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STATISTICAL POPULATION RECONSTRUCTION USING WINGS FROM HARVESTED NORTHERN BOBWHITES CAN INFORM MANAGEMENT

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ABSTRACT

Despite the widespread collection wings from harvested northern bobwhite (*Colinus virginianus*) by state wildlife agencies and private entities, age-at-harvest information has been largely underutilized for guiding management decisions for this species. Statistical population reconstruction (SPR) techniques can use age-at-harvest information and provide a valuable tool for monitoring trends and the status of bobwhite (and other game bird) populations. However, SPR has not been applied to bobwhite. We evaluated the utility of statistical population reconstruction models, which have been applied successfully to other species (e.g., elk, *Cervus elaphus*; black-tailed deer, *Odocoilues hemonius*; and greater sage-grouse, *Centrocercus urophasianus*), to reconstruct annual abundance and demographic attributes for a bobwhite population in southwest Georgia. During 1998 – 2016, we collected wings from harvested birds ($n = 17{,}448$; $n_{annual} = 969 \pm 104$) in conjunction with survival information from mark-recapture. We derived independent estimates of fall abundance from the same site using covey call counts and a standardized measure of hunting success (coveys moved per hour). SPR models suggested that population change was stable ($\lambda = 1.00$; CV $= 0.19$) compared to moderate population growth ($\lambda = 1.05$; CV $=$ 0.29) indicated by the covey call quadrat method. Abundance estimates from SPR and covey call counts were moderately correlated ($r = 0.48$) with only 3 out 18 years statistically different. Abundance estimates from SPR and hunting success (coveys moved per hour) was highly correlated ($r = 0.86$). SPR provides valid, conservative abundance estimates for bobwhite age-at-harvest data. Therefore, we endorse the use of SPR for bobwhites where age-at-harvest, hunter effort and another source of auxiliary data are readily available. As such, given that the collection of harvested wings is simple and low cost, we recommend managers and state agencies consider incorporating this technique into their management program.

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Key words: age, harvest, *Colinus virginianus*, northern bobwhite, statistical population reconstruction, wing data

Upland game birds are important wildlife resources for most states in North America, providing substantial revenue to state wildlife programs and recreational opportunity (e.g., hunting and wildlife viewing) for the public (Burger et al. 1999). A common management objective for state and federal agencies in the United States is often to increase or maintain populations of game birds to levels consistent with the demands of consumptive and non-consumptive users (U.S. Fish and Wildlife Service 1990, Brennan and Jacobson 1992). As such, long-term population declines of several game birds such as the American Woodcock (*Scolopax minor*), the northern bobwhite (*Colinus virginianus;* hereafter, bobwhite) and the Greater Sage-grouse (*Centrocersus urophasianus*) underscores the importance of population monitoring to aid in their conservation and management, especially on public lands (Brennan 1991, Connelly and Braun 1997, Peterson et al. 2002, Schroeder et al. 2004, Link et al. 2008, Cooper and Rau 2014).

The annual establishment of hunting regulations is the product of managers understanding the population status, dynamics, and the anticipated hunting effects on

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exploited species. Reliable estimates of annual abundance, among other demographic information (e.g., harvest estimates, recruitment, etc.), is essential for guiding management decisions and conservation of a game bird species. But, these data are often lacking because they can be difficult or impractical to obtain. Several survey methods, requiring variable inputs, for estimating bobwhite abundance exist (Rusk et al. 2007, Kuvlesky, et al. 1989) such as: mark-recapture, mark-recovery, or trap-removal (O'Brien et al. 1985, Guthery 1989, Williams et al. 2001); distance sampling using covey call counts, (DeMaso et al. 1992, Seiler et al. 2002, Wellendorf et al. 2004), line transects (Brennan and Block 1986, Guthery 1988), and helicopter surveys (Shupe et al. 1987, Schnupp et al. 2013). Each of these survey techniques offer distinct advantages over the others, but many of them are limited in their application. For example, some require large amounts of data (mark-recapture) and/or are labor intensive (distance sampling, mark-recapture), expensive (helicopter surveys), or impractical at large spatial scales (e.g., covey call quadrat surveys) to implement effectively. Commonly collected by bobwhite managers, records of hunt success (coveys found per hour) have been used as an index to bobwhite abundance (Rosene 1969, Brennan et al. 1997, Stribling and Sisson 2009). Hunt success data can provide reliable trend information when protocols are standardized (Palmer et al. 2002) but they lack a measure of precision and have limited application for decision making, especially if on-site conditions change (e.g., hunting style, habitat, etc.).

