for future studies. After pooling blocks 1 and 2 to account for variation between blocks, we did not detect a decrease in forager abundance, but still documented a decrease in mound density. These results could be due to restrictions of density dependence; when there are too many mounds, resources to produce foragers are limited. With a reduction in fire ant mounds from treatment, more resources could be available for a single mound to produce more foragers. Our results differed from Caldwell et al. (2017), who treated a 3,744-ha area with Extinguish Plus and found that fire ant abundance was reduced 2 out of the 3 years following treatment. They implicated flooding as a reason why there was not a decrease in fire ants for 1 of the 3 study years and this is similar to flooding in our study. In June 2018, our study sites received approximately 36 cm of rainfall, which was higher than the average of 10 cm for the area (NOAA 2019) and flooded areas of our study sites for approximately 2 weeks. Fire ants have been observed using their combined bodies to form floating rafts and drift to different locations, which likely happened during these flooding events (Adams et al. 2011). Collectively, these results indicate that the insecticide efficacy varies based on environmental conditions following application.

Bobwhite Demography

Survival.— We used both Kaplan Meir and Program MARK to analyze bobwhite survival since Program MARK selected the best model, but there was no assessment of how well the model fit the data. Kaplan Meir allowed us to compare the survival distributions with a corresponding p-value. Bobwhite survival was not influenced by fire ant mound density or distance to nearest fire ant mound. In addition, bobwhite survival was similar in the treatment and control units before and after insecticide application. However, 4 weeks following application, when the treatment became fully effective, bobwhite survival remained relatively stable in the treatment units but decreased in the control units. This result provides evidence for possible biological significance that the fire ant treatment benefits bobwhite survival even though the difference between treatment and control was not statistically significant in our study. Fire ants do have the potential to sting and harm full-grown bobwhites, but bobwhites in our study did not appear to be directly affected by fire ants. We never observed any confirmed bobwhite mortalities caused by fire ants although given the warm ambient temperatures during much of our study and abundant scavengers, it would be difficult to document deaths caused by fire ants. Rather, predation appeared to be the most common cause of mortality in this study, although fire ants could have indirectly caused some of these predation events. Pedersen et al. (1996) observed that pen-raised bobwhites exposed to fire ants had less time for pecking, loafing, and sleeping, which could lead to weakening and increased vulnerability of the individual, resulting in increased predation risk. Despite this possibility of direct mortality, our results are similar to those of Johnson (1961), Brennan (1993), and Brennan et al. (1991), who suggested that fire ants do not substantially affect demographic performance of bobwhites.

Reproduction.—Nest survival also was not influenced by fire ant mound density or distance of nearest fire ant mound to nest. Similar to survival, we never observed a nest failure caused by fire ants. We did observe an instance where a nesting hen was found dead on top of the nest covered in fire ants. It is possible that the fire ants overpowered the bird and caused the mortality and nest failure, but this could not be confirmed. Even if this nest failure is assumed to be caused by fire ants, our overall results were similar to a study by Simpson (1976), who found that only 1 of 1,072 bobwhite nests was lost to fire ants. Our results differed from Rader et al. (2007), who documented failure of 5 out of 43 (12%) bobwhite nests caused by a similar fire ant species, the native southern fire ant (*Solenopsis xyloni*), in South Texas. Our findings were similar to the results of Mueller et al. (1999),

who hand-treated individual bobwhite nests with Amdro® (Ambrands, Atlanta, GA, USA) fire ant insecticide and did not document a difference in nest success when compared to untreated control nests. Mueller et al. (1999) did not report any bobwhite nests lost to fire ants but observed fire ants feeding on unsuccessful eggs in nests that were not treated with fire ant insecticide. Furthermore, no fire ants were found feeding on unsuccessful eggs in nests hand treated with fire ant insecticide. Mueller et al. (1999) treated individual nests with insecticide whereas we applied insecticide to pastures, but neither study reported significant differences in treatment effects on nest success.

Though we did not detect a statistical difference in bobwhite nest success between control and treated areas, apparent nest success did increase in treated areas, which provides evidence of possible biological significance. Because there was low statistical power, it was unlikely for us to demonstrate a statistical difference if one existed. The indirect effects of the treatment such as increased invertebrate richness and biomass may be beneficial for adult bobwhites and bobwhite chicks. Morrow et al. (2015) assessed the impacts of using a fire ant treatment to increase insect abundance. They treated fields with the same insecticidal ant bait used in this study and discovered 27% more individual invertebrates and 26% higher invertebrate biomass compared to control fields (Morrow et al. 2015). We did not sample invertebrates, but this is something to consider for future studies. Another point of consideration would be whether application of a fire ant treatment affects bobwhite brood survival. Mueller et al. (1999) documented an increase in proportions of brood surviving to 21 days of broods from treated nests (n = 25 broods, 53.5 ± 8.6%) compared to control nests (n = 25 broods, 24.7 ± 6.6%). Morrow et al. (2015) observed higher survival of Attwater's prairie-chicken broods that spent all of their time in areas treated to reduce fire ants compared to broods in untreated areas. We were unable to calculate brood survival due to the small sample sizes and the inability to count chicks in the tall prairie grass; we also suspected that some broods of chicks left radio-marked parents to join other broods, which would affect results.

Density.—Similar to our results for survival and nest success, we documented no difference in bobwhite relative abundance between treatments. One possible reason why we did not see an increase in bobwhite density after treatment is that with an already low density of bobwhites in the area, treatment may be less effective than if bobwhite density were high. For example, if there are fewer bobwhites in the area, there is greater opportunity to select high quality habitat and areas with already low fire ant abundances. In addition, there was no relationship between bobwhite relative abundance and fire ant mound density. These results are similar to Caldwell et al. (2017), who treated areas for fire ants; despite a documented decrease in fire ants, there was no increase in the number of female bobwhites during the nesting season, the number of females with broods, or the mean brood size per female.

