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An Evaluation of Northern Bobwhite Conservation Research: A Call for Large-Scale Studies

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AN EVALUATION OF NORTHERN BOBWHITE CONSERVATION RESEARCH: A CALL FOR LARGE-SCALE STUDIES

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) populations have declined throughout the species' range since the 1960s. Habitat loss and degradation are thought to have largely contributed to this decline by reducing the amount of space and resources required to sustain viable quail populations. Previous studies have attempted to address this issue by focusing on ranch-level management of bobwhites instead of on the effectiveness of large-scale techniques. Here, we review current and historical studies that have facilitated the implementation of management techniques on multiple scales. In doing so, we will also reveal the shortcomings of such studies by highlighting their narrowed focus on small-scale management and research, and reiterate the need for large-scale studies.

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The decline of northern bobwhites (*Colinus virginianus*) has been apparent for decades, with populations across their range currently deteriorating at a rate of >4.0%/annum (Sauer et al. 2014). This decline continues despite efforts to reverse the trend, indicating that predominate management strategies are either ineffective or lacking in some critical aspect. In the past, much of the effort in bobwhite management has been focused on a ranch or regional level, with little focus on large or landscape-level management (Brennan 1991, Williams et al. 2004*a*, Hernandez et al. 2013). Though many difficulties are associated with large-scale studies and implementing broad-scale management plans (Clark et al. 2015), there is increasing evidence that adopting a broad-scale management plan will be essential to the conservation of both bobwhites and other species associated with bobwhite habitat (Brennan and Kuvlesky 2005). The past 2 decades have seen the rise of large-scale management strategies for bobwhites; however conservation research trends may be slow to reflect these large-scale goals. A potential disconnect between research and management practices presents a challenge to conservation because small-scale research findings may not translate to the scale at which management is carried out.

In this review, we evaluate the relationship between bobwhite conservation management and research practices. We first examine the benefits and shortcomings of current and historical management and research. Second, we discuss changes in bobwhite research from the past 2 decades. Finally, we discuss 2 fundamental research questions that have yet to be answered and provide specific suggestions to improve research in both areas.

CHANGING PERSPECTIVES ON BOBWHITE MANAGEMENT

Northern bobwhites have historically been a popular game bird; and though the number of bobwhite hunters has decreased in tandem with the species' decreasing abundance, interest in conserving this species for sustainable harvest has persisted (Burger 2002, Williams et al. 2004*a,* Johnson et al. 2012). This popularity has both helped and hindered its conservation. Although hunter interest has aided in raising funds and awareness to protect bobwhites, this interest has ultimately abetted the precipitation of a culture and management style that was not designed to be primarily beneficial for large bobwhite populations. Rather, early management practices were meant to provide the greatest benefit to hunters and landowners by increasing quail abundance at minimum expense at a local level (Leopold 1933, Lehmann 1937, Johnson 1948, Williams et al. 2004*a*). This narrow interest led to the adoption of a symptomatic approach to quail management, whereby factors with potential negative impact on bobwhite populations were treated at a local level rather than addressed at a broad scale (Williams et al. 2004*a*). This symptomatic approach has included management measures such as food plots, predator control, and restrictions on bag limits (Guthery 1997). Although these approaches have the possibility of reaping beneficial impact on a local scale, they are

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impractical and have not been shown to affect broad-scale decline (Brennan 1991). Other issues addressed, such as red imported fire ants (Brennan 1993, Allen et al. 1995, Giuliano et al. 1996), helminthic parasites (Reed et al. 1981, Dunham et al. 2014), and mammalian generalist predators (Cox et al. 2004), as well as assessment of environmental factors such as precipitation (Hernandez et al. 2005) and thermal stress (Guthery et al. 1997, 2005; Hernandez et al. 2002*a*; Reyna and Burggren 2012), may have an impact on a broad scale but have mostly been studied at a local level.