In North America, however, wings from harvested game birds are often collected from hunters by wildlife agencies or can easily be incorporated into a management program. These wings provide easy-to-access information (such as age and sex) on population structure and demographic rates, which may inform management decisions when used appropriately and/or when used in conjunction with ancillary data. Age-at-harvest data can be utilized in a statistical population reconstruction (SPR) framework to derive robust estimates of population parameters, such as abundance, that may otherwise be difficult to obtain (Downing 1980, Gove et al. 2002). SPR techniques involve fitting population demographic models of harvested wildlife populations using age-at-harvest data as the primary input, an additional auxiliary source of demographic data to aid parameter identifiability (Deriso et al. 1985, Skalski et al. 2007, 2012 a, b, Clawson et al. 2013), and a measure of capture (or hunter) effort. In many scenarios, SPR can be a useful tool for monitoring long-term population trends as well as help establish harvest limits for game populations. Although SPR has been successfully applied to game species such as elk (*Cervus elaphus*; Gove et al. 2002), wild turkey (*Meleagris gallopavo*; Clawson et al. 2015), and greater sage-grouse (Broms et al. 2010*)*, it has not undergone a rigorous evaluation for accuracy in bobwhite populations.

To our knowledge SPR techniques have not been applied to bobwhite despite collection of wings from harvested birds by some state wildlife agencies and other private entities ostensibly because few techniques are readily available, or perhaps known, to incorporate such data. Given that inventorying wild bobwhite populations remains one of the greatest challenges facing state wildlife agencies, SPR may provide a useful and cost-effective tool for monitoring the status of bobwhite populations on wildlife management areas and/or focal regions comprised of either or both public and private properties. Furthermore, a salient challenge of large-scale, multi-state population recovery efforts, such as the National Bobwhite Conservation Initiative (Palmer et al. 2011), is the coordination of monitoring to provide a consistent, accurate abundance estimate using minimal data and effort across individual states. Thus, our objectives were to estimate population abundance and temporal trends in abundance of bobwhite on a private plantation located in southwest Georgia, U.S.A. from 1998-2016, and evaluate the efficacy of SPR techniques for utilizing bobwhite age-at-harvest data to estimate abundance.

STUDY AREA

We conducted the study on a private property (8,094 ha) located in Baker county in southwest Georgia, USA. The study site was located in the Upper Coastal Plain physiographic region and comprised of old field pine (*Pinus* spp.) forests (80%) with relatively low basal area (3–9 m^2/ha) and small (e.g., <2 ha), scattered fields (20%). The study area has been under intensive bobwhite management for >50 years. Habitat management techniques included frequent burning (50–70% burned annually), timber thinning, seasonal disking, chopping and mowing, supplemental feeding, and mammalian nest predator control. Typical field management consisted of disking in fall and late winter to stimulate annual weed production and arthropods. As a result of these intense management regimes, our study areas maintained abundant wild bobwhite density ranging from 2.5 to 7.4 birds per hectare (Yates et al. 1995; Burger et al. 1998, Stribling and Sisson 2009).