Another possible alternative explanation for the lack of a population response to the fire ant treatment in our study may be the strong influence that environmental factors such as rainfall have on bobwhites. In the semiarid portions of the bobwhite geographic range, populations have been linked to precipitation, where populations can drastically increase during wet periods and decrease during drought (Hernández et al. 2005, Parent et al. 2016). However, in the Gulf Coast Prairie, too much precipitation can lead to flooding. Large areas of our experimental units were flooded during December 2018, possibly influencing our helicopter surveys and thus comparisons between control and treatment sites. Hurricane Harvey passed over all 3 of our study areas on August 25, 2017, causing damage and flooding at the end of our first field season. Maximum sustained winds ranged between 177–209 km/hr and rainfall exceeded 40 cm (NOAA 2017). We monitored 25 adult bobwhites before Hurricane Harvey hit and when we could re-enter our study areas 2 weeks later, there was 25% mortality (n = 7 bobwhites), of which 12% (n = 3 bobwhites) were located underwater. Hurricane Harvey was a powerful natural disaster that struck our study sites and may have impacted both bobwhite and fire ant populations in the area.

Collectively, there are a few possible explanations why we did not statistically detect influences of the fire ants or fire ant treatment on bobwhites in our study. We had low statistical power throughout our study which made it difficult for us to demonstrate a statistical difference if one existed. One biological reason is that fire ants would have to be the limiting factor for bobwhite populations in our study in order for a fire ant treatment to result in a population response. In our study, it is possible that the amount of habitat was a more influential factor than fire ants in bobwhite survival, nest success, and density. Although Allen et al. (2004) documented that bobwhite populations decreased over time following fire ant invasion in the Texas Coastal Bend, other researchers have highlighted that bobwhite habitat also has declined considerably in this area during the same timeframe (Allain 1999, Perez 2007). Another possible explanation for our results is that our sample sizes of radio-marked bobwhites, nests, and covey detections were low both years due to low bobwhite populations in the ecoregion (Perez 2007) and especially in our study area after the passage of Hurricane Harvey. As a result of these low sample sizes, our analyses may not have had the statistical power necessary to detect differences in survival, nest success, and bobwhite relative abundance between treatments. Additionally, because treatment efficacy as indicated by the number of foraging fire ants was poor on 1 of the 2 study blocks, we pooled data from the 2 blocks to evaluate treatment effects on bobwhites. This unfortunately may have diluted any effects that may have resulted from successful reduction in foraging fire numbers. Last, bobwhite response to fire ant treatment may require more than single applications or may exhibit a lag response, with effects appearing in future years. Thus, with repeated annual treatment, it is possible that fire ant densities would be reduced with a corresponding bobwhite response.

MANAGEMENT IMPLICATIONS

Even though fire ants have the potential to directly impact bobwhites, we did not statistically detect an influence of fire ants on bobwhites at the point-of-use or pasture scales in this study. However, after application of a fire ant treatment (Extinguish Plus), bobwhite survival and apparent nest success were higher than untreated control units. These trends indicate potential effects of treatment. Even though demographic performance of bobwhites was better in the treatment than control units, we did not detect a difference in overall bobwhite relative abundance 8 months post-treatment. Based on these findings, the following key points may be useful in managing bobwhites:

1. Fire ant treatment is expensive and may be impractical at a large scale.
2. Time, money, and effort may be better spent on creating habitat or increasing overall usable space to benefit bobwhites.
3. Given the relatively small sample sizes and potentially confounding effects of weather on our study, some results of our study (e.g., adult survival, apparent nest success) suggest that additional research on this issue is warranted.

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CLIMATE IMPACTS ON NORTH AMERICAN QUAIL

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ABSTRACT

North America's quail population trends are often linked to regional climate. Extreme climate events such as severe drought, hard freezes, or excessive winter precipitation can reduce quail populations by as much as 84%. Above-average spring and summer temperatures coincident with drought can reduce the laying season for quail by ≤60 days. Exposure of quail eggs to high temperatures during preincubation can initiate and alter embryonic development. Here, we review the impacts of extreme climate events and a changing climate on the survival, reproduction, and population trends of 6 North American quail species: California quail (*Callipepla californica*), Gambel's quail (*Callipepla gambelii*), Montezuma quail (*Cyrtonix montezumae*), mountain quail (*Oreortyx pictus*), northern bobwhite (*Colinus virginianu*s), and scaled quail (*Callipepla squamata*). Climate change scenarios are especially troubling when considered in conjunction with the heat stress hypothesis, which suggests that reproduction is reduced during heat and drought events by elevated corticosterone levels due to heat stress. Global climate change is predicted to increase the west-to-east precipitation gradient across North America. While eastern North America will see more frequent heavy precipitation events, western North America will experience more frequent and severe spring heat waves, droughts, and wildfires. These will further imperil western quail populations in the near term by decreasing the frequency of successful reproductive events. Over the long term, we expect both an elevational increase and southwest-to-northeast shift in species ranges, and concordant extirpation of local populations. Of North American quail species, California quail may see its range contract the most, approximately 50% under a 3° C global temperature increase scenario. Conversely, milder winters may increase the area over which climate is favorable to bobwhites by approximately 25%. However, these gains will largely be contiguous with regions where bobwhite populations are rapidly declining, or have been extirpated, due to intensive agriculture and other land use changes. Extirpation of local populations may not be reversible, as there are few examples of successfully reestablished populations. There is a critical need for a national recovery plan that incorporates the impacts of future climate change on quail populations. We recommend that incorporating quail and other grassland birds into agricultural enterprises become standard practice. Long-term solutions will require increasing habitat quantity and connectivity. We also recommend research to further test and expand upon the heat stress hypothesis, and we recommend land management practices to mitigate the negative consequences of climate change.