Of the proposed causes for decline, the state of bobwhite habitat is now recognized as perhaps the most influential factor. Habitat management has always been a part of bobwhite management as the proper management of forest, prairie, and scrubland is paramount to sustaining and increasing quail abundance where quail are already present (Stoddard 1931, Brennan 1991). The importance of habitat has made it increasingly apparent that all of the aforementioned factors of decline are still yet symptoms of a larger problem—habitat degradation and fragmentation on a national scale. An estimated 80% of grass and shrub-land habitat has been lost in North America since the mid-19th century (Brennan and Kuvlesky 2005). Though quantifiable evidence of the bobwhite decline exists only as far back as the Breeding Bird Survey—approximately 60 years—this loss of habitat precedes estimates of the beginning of the bobwhite decline, circa 1875 (Peterson et al. 2002). Habitat loss is chiefly attributed to large, national-scale issues such as monoculture agriculture (Exum et al. 1982, DeMaso and Dillard 2007, Peterson 2007), afforestation (Brennan and Kuvlesky 2005), pesticide use (Brennan 1991), and urban or suburban development (Veech 2006); better said, human impact is likely the largest contributor to the bobwhite decline. This has caused conservationists to recognize 2 crucial concepts: 1) effective wildlife management is less about managing wildlife and more about managing people (Leopold 1933) as we are essentially battling ourselves to restore this species; and (2) a large-scale problem such as habitat loss warrants a large-scale response. In this way, previous small-scale management techniques and research have fallen short—their scope has been too narrow.

For the past 2 decades, bobwhite conservation has undergone a refocusing of scope; considerable effort has been made to manage bobwhites on a broad scale through programs such as the National Bobwhite Conservation Initiative, the North Texas Quail Corridor, and North Carolina's Cooperative Upland Habitat Restoration and Enhancement program, among others. These programs coordinate with local entities to manage vast quantities of land for bobwhites, and emphasize landscape-scale management (McKenzie et al. 2015). Although these efforts are laudable, it is not clear if the current scale of bobwhite conservation research reflects management scale, or if small-scale results can be generalized to management scale.

TWO DECADES OF BOBWHITE RESEARCH

To ascertain the prevalence of landscape-scale research, we conducted a scoping literature survey using the databases Wiley Online (John Wiley and Sons, Inc., Hoboken, NJ, USA) and Google Scholar (Google Inc., Mountain View, CA, USA). We also surveyed journal and symposia literature published in the past 2 decades of the National Quail Symposia (IV–VII). We limited our search to fieldwork and habitat or population studies of northern bobwhite quail published between 1996 and 2015, for which study area was described and size given or region described, if conducted on the regional level. We included studies in the National Quail Symposia for which only abstracts were available only if study area size was given in the abstract. We included studies that examined predation, survival, nest success, management practices and habitat manipulation, measures of abundance or density, migration or dispersal, modeling, and other features of population dynamics. We converted all study area sizes into hectares (ha) for analysis, unless only a region was described.

We chose to categorize studies into 3 rankings: ranch-level, landscape-level, and region-level. Choosing how to categorize studies based on study area size presented a challenge in that no formal definitions were found for these rankings. Ranch-level has been described as $\leq$2,000 ha (Sands et al. 2012*b*); however, this approximation appears rather conservative (Perez et al. 2002). Landscape-level has been described as areas encompassing approximately 1,000,000 ha (Sands et al. 2012*b*) but consistent measures have not been seen in the literature. Region is generally designated by ecoregion or as an area encompassing several landscapes. We chose to analyze the data using a slightly less conservative definition of ranch-level; we defined ranch-level as $\leq$5,000 ha, and landscape-level as $>$5,000 ha and $\leq$1,000,000 ha. Region was defined as an area greater than landscape-level ($>$1,000,000 ha). Many publications used more than one study area, so we chose to analyze the data by only looking at the largest study area listed. As a result of our broad definition of landscape-level and the fact that we omitted several articles at the ranch-level because they did not provide a study area size (e.g., Henke 2002), we assert that ranch-level studies are likely underrepresented in this analysis.

This scoping survey yielded 139 publications (Table 1). In our initial analysis, we divided studies into 2 time frames, each spanning approximately 1 decade. We then calculated the percentage of literature that each scale-rank made up, for each decade respectively. For the years 1996–2005, ranch-level studies made up 64.5%, landscape-level studies made up 22.6%, and region-level studies made up 12.9%. For the years 2006–2015, ranch-level studies made up 59.7%, landscape-level studies made up 31.2%, and region-level studies made up 9.1%. We conducted a second analysis wherein we pooled studies from both decades. For the combined years 1996–2015, ranch-level studies made up 61.9%, landscape-level

studies made up 27.3%, and region-level studies made up 10.8%.