METHODS

We trapped wild bobwhites during October–November and March–April 1997–2016 using confusion-style, baited funnel traps (Stoddard 1931), placed at an average trap-density of approximately 1 trap per 2.56 ha. We camouflaged traps by covering them with brush (e.g., fresh-cut pine boughs) to minimize stress on captured birds. We classified bobwhites by age and sex, and we weighed, and leg-banded them with a unique identifier (#7, aluminum band from National Band and Tag) and released them at capture sites.

Harvest was conducted annually on the study site during the hunting season (November–February), contributing substantially to recovery data. Hunting was conducted from horseback, and mule-drawn wagon, using trained pointing bird dogs as well as retrieving dogs to locate lost harvested birds. The reporting rate was assumed to be 100% because we conducted this research

Table 1. Northern bobwhite age-at-harvest date for private property located in Albany, Georgia, USA, 1997 – 2007.

Year	Juvenile	Adults	Total	Capture Effort (hrs)
1998	858	247	1,105	286.25
1999	739	279	1,018	300.25
2000	1,130	327	1,457	321.75
2001	1,028	360	1,388	292.5
2002	1,098	494	1,592	339
2003	1,141	436	1,577	345
2004	1,055	551	1,606	342.25
2005	990	345	1,335	328.75
2006	666	329	995	274.25
2007	422	132	554	196
2008	582	221	803	243
2009	624	249	873	230.5
2010	550	268	818	247
2011	271	131	402	144
2012	352	94	446	179.75
2013	518	206	724	206.75
2014	214	127	341	133.25
2015	284	130	414	166.75
Total	12,522	4,926	17,448	4577

on private property, hunting and harvest was controlled, and all harvested birds was entered into a centralized research database. We constituted a year beginning on 1 October and ending 30 September of the following calendar year to fully incorporate each hunting season (November–February). Each bird harvested was handled by research staff prior to cleaning; during this time, we determined age and sex (juvenile or adult) using molt patterns on the wings (Petrides and Nestler 1943, Rosene 1969) and recorded band information if present. For each hunt, plantation staff recorded start and end times and collected information on hunt encounters (coveys pointed, coveys shot, wild flushes, etc.), number of birds harvested, covey size and number of hunters (observers). We used these data to develop capture (hunt) effort (Table 1) and deduce hunting success metrics (coveys moved per hour). All methods followed Institutional Animal Care and Use Committee approved protocol (Protocol Review No.: A1999-10028; A2001-10100; 2002-0364).

We used covey call counts (DeMaso et al. 1992, Seiler et al. 2002, Wellendorf et al. 2004) to estimate fall bobwhite abundance during 1999 – 2015. We conducted covey call quadrat surveys from mid-October through late-November and estimated bobwhite density following protocols of Wellendorf et al. (2004).

Statistical Analysis

For the SPR analysis, we used the software PopRecon 2 to construct and analyze a joint-likelihood model based on three separate likelihoods: the likelihood of age-at harvest (wing data), the likelihood of survival (mark-recapture data), and the likelihood of harvest probability (band recovery data). PopRecon 2 uses maximum likelihood estimation methods to estimate abundance for each age class and year, as well as associated confidence intervals (see Gast et al. 2013a, b). It uses a 2-stage estimation method wherein survival and harvest parameters are estimated solely based on the age-at-harvest and hunter effort data, then a Horvitz-Thompson type estimator is used to incorporate the binomial sampling process (inherent in the harvest process) into the estimates of abundance (Gast et al. 2013a, b, Horvitz & Thompson 1952).