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Key words: California quail, *Callipepla californica, Callipepla gambelii, Callipepla squamata,* climate, *Colinus virginianus, Cyrtonyx montezumae,* development, drought, Gambel's quail, heat stress, Montezuma quail, mountain quail, northern bobwhite, *Oreortyx pictus*, reproduction, scaled quail

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EXAMINING A HABITAT–WEATHER THRESHOLD FOR NORTHERN BOBWHITE POPULATIONS IN THE SOUTHWESTERN UNITED STATES

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ABSTRACT

In semiarid portions of the northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) geographic distribution, weather is a strong driver of interannual abundance. However, the strength of this relationship may depend on habitat amount. Given this habitat–weather dependence, there is likely to be a threshold value for habitat that determines how strongly a bobwhite population responds to weather. Our objective was to evaluate the relationship between habitat amount and the relative influence of weather on bobwhite abundance in Texas and Oklahoma, USA and determine a potential land-cover threshold value. We collected bobwhite abundance and land-cover data from the Breeding Bird Survey and National Land Cover Database, respectively, for 2 time periods which corresponded to historical lows (2012–2013) and highs (2015–2016) of bobwhite abundance within this region. We reclassified land cover into grassland, shrubland, pastureland, cropland, forest, and urban cover, and combined grassland and shrubland categories to represent bobwhite habitat. We used weighted linear regression to model the difference between mean bobwhite abundance between each time period as a function of habitat amount, hypothesizing a positive, linear relationship given the theorized greater influence of weather on populations within higher habitat amounts. To evaluate a potential habitat threshold, we modeled mean bobwhite abundance, for each time period, and all individual land-cover variables using a generalized additive model with a negative binomial distribution. We detected a positive, linear relationship between habitat amount and the difference between high and low bobwhite populations (r^2 = 0.30), per our hypothesis. Models of land-cover variables differed between low- and high-abundance time periods. The time period of lower abundance (2012–2013) model included all land-cover variables except cropland and showed significant positive, linear relationships with grass and hay cover, and negative, linear relationships with forest and urban cover. Shrubland cover was the only nonlinear term, increasing to approximately 50–60% cover, then decreasing sharply with increasing cover. Deviance explained for this model was 41.2%. For the period of high abundance (2015–2016) the model explained approximately 25% of the deviance and was reduced to only negative, linear relationships with forest and urban cover. Our results provide some evidence toward the habitat–weather threshold hypothesis. Additionally, while no land-cover values showed a threshold-like relationship with bobwhite abundance, we did document differences in variable selection for each time period. Stressors on bobwhite habitat seem to have a more dramatic impact on bobwhite populations than available habitat, especially in periods of higher abundance, whereas periods of lower abundance also included habitat variables.

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Key words: *Colinus virginianus,* Great Plains, habitat, northern bobwhite, Oklahoma, Texas, threshold, weather

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EFFECTS OF CLIMATE CHANGE ON NORTHERN BOBWHITE NESTING CHRONOLOGY AND CLUTCH SIZE

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ABSTRACT

Widespread changes to breeding bird phenology in response to climate change have been apparent in North America for several decades. While the impact of an earlier breeding season may be minimal by itself, changes in community-level interactions can be greatly influenced because of varying responses to climate change in different trophic levels. Climate change has been shown to alter the onset of breeding season and chick survival, and lead to population declines for game birds in high latitudes, at high elevations, and on the periphery of their range. The topic of climate change in relation to northern bobwhite (*Colinus virginianus*; hereafter, bobwhite) populations has attracted interest in the past 2 decades. Some researchers have hypothesized that climate change has the potential to cause the breeding season to initiate sooner and have a shorter duration. Using a 29-year dataset (1992–2020) with 1,171 individual bobwhites, we analyzed how temperatures prior to the breeding season affected the timing of nest initiation and clutch size, and how the length of the breeding season varied over time. We determined that the average minimum daily temperatures 30 days prior to the breeding season warmed by 0.07° C/year from 1992–2020. For any given year, we found that nest initiation could occur 1.12 days earlier for every 1° C increase in temperature. Overall, we determined that the timing of the nesting season had not changed from 1992–2020. The overall average breeding season length (135 days) or last average initiation date (27 Aug) did not change over the course of our study. We did not find that clutch sizes have changed over time and they were not correlated to pre-laying temperature. We attribute the lack of significant change in nesting chronology to plasticity of populations within the core of the range and the intensity of bobwhite management on the landscape.

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Key words: breeding phenology, *Colinus virginianus*, nest initiation, northern bobwhite, temperature

Climate change has the potential to adversely affect wildlife to the extent of threatening the population persistence of those that cannot adapt to adverse extrinsic environmental factors. Studies have demonstrated that climatic changes can affect avian distributions (Root 1988), migration patterns (Sparks 1999), reproductive output (Torti and Dunn 2005), and survival rates (Barbraud and Weimerskirch 2001). Researchers have suggested that animal populations in higher latitudes are much less stable as compared to low- or mid-latitude populations (Hampe and Petit 2005) in the face of climate change. Researchers of game bird species have documented changes in the breeding phenology of high latitude populations of black grouse (*Lyrurus tetrix*) in Finland (Ludwig et al. 2006) and red grouse (*Lagopus lagopus*) in Scotland (Fletcher et al. 2013) as a result of warming spring temperature prior to the onset of breeding. While populations at such latitudes may be at a heightened risk when challenged by warming temperatures, other research suggests that populations found in more southerly latitudes are actually more prone to extinction (Sinervo et al. 2010). Researchers suggest that species found in the lower and mid-latitudes may not have the ability to adapt quickly to climatic extremes given they are acclimated to more temperate weather conditions (Sheldon 2019).

The northern bobwhite (*Colinus virginianus*; hereafter, bobwhite), like other imperiled ground nesting species, is also potentially vulnerable to a changing climate, especially on the fringe of its range. The potential effect of climate change on bobwhite population persistence has importance beyond the conservation of a single species. Bobwhite serve as an umbrella

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species for other wildlife (Crosby et al. 2015) and lands that are conserved in the name of intensive bobwhite management have an immense economic impact on local economies (Burger et al. 1999, Fleckenstein 2020).