The call-to-action for large-scale bobwhite management was initiated a little more than 2 decades ago (e.g., Brennan 1991); therefore, we expected to see an increase in the number of landscape-scale studies from one decade to the next and this was true overall. From 2006 to 2015, studies performed at the landscape level made up 8.6% more of the literature than in the previous decade. However, during 2006–2015, ranch-level studies still accounted for 28.6% more of the literature than landscape-level. Furthermore, when considering literature in both decades combined, ranch-level studies made up 61.9% of the literature alone. We reiterate that ranch-level studies are likely underrepresented.

From the results of this scoping review, we observe that bobwhite conservation research is still being performed predominately at ranch-level. Although we contend that not all research should be performed at a landscape-level, we do stress that small-scale studies may not yield results that are generalizable or able to direct broad-scale management. It is important that scientists invested in bobwhite conservation expand their inquiries to the landscape-scale at which the previously listed conservation initiatives take place.

FUNDAMENTAL RESEARCH CONCERNS RELATED TO SCALE

Based on our literature review, we believe there are presently 2 fundamental concerns that have yet to be answered by current scientific pursuits. The first is how much space a viable population requires; and the second is what ecological processes affect the persistence of local populations and how those processes are affected by landscape features. Here, we exemplify the importance of these concerns and how research has potentially been unsuccessful in addressing them.

Habitat and Space

The first fundamental concern of bobwhite research is to determine how much space a viable population needs. Guthery (1999) postulated that quail abundance is density-dependent, primarily restricted by the amount of viable habitat in a particular space and time (Guthery 1999, Lusk et al. 2002). Recent research has led further credence to the importance of understanding and incorporating density-dependence into population models (DeMaso et al. 2013). Considering both bird density and space requirements, several models have been developed to estimate the spatial requirements of a viable population. Guthery et al. (2000) suggested 800 bobwhites would be stable in approximately 650 ha; Twedt et al. (2007) suggested a sustainable population of >400 birds was possible at 5,000 ha; and Sands et al. (2012*b*) suggested that a stable population may need anywhere from 800 to 9,600 ha. Whether or not such stable populations actually exist in the tested conditions is not clear, generating concern regarding usable space and using current bobwhite research to make management decisions—stable and viable populations of quail could potentially be larger than what pasture-scale research takes into account. Studies of declining populations of bobwhites have concluded that there is a need to increase the quantity of breeding habitat for quail, though whether or how far breeding habitat should be increased beyond the scope of ranch-level management is unclear (Collins et al. 2009). Crosby et al. (2013) demonstrated the unsuitability of pasture-scale management via habitat restoration through the Quail Habitat Restoration Initiative. The study examined 29 areas over a period of 3 years to determine whether habitat restoration projects by the initiative had a positive impact on bobwhite abundance. The study concluded that no positive impact could be observed and postulated that this lack of impact could be explained by the fact that bobwhite population ecology operates on multiple scales, and that pasture-scale management and study would not necessarily take all scales or associated processes into consideration (Crosby et al. 2013). Furthermore, Williams et al. (2003*a*) showed that density-dependent abundance in bobwhites varies within their geographical range; variation was highest in the periphery of their range and the authors postulated that this was likely due to environmental factors affecting habitat quality. Terhune et al. (2010) have also suggested that habitat of poorer quality may need to be larger in area to accommodate a stable population of bobwhites, though to what degree habitat quality affects increased spatial needs has not been elucidated. Therefore, the spatial needs of stable and viable populations could potentially be greater than study areas on which research is performed and from which management decisions are made.