We generated 2 types of auxiliary data for SPR: survival and band recovery data. For the auxiliary survival likelihood (mark-recapture data), we used Burnham's Live-Dead Recovery model (Burnham 1993) in program MARK to estimate survival for both age classes (juvenile and adult) in each year from 1998-2007 during which large sample sizes of banded birds were maintained. We determined age as adult (>1 yr) or juvenile (<1 yr) at time of initial capture and we assigned each individual a binary covariate. We deductively determined age for subsequent encounter occasions, whether recaptured or not, based on maturity time (Stoddard 1931, Rosene 1969). We modeled age as a time-varying indicator in MARK (using 8 indicator variables: age1, age2, age3, ..., age8) to delineate 2 groups: juveniles and adults, coded as 0 and 1, respectively. Because bobwhites were juveniles for only 1 year (i.e., 2 encounter occasions) we needed only 8 covariates (i.e., no. capture occasions/2) to model this parameter. We coded adult birds captured during spring or fall seasons as adult for the initial trapping session and each encounter occasion thereafter. We coded bobwhites classified as juveniles captured during fall as juvenile for the initial and subsequent (i.e., spring) trapping occasions and adults for remaining encounter occasions, whereas bobwhites classified as juveniles and captured during the spring we coded as juvenile for the initial trapping occasion and as adult for each subsequent encounter occasion.

For the likelihood of harvest probability, we summarized the number of individuals and banded birds recovered from harvest for each year and age class.

We used Pearson Product-Moment Correlation (R Development Core Team 2015) to measure the strength of a linear association between abundance estimates derived from covey call counts and PopRecon independently.

RESULTS

The total number of harvested birds (n = 17,448) varied by year and age class (Table 1). Average annual survival was 20.0% (SE = 3.97) and 25.24% (SE = 4.94) for juvenile and adult bobwhites, respectively (Table 2). We banded a total of 5,675 birds of which 299 were harvested during the course of the study (Table 3). Annual harvest effort was high overall ($\bar{x}$ = 254 hours/year; SE = 16.63; see Table 1), but harvest effort was higher in the first 9 years compared to the second 9 years ($\overline{x_{1998-2005}}$ = 194.11 hours/year; SE = 8.87; $\overline{x_{2007-2015}}$ = 194.11 hours/year; SE = 13.87, see Table 1). Similarly, hunt success (birds harvested) declined through time whereby the first 9 years (1998 – 2006) of the study an average of 4.2 birds was harvested per hour compared to

Table 2. Annual survival estimates, used as auxiliary data for statistical population reconstruction, and associated standard errors derived from Burnham's joint live-dead recovery model in program MARK for juvenile and adult northern bobwhite on a private property in Albany, Georgia, USA, 1997 – 2007.

	Juvenile		Adult	
Year	Survival	SE	Survival	SE
1997 - 1998	0.1313	0.0307	0.1434	0.0337
1998 - 1999	0.1292	0.0215	0.1828	0.0259
1999 - 2000	0.2576	0.0250	0.2922	0.0221
2000 - 2001	0.1645	0.0176	0.1886	0.0187
2001 - 2002	0.3111	0.0238	0.3978	0.0183
2002 - 2003	0.1892	0.0212	0.2147	0.0211
2003 - 2004	0.2377	0.0445	0.3303	0.0733
2004 - 2005	0.2484	0.0689	0.3193	0.0746
2005 - 2006	0.2219	0.0780	0.2426	0.0710
2006 - 2007	0.1420	0.0389	0.2539	0.0759
2007 - 2008	0.1625	0.0666	0.2116	0.1089

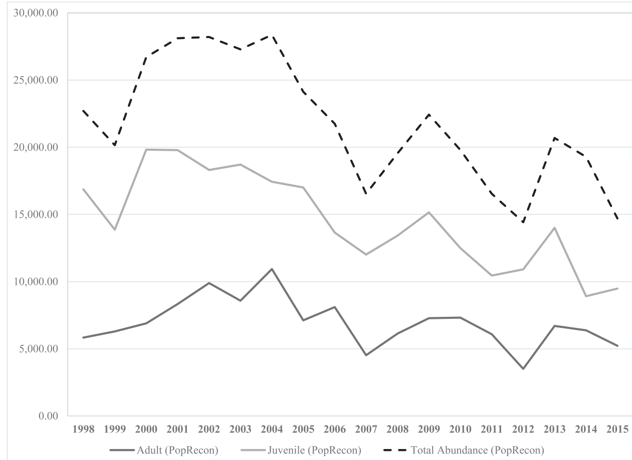

Fig. 1. Statistical population reconstruction abundance estimates for northern bobwhites (adult, juvenile and pooled) as derived from PopRecon2, during 1998 – 2015.