With bobwhite populations decreasing significantly over the last 60 years range-wide (Sauer et al. 2017), researchers and managers alike have hypothesized on potential causes of the decline. Outside of the relatively well understood issues that bobwhite are facing such as habitat loss, habitat fragmentation, and predation (Brennan 1991, Rollins and Carroll 2001), climate change effects on bobwhite populations are mostly unknown. To our knowledge, there have been no studies that have analyzed the relationship between bobwhite demographics and climate change using long-term empirical data. In studies conducted using short spans of data or data based on simulation modeling, researchers have suggested that there is the potential for shorter breeding seasons, reduced reproductive output, and altered ranges in some localities (Guthery et al. 2000, Lusk et al. 2001, Rolland et al. 2011). Most earlier studies have been conducted on the edge of the bobwhite range, where extreme weather events (e.g., drought, prolonged freezing weather, flooding) are much more likely to impact bobwhite demography. It is currently unknown how changing climatic conditions are affecting bobwhite populations in the core of their range. The topic has gained much attention as researchers have reiterated the need for studies on how climate could be affecting bobwhite populations and how potential impacts will influence future management decisions (Guthery 2000, Lusk et al. 2001, Rolland et al. 2011, Martin 2012, Hernández et al. 2013).

Researchers need long-term datasets to study how critical issues such as climate change may affect bobwhite and to help resource managers make informed decisions. Given researchers' growing concern about bobwhite and climate change over the last 2 decades, we wanted to determine whether a relationship existed between climate and bobwhite breeding ecology in low altitude and low latitude populations within the core of the bobwhite range. Our objectives were to analyze the effects of temperature on the timing and duration of the bobwhite nesting season and the resulting effect on clutch sizes and to determine whether any of these variables have changed over 3 decades in any biologically meaningful ways. We hypothesized that bobwhite breeding chronology or clutch size would not vary significantly over time. We predicted that because our study area was located within the core of the bobwhite range, climate variables were less likely to affect populations as compared to populations found on the periphery.

STUDY AREA

Our study was conducted on an 8,000-ha privately owned property in Baker County, Georgia, USA that has been intensively managed for bobwhite hunting since the mid-1900s. The site is among similarly managed properties in the Albany, Georgia area totaling approximately 100,000 ha within the core of the bobwhite range (i.e., centrally located within the historical bobwhite range). The property is primarily low basal area upland pine (60%) consisting mostly of slash pine (*Pinus elliottii*), longleaf pine (*P. palustris*), and loblolly pine (*P. taeda*) with occasional live oak (*Quercus virginiana*) hammocks (5%) interspersed, planted loblolly pine for timber production (10%), and few hardwood drains and wooded wetlands (5%) along the Flint River. Annually disked fallow fields (20%) are found throughout the uplands and primarily consist of common ragweed (*Ambrosia artemisiifolia*) and camphorweed (*Heterotheca subaxillaris*). Ground cover in the uplands is primarily forbs (e.g., *Chamaecrista nictitans, Desmodium* spp., *Lespedeza* spp.) and native warm-season grasses. A detailed description of this site can be found in Yates et al. (1995), Burger et al. (1998), Hughes et al. (2005), and Terhune et al. (2006). This site is 50 m above sea level, receives approximately 130 cm of rainfall annually, and has an average daily high temperature of 25.6° C and an average daily minimum temperature of 12.2° C. In the breeding season (i.e., Apr–Sep), the site receives approximately 69 cm of rainfall and has an average daily high temperature of 31° C and an average daily minimum temperature of 18.9° C.

METHODS

Bobwhite Metrics

Adult bobwhites were trapped twice per year (Oct–Nov and Feb–Mar) using baited funnel traps (Stoddard 1931) from 1992–2020. Individuals captured were aged, sexed, weighed, banded with aluminum leg bands, and released at the trap site. A subset of individuals that weighed ≥132 g were radio-tagged with 6.2 g pendulum-style transmitters equipped with an activity switch (Holohil Systems, Ltd., Carp, Ontario, Canada). Bobwhites were tracked ≥2 times/week during the breeding season (1 Apr–30 Sep) to locate nests and determine nest fate. Individuals located in the same location for consecutive days were assumed to be incubating. Incubating nests were visited daily to monitor nesting progress until they were determined to be successful or failed. When the radio-tagged bobwhite was not present at the nest, eggs were counted to determine clutch size. Nests that began incubation on or before 1 June were considered to be the first nesting attempt for that individual bird. We calculated the nest initiation date using (incubation date) – (1.2 × clutch size) (Klimstra and Roseberry 1975) for each nest as ordinal date (1 Jan = 1). The population-level first nesting attempt was defined as the average date of incubation for the first nesting attempts for all individuals, and the earliest nest initiation date was defined as the first attempt of any individual for that year.

Climate Data Variables

Historical climate data for the study were obtained (NOAA National Centers for Environmental Information 2021) for the Southwest Georgia Regional Airport in Albany, Georgia (~20 km from study site). Daily precipitation, minimum temperature, maximum temperature, and average daily temperature were collected for each day throughout the study period. Bobwhite

hens begin increasing in weight approximately 1 month before producing eggs (Roseberry and Klimstra 1971). Therefore, we decided that the pre-laying temperature (PLT) that could affect the onset of incubation was 30 days before the onset of incubation. We used the average PLT for the 30-day pre-laying period of the first 5 years of the study as our baseline to determine whether temperatures were changing on our study area.