Improvements to habitat study and management.—Characterizing habitat has been a large part of bobwhite management, though the majority of attempts to characterize habitat occur at a pasture-scale (Peterson et al. 2002). To better implement large-scale management, further research should be aimed at characterizing habitat at a landscape scale. Although habitat quality may seem to be the most important feature at a local scale, the importance of habitat patch size, configuration, type, and connectivity may be more apparent at the landscape level (Riitters et al. 1997, Duren et al. 2011). For bobwhite habitat, efforts have been made using tools such as GPS and LANDSAT imagery (Roseberry and David 1994, Roseberry and Sudkamp 1998, Schairer et al. 1999) natural and agricultural resource databases (Peterson et al. 2002, Veech 2006), models (Baker 1996), and aerial photography (Exum et al. 1982, Guthery et al. 2001, Weber et al. 2002), but methods should be further refined. Habitat modeling at multiple scales, such as that performed by Duren et al. (2011), may provide much-needed insights to different habitat variables, which can be used to guide management of a particular landscape.

Research findings indicate that restoration and proper management of large, contiguous tracts or patches of habitat should continue to be the goal of bobwhite conservation (Brennan 1991, Hernandez et al. 2013). Although current large-scale restoration and management

Table 1. Referenced articles published between 1996 and 2015 that we examined while evaluating the relationship between northern bobwhite conservation management and research practices, categorized according to scale-rank, with largest study area size listed. Multiple study areas in a single reference were treated as separate unless they were specifically described to be continuous, in which case study areas were combined.

Reference	Study area
Ranch	
Arredondo et al. 2007	1,966 ha
Brennan et al. 1997*a*	1,500 ha
Brennan et al. 1997*b*	1,500 ha
Brooke et al. 2015	3,330 ha
Crosby et al. 2013	192 ha
DeMaso et al. 2002	283 ha
DeMaso et al. 2011	1,966 ha
DeMaso et al. 2013	1,966 ha
DeMaso et al. 2014	1,966 ha
Dietz et al. 2006	607 ha
Doerr and Silvy 2002	260 ha
Guthery et al. 2001	200 ha
Guthery et al. 2004	796 ha
Guthery et al. 2005	796 ha
Haines et al. 2004	1,563 ha
Haines et al. 2006	1,563 ha
Harveson et al. 1997	48 ha
Hernandez et al. 2005	2,000 ha
Hernandez et al. 2006	2,000 ha
Hiller and Guthery 2005	802 ha
Hiller et al. 2007	796 ha
Holt et al. 2006	2,300 ha
Holt et al. 2012	2,300 ha
Janke and Gates 2012*a*	1,200 ha
Janke and Gates 2012*b*	1,200 ha
Janke et al. 2013	1,200 ha
Jones and Chamberlain 2004	700 ha
Jones et al. 2010	66 ha
Kuvlesky et al. 2002	1,093 ha
Liberati and Gates 2012	1,200 ha
Liu et al. 1997	563 ha
Liu et al. 2002	563 ha
Lusk et al. 2006*a*	796 ha
Madison et al. 1997	5 ha
Manley et al. 1997	2,900 ha
Martin et al. 2006	2,368 ha
Miller et al. 2012	1,570 ha
Nedbal et al. 1997	610 ha
Oakley et al. 2002	3,900 ha
Osborne et al. 2011	10.8 ha
Palmer and Wellendorf 2007	1,568 ha
Palmer et al. 2005	250 ha
Palmer et al. 2002	445 ha
Palmer et al. 2012	1,568 ha
Parsons et al. 1997*a*	563 ha
Parsons et al. 1997*b*	563 ha
Peters et al. 2015	3,330 ha
Piispanen and Riddle 2012	1,619 ha
Potter et al. 2011	2,360 ha
Puckett et al. 1997	640 ha
Rader et al. 2007*a*	2,000 ha
Ransom and Schulz 2007	499 ha
Rollins and Koennecke 2012	1,900 ha
Rusk et al. 2007	1,200 ha
Sands et al. 2012*a*	750 ha
Sands et al. 2012*c*	1,900 ha
Seckinger et al. 2006	2,217 ha
Sisson et al. 1997*a*	380 ha
Sisson et al. 1997*b*	316 ha
Sisson et al. 2002*a*	3,734 ha
Sisson et al. 2002*b*	324 ha
Smith and Burger 2006	3,172 ha
Staller et al. 2002	1,568 ha
Staller et al. 2005	1,568 ha
Suchy and Munkel 1997	793 ha
Tanner et al. 2012	3,300 ha
Taylor and Burger 1997	320 ha
Taylor et al. 1997*a*	320 ha
Taylor et al. 1997*b*	2,850 ha
Taylor et al. 1999	2,850 ha
Terhune et al. 2006*b*	3,734 ha
Terhune et al. 2007	304 ha
Terhune et al. 2010	1,092 ha
Townsend et al. 1999	284 ha
Trewella et al. 2012	800 ha
Unger et al. 2012	3,300 ha
Unger et al. 2015	3,300 ha
Villarreal et al. 2012	1,902 ha
Wellendorf and Palmer 2006	1,568 ha
West et al. 2012	515 ha
White et al. 2005	3,898 ha
Whitelaw et al. 2006	1,568 ha
Williams et al. 2000	2,849 ha
Williams et al. 2003*b*	259 ha
Williams et al. 2004*b*	259 ha
Williamson et al. 2002	4,048 ha
Landscape	
Berkman et al. 2013*a*	757,300 ha[a]
Berkman et al. 2013*b*	757,300 ha[a]
Blank 2012	340,065 ha[a]
Buckley et al. 2015	5,665 ha
Collins et al. 2009	12,500 ha
Cook et al. 2006	13,300 ha
Cox et al. 2004	6,475 ha
Cox et al. 2005	6,475 ha
Cram et al. 2002	>60,000 ha
Cram et al. 2006	60,000 ha
DeMaso et all. 1997	6,475 ha
Dunham et al. 2014	120,000 ha
Duren et al. 2011	State of Delaware
Flock et al. 2012	6,480 ha
Godbois et al. 2003	11,700 ha
Godbois et al. 2004	11,700 ha
Hall and Silvy 2006	9,500 ha
Lohr et al. 2011	12,500 ha
Lusk et al. 2005	6,475 ha
Masters et al. 2006	60,000 ha
Michener et al. 1997	11,500 ha
Miley and Lichtler 2006	42,430 ha
Perez et al. 2002	13,760 ha
Peterson et al. 1997	15,500 ha
Rader et al. 2007*b*	15,000 ha
Rader et al. 2011	15,000 ha