only 3.0 birds per hour during the last 9 years (2007 – 2015). Similarly, a banded bird was harvested approximately every 14 hours of hunting during 1998 – 2006, whereas 59 hours of hunting during 2007 – 2015 was required, on average, to harvest a banded bird (Table 1 & 3).

Using PopRecon2, we estimated the finite rate of population change to be $\lambda = 1.00$ (CV = 0.19) compared to $\lambda = 1.05$ (CV = 0.29) for covey call quadrat method. Using the fitted capture coefficient and annual adjustments to harvest effort (hours hunted), we estimated the average harvest probability of 0.0414 (SE = 0.003) which was similar to that estimated via program MARK, band recovery models (Terhune et al. 2007). The SPR produced reasonable annual abundance estimates for adults and juveniles (Figure 1). During the 18-year period, population reconstruction estimates from PopRecon2 and covey call counts were moderately correlated (Figure 2, $r = 0.48$); and when we removed outliers for 3 years (2007, 2012 and 2015), associated with dramatic population increases, the linear relationship increased substantially ($r = 0.71$). Population abundance estimated from SPR was more strongly correlated ($r = 0.86$) with hunt success (coveys moved per hour; see Figure 3).

Table 3. Northern bobwhite band recovery and capture effort data, used as auxiliary data for statistical population reconstruction, for a private property in Albany, Georgia, USA, 1997 – 2007.

	Banded		Harvested		Total	
Year	Adult	Juvenile	Adult	Juvenile	Banded	Harvested
1998	79	343	8	19	422	27
1999	162	639	5	32	801	37
2000	75	488	8	23	563	31
2001	125	573	11	27	698	38
2002	194	492	14	19	686	33
2003	96	204	7	7	300	14
2004	104	205	6	14	309	20
2005	73	234	4	13	307	17
2006	92	161	0	11	253	11
2007	30	106	0	4	136	4
2008	29	97	1	3	126	4
2009	31	106	1	8	137	9
2010	52	82	5	3	134	8
2011	28	79	0	6	107	6
2012	39	76	1	3	115	4
2013	32	64	1	1	96	2
2014	34	60	0	1	94	1
2015	24	61	0	0	85	0
Total	1346	4329	76	223	5675	299

DISCUSSION

Statistical population reconstruction appears to be a promising tool for estimating bobwhite abundance using age-at-harvest data. We found that SPR provided more conservative abundance estimates during most years compared to fall covey call counts such that evaluation

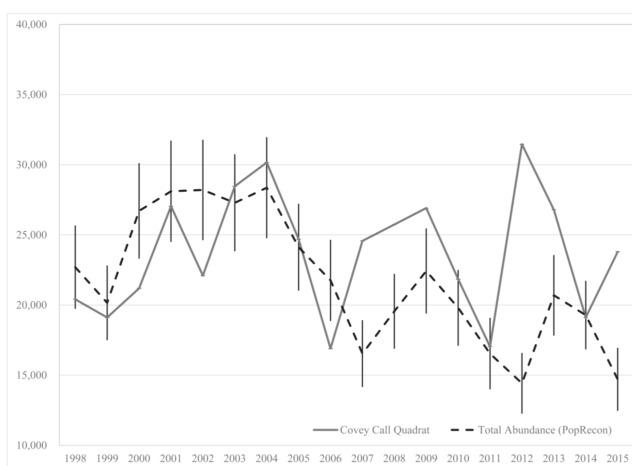

Fig. 2. Annual abundance estimates for northern bobwhites derived from statistical population reconstruction using PopRecon2 and covey call counts, during 1998 – 2015.