Analysis

We used linear regression to model the relationship between climate variables and year. We tested for serial correlation in the error terms using the "acf" function in R (R Version 1.3.1093, www.R-project.org, accessed 10 Feb. 2021) but no correlations were detected, negating the need for more complex error terms. We used generalized linear models to test the effect of climate variables on nest initiation and clutch size using the lme4 package (Bates et al. 2015). Year was treated as a random effect because multiple individuals were included per year. A Gaussian error term was used for the nest initiation models and a Poisson error term with a log link was used for the clutch size models. We used likelihood ratio tests to determine whether covariate models were more supported than the null model. For all models fitted, an alpha of <0.15 and 85% confidence limits were used to be able to detect change more liberally. We used marginal r^2 based on Nakagawa and Schielzeth (2013) to determine the amount of the variance explained by the fixed effect in the mixed effects models. Conventional r^2 was used for the simple linear regressions.

RESULTS

The average daily pre-laying temperature (PLT) was 19.8° C (SE = 0.06, range = 17.1–23.7) between 1992–2020 and showed no trend during the time series ($P = 0.28$, $df = 27$). The average maximum daily PLT was 27.0° C (SE = 0.06, range = 24.3–29.7) between 1992–2020 and also showed no trend ($P = 0.83$, $df = 27$). The average minimum daily PLT was 12.5° C (SE = 0.08, range: 8.6–17.7) between 1992–2020 and increased by 0.07° C/year ($P = 0.13$, $df = 27$, CI = 0.004–0.14; Figure 1). Average total precipitation 30 days prior to the onset of nest initiation was 7.6 cm (SE = 1.01, range = 1.27–21.08) and did not vary across years ($P = 0.35$, $df = 27$).

We collected nest data from 1,171 individual bobwhites from 1992–2020 that produced 1,598 total nesting attempts. We determined that 548 of those were considered first nesting attempts (i.e., nest initiation occurred on or before 1 Jun). The average population-level nest initiation date of first attempts across years was 8 May (day 127) (SE = 0.62, range of annual means: 26 Apr–18 May, day 115–137) and showed no trend ($P = 0.25$, $df = 27$) between 1992–2020 (Figure 2). The earliest nest initiation of the season did not vary across years ($\bar{x}$ = 14 Apr, SE = 0.51, $P = 0.185$, $df = 27$, range: 12 Mar–13 May).

According to the likelihood test, the pre-laying temperature model fit the data better than the null model (χ^2=3.95,df=1,P=0.05). For every 1° C increase in the 30-day pre-laying temperature period, nest initiation occurred 1.12 days earlier ($P = 0.06$, $df = 26.2$, CI = –1.92 to –0.33; Figure 3); however, the model explained very little variation (marginal $r^2 = 0.01$). Precipitation 30 days prior to the nesting season was not shown to affect nest initiation timing ($P = 0.19$, $df = 27$). The average clutch size for all nests was 12.3 eggs (SE = 0.32, range = 2–29) while the clutch size of first attempt nests averaged 14.32 eggs (SE = 0.15, range = 4–29). Clutch size

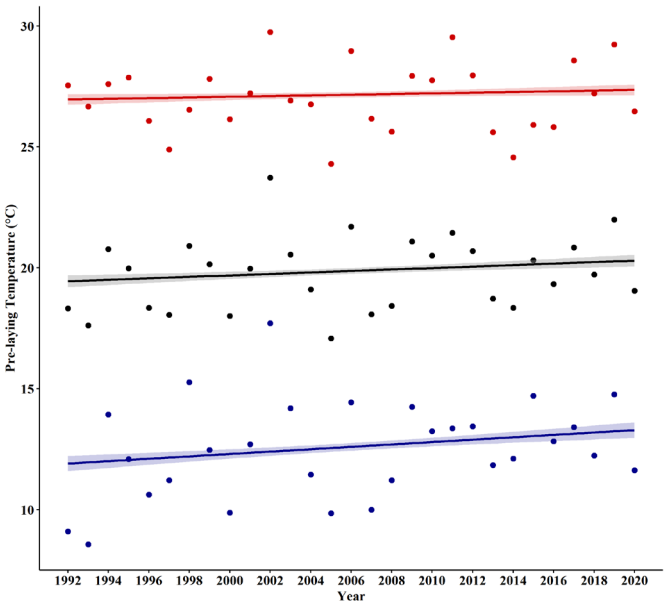

Fig.1. Average daily minimum (blue), mean (black), and maximum (red) pre-laying temperatures from 1992–2020 on privately owned property in Baker County, Georgia, USA and model predicted trendline with 85% credible intervals ($r^2 = 0.03$, $P = 0.28$).

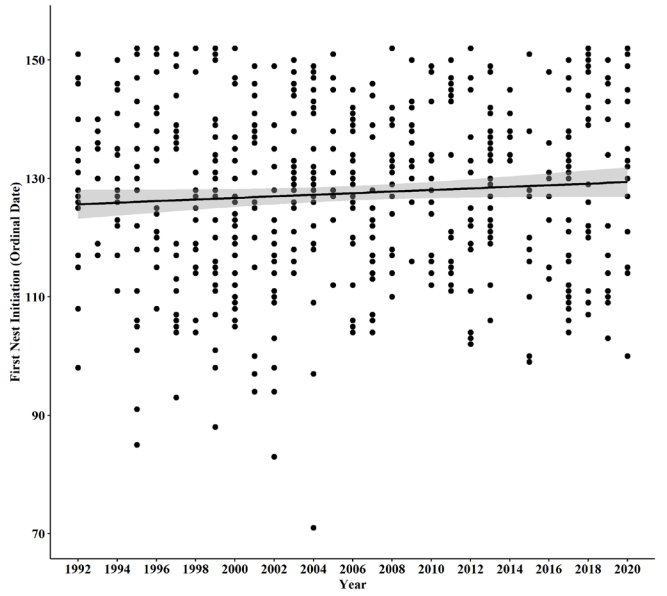

Fig. 2. Model-estimated mean nest initiation date from 1992–2020 and 85% credible intervals on a privately owned property in Baker County, Georgia, USA ($r^2 < 0.01$, $P = 0.25$).

did not vary by year ($P = 0.355$, $df = 27$) and was not affected by any climate variable (Figure 4). The average length of the nesting season (i.e., when nests were being initiated) was 135 days (SE = 3.11, range = 90–168) that lasted on average from 14 April–27 August (Figure 5). We detected no change in the last initiation date ($P = 0.18$, $df = 27$) or the overall nesting season length ($P = 0.957$, $df = 27$).