Table 1. Continued.

Reference	Study area
Ransom et al. 2008	12,000 ha
Rolland et al. 2011	26,799 ha
Sisson et al. 2006	20,000 ha
Terhune et al. 2006*a*	8,490 ha
Terhune et al. 2006*c*	12,980 ha
Terhune et al. 2008	8,490 ha
Townsend et al. 2001	6,475 ha
Townsend et al. 2003	6,475 ha
Turner et al. 2008	12,000 ha
Wellendorf et al. 2002	6,084 ha
Wellendorf et al. 2004	6,084 ha
Williams et al. 2012	12,500 ha
Region	
Bridges et al. 2002	Ecoregion
Evans et al. 2013	Eastern and Central U.S.
Hernandez et al. 2002*b*	Ecoregion
Lusk et al. 2001	State of Oklahoma[b]
Lusk et al. 2006*b*	Ecoregion
Lusk et al. 2007	Ecoregion
Peterson et al. 2002	Eastern and Central U.S.
Roseberry et al. 1998	State of Illinois
Scott et al. 2012	Ecoregion
Thogmartin et al. 2002	Southern Illinois
Tri et al. 2012	9,000,000 ha
Twedt et al. 2007	21,000,000 ha
Veech 2006	Eastern and Central U.S.
Weber and Roseberry 2002	11 Illinois counties
Williams et al. 2003*a*	State of Kansas

[a] Converted from county descriptions.
[b] Excluding Oklahoma and Tulsa counties.

programs have met with success (McKenzie et al. 2015), published research has not effectively addressed this issue and restoration of large habitat patches may not be a viable option in all cases. For one, much of the historical bobwhite habitat has been repurposed, often for agriculture and related industries, sometimes for afforestation (Crosby et al. 2015); displacing highly productive agricultural settlements for the sake of restoring bobwhite habitat is neither logically sound nor economically advisable (Peterson et al. 1997, Veech 2006). Still, landscapes wherein bobwhite habitat occurs primarily as patches are not necessarily beyond salvaging. Although mainly associated with grassland, scrubland, and pine (*Pinus* sp.) forest, bobwhites make use of several different kinds of habitat, and apparent "slack" in patch configuration could be beneficial (Guthery 1999). However, severe fragmentation may not be as easily navigated and other solutions must be found.