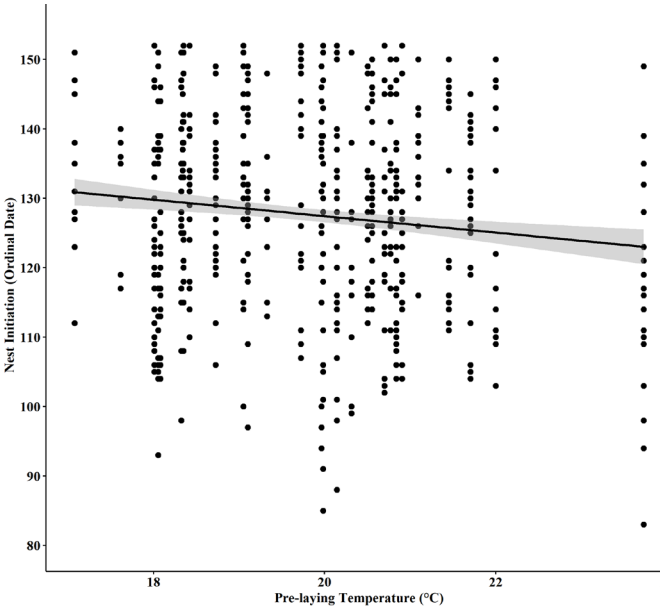

Fig. 3. Relationship between pre-laying temperatures collected and nest initiation dates of northern bobwhite (*Colinus virginianus*) from 1992–2020 on a privately owned property in Baker County, Georgia, USA and model-predicted trendline with 85% credible intervals ($r^2 = 0.01$, $P = 0.06$).

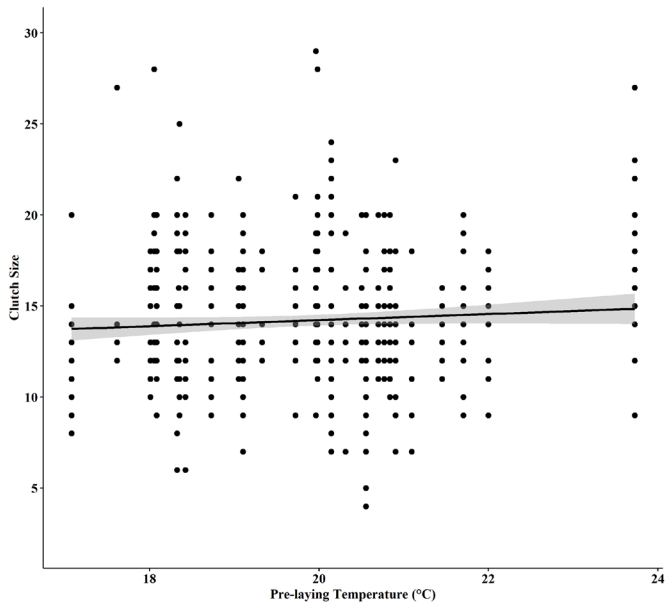

Fig. 4. Relationship between clutch sizes of first nesting attempts of northern bobwhite (*Colinus virginianus*) and pre-laying temperature from 1992–2020 on a privately owned property in Baker County, Georgia, USA and model-predicted trendline with 85% credible intervals ($r^2 < 0.01$, $P = 0.13$).

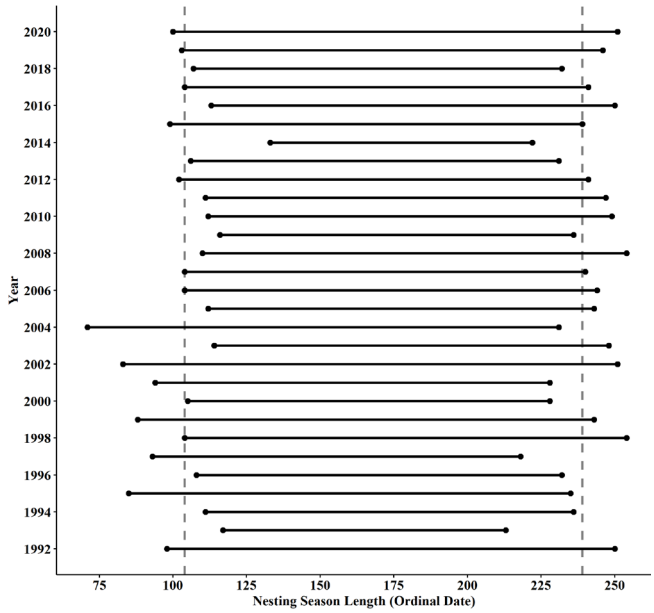

Fig. 5. Northern bobwhite (*Colinus virginianus*) nesting season length (displayed as ordinal dates, 75 = Mar 17, 250 = Sep 8, horizontal solid lines) and average start and end dates (vertical dashed lines) from 1992–2020 on a privately owned property in Baker County, Georgia, USA.

DISCUSSION

Our results suggest that while pre-laying temperatures have warmed slightly over the last 3 decades, a warming climate has not had a biologically meaningful influence on bobwhite nesting chronology or clutch size on our study area. While annual temperatures across the United States have averaged 0.75° C higher from 1992–2020 as compared to the preceding 97 years, temperatures in our study area have been only 0.46 °C higher across the same time period (NOAA National Centers for Environmental Information 2021). It is possible that climate during the spring and early summer months may be changing at a slower pace in southern latitudes and low elevation as compared to more northern latitudes and higher elevations (Flato and Boer 2001).