Fragmentation is a limiting factor to both population size and gene flow (Segelbacher et al. 2010, Robert 2011) and research increasingly supports the notion that observable effects of fragmentation are influenced by both temporal and geographic scale (Stephens et al. 2004, Smith et al. 2011, Reino et al. 2013). The importance of connectivity among habitat patches has been enumerated throughout conservation literature (Taylor et al. 1993, Metzger and Decamps 1997, Pascual-Horta and Saura 2006, Foster et al. 2016). However, studies of how bobwhites navigate fragmented habitat are few and it is evident that more research should be conducted in this area (Fies et al. 2002, Terhune et al. 2010, Scott et al. 2012).

One technique that has been proposed in the wider conservation literature to palliate the effects of fragmentation is to establish conservation corridors. In theory, corridors are an elegant solution to habitat fragmentation, though there has been considerable skepticism regarding their true efficacy (Simberloff and Cox 1987, Hobbs 1992, Harrison and Bruna 1999). Much of this skepticism arises from models of corridors (Falcy and Estades 2007) and from corridor experiments that neglect to account for the behavioral ecology and dispersal capabilities of the species they were meant to help (Chetkiewicz et al. 2006). Despite skepticism, research continues to pursue corridors as useful conservation tools and corridor design continues to be improved (Beier and Noss 1998, Chetkiewicz et al. 2006, Pascual-Hortal and Saura 2006). A model by Hudgens and Haddad (2003) predicted that corridors will most likely benefit slow-growing populations that experience high mortality rates when traversing matrix habitat, and stress that the benefits of corridors depend on the temporal scale of conservation. A model by Falcy and Estades (2007) demonstrated that habitat patch enlargement is preferable to corridor construction, but corridors may be useful in connecting larger but spatially distant habitat patches or in patches where enlargement is not possible. The use of corridors in bobwhite habitat management has been explored primarily at the local scale with field borders (Palmer et al. 2005, Riddle et al. 2008, Piispanen and Riddle 2012), with the exception of a study by Bowling et al. (2014), which both assessed the influence of field borders on bobwhite abundance and characterized landscape surrounding field borders. Studies utilizing large corridors have not been published. Determining whether or not corridors would be an effective management tool for bobwhites requires further study. Even if corridors are deemed not a viable conservation tool for bobwhites, more research should be focused on the value and increase of connectivity in the landscape of bobwhite habitat.

Ecological Processes

Scale of study and management often hinge on the population dynamics of a species. Bobwhites exhibit *r*-selective reproductive strategies with immense reproductive capabilities (Halley et al. 2014), capable of producing large clutches and multiple-broods during the breeding season (Hernandez and Peterson 2007). These factors result in bobwhite populations that exhibit a yearly boom–bust phenomenon, typically associated with environmental factors such as precipitation (Hernandez et al. 2005, Hernandez and Peterson 2007). Populations display drastic seasonal fluctuations, with unexploited populations of bobwhite quail sustaining calculated annual losses of 56% (Guthery et al. 2000) and hunted populations experiencing losses as great at 80% (Brennan 1991). The cyclic nature of bobwhite-boom bust dynamics has

been observed at the regional level on large temporal scales (Thogmartin et al. 2002, Williams et al. 2003*a,* Lusk et al. 2007). Markedly few studies consider range-wide trends in bobwhite population ecology and dynamics (e.g., Parent et al. 2012). Most estimates of seasonal loss and fluctuations across years are based on studies performed at ranch-level. The possibility that stable populations of quail are larger and exist at greater spatial scales than are currently under study has the potential to change what we know about bobwhite population dynamics.

Population dynamics of most species are affected significantly by habitat loss and fragmentation. Bobwhite quail are no exception (Terhune et al. 2010) and it may be useful to apply principles from island biogeography to examine fragmented populations (Sands et al. 2012*b*). Smaller, more isolated, and more fragmented patches of habitat are likely to support populations more prone to extinction (Harrison and Bruna 1999). Proximity of biological islands (i.e., habitat patches) is critical because more closely grouped fragments may allow species to exhibit metapopulation dynamics. Metapopulation theory postulates that dispersal by individuals from one subpopulation to another will increase the viability and persistence of the metapopulation and that the local extinction or deterioration of one subpopulation can be recovered by individuals from nearby subpopulations (Stacey et al. 1997, Harrison and Bruna 1999, Martin et al. 2000, Hanski and Gaggiotti 2004). It is possible that our current estimations of what bobwhite populations can handle in regard to natural mortality and harvest pressure do not take metapopulation effects into account (Sands et al. 2012*b*). That is, a local population that sustains an annual mortality rate of 80% may only be able to do so because individuals from nearby subpopulations replenish the diminished population (source–sink dynamics). Metapopulation dynamics of this kind may not be seen at a ranch level examining a single patch of habitat. This presents a problem for bobwhite research performed at the ranch level because these habitat patches may be too small to support stable populations, given useable space and density-dependence. Bobwhite demographic patterns and characteristics have been studied using life stage analysis (LSA) models, which provide vital insight into factors that most strongly affect mortality and population persistence (Sandercock et al. 2008, Gates et al. 2012, Williams et al. 2012). Life-stage analysis models are useful in that they can provide demographic parameters for species about which little is known, in comparison with population viability analysis models (PVA), which generally work best for species about which much is known (Boyce 1992, Williams et al. 2012). However, because LSA models are often based on local data, they may not be capturing the entire picture.

Bobwhites have historically been regarded as a generally sedentary species. Though dispersal behavior across shorter distances is commonly observed, great dispersals by individuals are thought to be rare (Townsend et al. 2003). However, there is some evidence that bobwhite commonly disperse over large distances during the spring (Fies et al. 2002, Liberati and Gates 2012). Dispersal frequency appears to increase with increased habitat fragmentation (Fies et al. 2002), lending support to the notion that dispersal occurs as a result of the unavailability of suitable habitat, either because of saturation (reaching density-threshold) or habitat changes rendering the habitat unsuitable. In such a case, it has been observed that dispersing bobwhites are also more likely to survive than nondispersers during the breeding season (Townsend et al. 2003). Unsurprisingly, survival among dispersers is correlated with dispersal distance, and distance–survival relationships alternate during breeding vs. nonbreeding seasons (Lohr et al. 2011). Though dispersal appears to have survival benefits, it also poses mortality risks because matrix habitat (habitat not suitable to the species) must be traversed, and predation may be more likely in the matrix for species predated by relatively more mobile generalists (Wilcove 1985, Gehring and Swihart 2003, Ryall and Fahrig 2006). It is possible that, in ideal habitat conditions, bobwhites are completely sedentary but habitat fragmentation has altered their behavior. Alternatively, Berkman et al. (2013*b*) hypothesized that bobwhites may not be as sedentary as we have been led to believe, but that their tendencies toward longer dispersal have been hampered by the sparsity of suitable habitat. To reiterate an earlier point, it is evident that more studies should examine the movements and population dynamics of bobwhites because habitat degradation may have, by this point, completely precluded normal dispersal and population behavior, an assertion that has been corroborated elsewhere (Liberati and Gates 2012, Sands et al. 2012*b*). Small-scale research may not be capturing such phenomena, hindering both our understanding of bobwhite dispersal behavior and, consequently, population dynamics.

Expanding population dynamics studies to include landscape genetics and metapopulations.—Improving our understanding of bobwhite population dynamics is critical to enhancing the efficacy of broad-scale management. For most existing studies focusing on population dynamics and natural movements of bobwhites, radiotelemetry has been employed; however, this method has been called into question as seriously underestimating survivorship (Osborne et al. 1997, Cox et al. 2004) and potentially handicapping radiotagged birds (Guthery and Lusk 2004). If telemetry devices are cumbersome enough to preclude normal movements or decrease survivorship, experiments utilizing current telemetry devices may not be able to accurately study large-scale dispersal. Improvement of radiotelemetry devices is recommended to aid this purpose. Furthermore, although radiotelemetry has provided insightful demographic information about bobwhite populations (Williams et al. 2000, Scott et al. 2012), it reveals little about how these individuals contribute to the genetic fitness of a population, which is important for population persistence (Reed and Frankham 2003). An alternative approach to monitoring population dynamics may be found in the nascent field of landscape genetics, which seeks to understand how landscape features affect gene flow; this, in turn, can be used to make valuable

inferences about ecological processes of populations (Holderegger and Wagner 2006).