We found that clutch size did not vary according to any climatic factor and did not vary by year. This finding is consistent with other studies that found no link between temperatures and clutch size (Pendlebury and Bryant 2005, Fletcher et al. 2013). It is likely that other factors such as timing during the breeding season (Perrins and McCleery 1989), the number of nesting attempts (Aslan and Yavus 2010), or changes in food availability (Lack 1947) affect clutch size more than ambient temperature. The average clutch size during our study was 12.3 eggs. A study conducted on a nearby property from 1967–1971 concluded that average clutch size was 12.0 eggs (Simpson 1972). When we compare our 29-year dataset and data from Simpson (1972), it does not appear that clutch size has changed in Southwest Georgia over the last 50 years.

We documented that bobwhite nesting on our study area was minimally affected by temperature and nests were initiated 1.12 days earlier for every 1° C increase in the 30-day pre-laying period during the spring. Our results indicated that the window for the beginning of bobwhite nest initiation could vary by a week depending on the average daily temperature leading up to the breeding season. While photoperiod is the primary environmental cue for breeding chronology (Dawson 2008), seasonal temperatures can also dictate the onset of breeding (Brown et al. 1999, Dunn 2004, Fletcher et al. 2013). If temperatures in the period prior to the onset of breeding begin to increase incrementally on an annual basis, there is a potential for a consistently earlier breeding season in bobwhite. While a shift in the bobwhite breeding by itself may pose little risk to the population, there is potential for a mismatch between the peak of hatching and food resource availability (Dunn and Winkler 1999). A potentially earlier start to the breeding season could also reduce the window of allowable time for managers to conduct annual prescribed burns, mowing, and timber harvests. Nonetheless, the current influence of climate on nest initiation is minor.

We did not observe any change in the timing of bobwhite nest initiation from 1992–2020. This outcome is contrary to the findings of many researchers who have determined that some bird species, particularly in high altitudes and latitudes, are nesting earlier (Ludwig et al. 2006, Fletcher et al. 2013). The results of these studies align with other research that suggests that animals existing in high altitudes and latitudes are more vulnerable to climate change (Hampe and Petit 2005). The population we studied, which is found in the core of the range, appears to be insulated from any apparent changes at this time. The length of the breeding season was fairly consistent across years as 93% (27/29) of all years were within 1 standard deviation of the mean season length. Of the 2 years that fell outside of one standard deviation from mean, both were severe drought years. While there were several years prior to 2005 where the nesting season began noticeably earlier, these were individual nests and most nests thereafter began within the normal window of time.

Our results did not align with predictions from Guthery et al. (2000), who suggested that the bobwhite breeding season length would decline over time and lead to a slow annual rate of decline. This hypothesis is likely to be more applicable on the fringe of the bobwhite range where weather patterns are more extreme. Hampe and Petit (2005) also suggested that animals are more likely to exhibit change in response to climate at range margins. We have not seen evidence of this within the core of the range, where population density has actually increased by 0.12 bobwhite/ha/year over the duration of the study. Compared to bobwhites on the edge of their range, it is likely that populations within a landscape of intentional bobwhite management such as the one in our study may be buffered from modest climatic changes that have occurred so far. In addition, cultural practices such as supplemental feeding (Sisson et al. 2000, Buckley et al. 2015) and meso-mammal predator removal (Jackson et al. 2018, Palmer et al. 2019, Yeiser et al. 2020) as part of the modern quail management strategy (Stribling and Sisson 2009) have likely aided in further stabilizing or increasing populations on our area despite mild climatic changes. Future research should explore how intensive cultural practices may serve as climate mitigation strategies on the fringe of the bobwhite range.

MANAGEMENT IMPLICATIONS

The present rate of change regarding the timing of the onset, duration, or termination of breeding is very minimal and should not currently warrant any changes in management on intensively managed bobwhite properties. Research in the future should continue to monitor how bobwhite are responding to climate change to ensure that management is optimized to benefit population growth and expansion. If there is future evidence that the bobwhite breeding season is beginning sooner by a matter of weeks, is of shorter duration, or is being impacted by weather extremes, it could abbreviate an already short window of time where it is logistically and biologically feasible to manage bobwhite habitat. Significant changes in the future to nesting chronology patterns could warrant changes to the timing of the hunting season, prescribed burning, and other pre-breeding-season activities (i.e., timber harvesting, mowing, and dog training); however, our results suggest changes are not necessary at this time.

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THE EVOLUTION OF QUAIL RESEARCH: TRENDS IN THEMES, COGNITIVE EXTENT, AND LEXICAL DIVERSITY

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EXTENDED ABSTRACT

Language is an interesting characteristic that is unique to humans. Language represents a method of human communication and is believed to reflect a person's view of reality (Kramsch 2004). The words used by a person or a community provide insight into the ideas, concepts, and worldview held by people (Pennebaker et al. 2003). In science, publications represent a primary form of communication of ideas among scientists. Publications provide a historical record of a discipline and reflect the relative interest of a scientific community in particular concepts during a given era (Kim et al. 2018). Consequently, how word use in publications changes over time can provide valuable insight into the evolution of a discipline and help identify possible shifts in thinking of the scientific community (McCallen et al. 2019).

Quail science is a research domain that is over a century old. Studies of the life history and ecology of quail began appearing by the late 1800s, and investigations into the management of quail were circulating by the early 1900s (Bent 1932). Research on quail continued and increased during the 20th century and remains active at the beginning of the new millennium. Despite this long-term and active research trajectory, quail science appears to be a stagnant domain of research, with the same general topics being investigated decade after decade (Hernández 2021). I explore this qualitative impression of quail science and quantitatively assess the level of novelty in quail research. My goal is to address 2 general questions: 1) What are the main themes of quail research? and 2) How has the frequency of these themes changed over time? My research hypothesis is that, although the amount of quail research has increased over the past century, the cognitive territory covered by this research has remained more or less the same.