Tools and methods of genetic study have become critical to modern conservation science. Studies of population genetics have been used in combination with demographic patterns to estimate viable population sizes (Lande 1988, Nunney and Campbell 1993), and genomic studies of ancient DNA have yielded valuable insights into the prehistoric population dynamics of species, including those of the bobwhite (Halley et al. 2014). However, population genetics studies rely on the supposition of large populations and spatial symmetry and do not incorporate detailed life-history data into their analyses (Segelbacher et al. 2010). In this respect, landscape genetic studies may be more useful for examining bobwhite populations, especially because they account for the effects of landscape features on genetic structure and thus gene flow. Information about genetic structure with relation to landscape features may be used with demographic information to improve the accuracy of models (e.g., LSA or PVA) and help determine the overall fitness of a population (Nunney and Campbell 1993, Robert 2011). Landscape genetics is showing increasing promise in the management of threatened species, and several studies of its practical application are evident in literature (Epps et al. 2005, Vignieri 2005, Riley et al. 2006, Segelbacher et al. 2008). However, relatively few studies have examined bobwhites in the context of landscape genetics. A single example for bobwhites exists in 2 studies by Berkman et al. (2013*a, b*) based on the same metapopulation of bobwhites.

The first study by Berkman et al. (2013*b*) examined the effects of a single landscape feature (highways) on gene flow in metapopulation of bobwhites in southern Illinois. Interestingly, this study found that highways did not present a significant barrier to gene flow; rather, geographic distance between subpopulations was cited as the factor contributing most to genetic differentiation (Berkman et al. 2013*b*). The second study by Berkman et al. (2013*a*) attempted to determine overall genetic structure in and among these same subpopulations. In this analysis, Berkman et al. (2013*a*) found that an isolation-by-distance pattern was not apparent for the subpopulations and that the subpopulations exhibited a low amount of genetic structure. The authors postulated that their results indicated early patterns of genetic drift resulting from the recently agriculturally modified landscape (Berkman et al. 2013*a*). Bobwhites are not regarded to be proficient dispersers, so one might expect to see an isolation-by-distance pattern in the genetic structure of several subpopulations (Townsend et al. 2003, Haig et al. 2011). Though a low amount of genetic structure was observed overall, significant genetic structure was apparent at distances up to 11.4 km; the authors suggested that metapopulation processes of extinction and colonization could have been responsible for the low genetic structure, and additionally suggested that the structure observed up to 11.4 km was due to difficulties in dispersal. The recommendation from both studies was for larger, contiguous tracts of habitat within dispersal range (Berkman et al. 2013*a, b*). These recommendations are corroborated by modeling efforts such as those conducted by Ovaskainen et al. (2002), which found that the equilibrium of metapopulation size was affected by the spatial connectivity of patches and that patches should be well within dispersal distance of a species.

Studies such as these based on landscape genetics are, by themselves, far from plenary. By nature, the models produced by landscape genetics have limitations (Segelbacher et al. 2010, Berkman et al. 2013*a, b*). However, the analyses by Berkman et al. (2013*a, b*) provide an example of how landscape genetics can be used to make landscape management decisions, and they lend further credence to the idea that habitat management for bobwhites must be undertaken on a landscape-scale with a conscious effort to acknowledge the impact of landscape features on bobwhite dispersal and, thus, the genetic fitness of populations. Landscape genetics should be combined with improved telemetry equipment to make inferences and predictions about demographic patterns and connectivity for management decisions about bobwhite conservation (Haig et al. 2011, Keller 2015).

CONCLUSION

We conclude that there is a possible, if not probable, disconnect between the scales of management and research practices for the conservation of northern bobwhites. Small-scale research is likely insufficient to answer 2 of the most pressing questions in bobwhite conservation: 1) how much space a viable population requires, and 2) what ecological processes influence the persistence of local populations, and how such processes are affected by landscape features. Future research should endeavor to address the northern bobwhite decline at a large scale and utilize technologies, such as landscape genetics, that have the power to answer those questions.

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