Addressing this hypothesis requires the definition of a few linguistical terms and concepts. In linguistics, *tokens* is the total number of words in a sample, and *types* is the number of different words in that sample (Malvern et al. 2004). For example, the phrase, "The bison herd grazed on the plains" has 7 tokens. Because 2 of the tokens represent a repetition (the word "the"), the phrase contains only 6 types. Linguistic scientists have used the ratio of types (number of different words) to tokens (total number of words) as a measure of *lexical diversity*, that is, the level of vocabulary richness (Malvern et al. 2004). Repetition of words causes an imbalance in the number of types to tokens; thus, higher repetition results in lower lexical diversity and vice versa (Jarvis 2013). *Cognitive extent* is a concept similar to lexical diversity but is based on the number of unique phrases appearing in a text (Milojević 2015). It operates at the level of phrases rather than single words, requires large unit quotas of text, and reflects the cognitive territory being covered by the literature (Milojević 2015).

I used the Proceedings of the National Quail Symposia as the literature base to conduct a linguistic assessment of quail science. I obtained the titles, authors, and abstracts of all articles appearing in the 8 volumes of the proceedings, a literature corpus that spanned 45 years (1972–2017). I determined the number of articles appearing per volume and the number of years between volumes to obtain a standardized measure of publication rate (number of articles/year). I also calculated the lexical diversity of article titles to obtain a measure of mean lexical diversity by volume. Because calculating cognitive extent requires large unit quotas, the sample size of articles appearing in the proceedings was too small to calculate cognitive extent for the proceedings. Thus, I conducted a literature search for quail-related articles in 11 ecological journals using the Web of Science database. These journals were Conservation Biology, Ecology, Ecological Applications, Ecological Monographs, Ecosphere, Journal of Animal Ecology, Journal of Applied Ecology, Journal of Wildlife Management, Oecologia, Wildlife Society Bulletin, and Wildlife Monographs. I calculated the cognitive extent of quail science using article titles of this larger literature corpus. For comparative purposes, I also calculated the cognitive extent of the general ecological research appearing in these journals. The amount of quail research published in the proceedings increased exponentially during the 45 years (Figure 1). The number of articles more than doubled from 1972 (n = 40 articles) to 2017 (n = 94 articles). The number of coauthors per article also increased from a median of 1 author (range: 1–4) in 1972 to 4 authors (range: 1–12) in 2017. Despite an apparent exponential increase in the amount of quail research, the cognitive extent of quail science appeared stagnant during 1973–2020 based on the 11 journals (Figure 2). In contrast, the cognitive extent of general ecological research in these journals steadily increased over the same time period (Figure 2).

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Historians of science suggest that the evolution of a discipline appears to follow a model of iterative and incremental growth, a pattern that has been described as cyclical development (Nunez-Mir et al. 2015). In such cyclical development, a scientific field (or domain of research) begins with a stage of theoretical conceptualization in which concepts are defined and central hypotheses are identified. This stage is followed by a stage of experimentation where theory is tested (Nunez-Mir et al. 2015). The knowledge gained from the experimentation stage results in refinement and expansion of the theory, which is broadened to include new concepts and perspectives arising from such experimentation. The refined theory then reenters the cycle, and the scientific field or domain of research advances in an iterative, incremental manner (Nunez-Mir et al. 2015). Ecological research appears to conform to such a model of cyclical development based on its incremental increase in cognitive extent over time. In contrast, quail research does not. No new ideas or concepts appear to be entering the domain given its relatively constant and unchanging cognitive extent. Stated differently, the quail scientific community appears to be retracing the same cognitive territory decade after decade. Consequently, quail research seems to be a domain suffering from a lack of novelty and creativity.

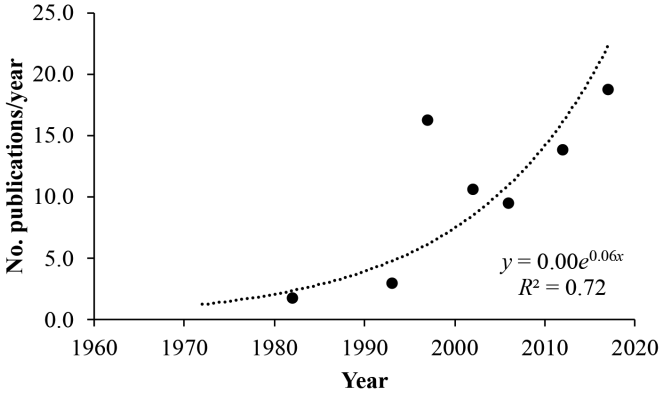

Fig. 1. Trend in publication rate (number of publications/year) in the Proceedings of the National Quail Symposia, 1972–2017.

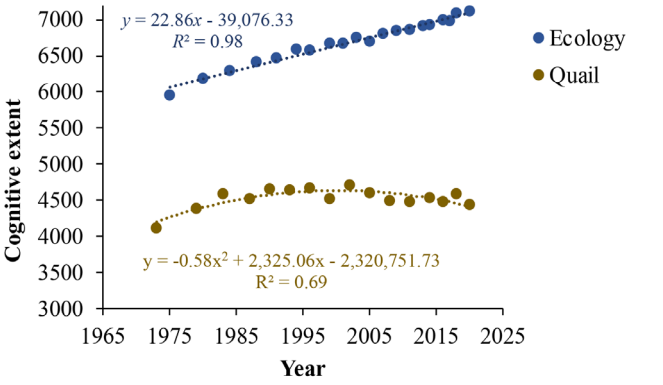

Fig. 2. Trend in cognitive extent for quail research and general ecological research appearing in 11 ecological journals, 1973–2020.

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Keywords: cognitive extent, content analysis, creativity, cyclical development, lexical diversity, northern bobwhite, quail, quail science, scientometrics, text mining

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