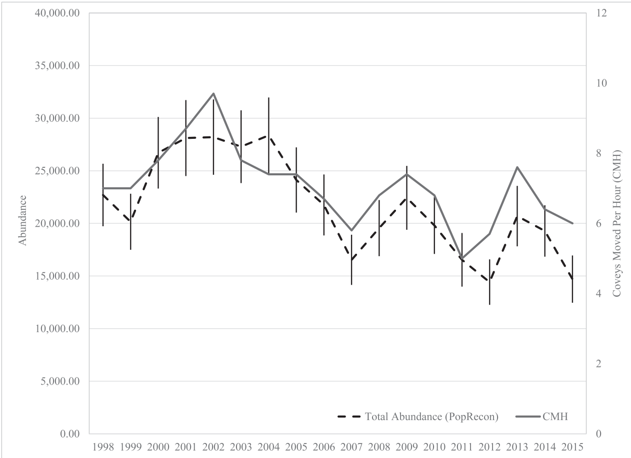

Fig. 3. Annual abundance estimates for northern bobwhites derived from statistical population reconstruction using PopRecon2 and hunting success represented as coveys moved per hour, during 1998 – 2015.

of these estimates inferred a stable population whereas traditional covey counts suggested a slightly growing population (4.6% increase per year). Covey call counts occurred on a small subset (<10%) of the study area whereas harvest of bobwhites occurred throughout the property potentially explaining some of the disparity among population estimates. SPR has been suggested to provide a minimum population estimate as opposed to true abundance (Davis et al. 2007), but further evaluation and comparison to other population estimation techniques (e.g., mark-recapture, Lincoln-Peterson) is warranted.

Annual trends from SPR may be misleading in certain years when annual survival or recruitment rates are highly variable (outside the long-term averages) over time as they can be for high-turnover species such as bobwhites. For example, during 3 years (2007, 2012, and 2015) where dramatic population increases occurred in covey call data, SPR abundance estimates differed from covey call estimates by more than 8,000 individuals. However, the strong relationship between hunt success (coveys moved per hour; Figure 3) and SPR abundance estimates suggests that bias associated with covey call counts is a plausible explanation for the difference during these 3 years. For instance, in 2007, the property was hit by a severe tornado which was debilitating to habitat in the area immediately followed by a new ground effect related to cleaning up with heavy equipment after the event (Palmer et al. 2000, Sisson et al. 2002). This new ground effect elicited a rapid bird response on a portion of the census plots, elevating population estimates for the area impacted. If SPR is insensitive to sharp upticks in abundance, inclusion of recruitment auxiliary data, such as broods produced per hen or chick survival, could help to mitigate this bias and inform the models for improved estimation (Gast et al. 2012). Davis et al. (2007) submitted that collapsing age classes was highly effective and provided more robust abundance estimates in these cases, but also recognized that certain violations of assumptions are known to impact abundance and trend estimates which might explain the difference we observed in 3 years experiencing precipitous population growth. Alternatively, because bobwhite wings from harvested birds can be backdated to incorporate multiple juvenile age categories (e.g., 1-month, 2-months, 3-months; see Rosene 1969, Petrides and Nestler 1943), improved reconstruction estimates during rapid population expansion years is plausible.

Beyond age-specific abundance, SPR provides demographic parameters such as probability of harvest, survival and recruitment that could inform management decisions or regulatory processes through adaptive management or complement harvest information programs (HIP). For instance, one could ostensibly use this method to determine which demographic (e.g., recruitment or harvest) is limiting population growth and potentially adjust management or harvest regulations accordingly (Skalski et al. 2011). In our study, probability of harvest was relatively constant and low (<%7), suggesting that recruitment and/or variation in annual survival was likely driving population fluctuation from year to year and not additive harvest mortality. In a similar vein, using SPR to investigate the sensitivity of hunter effort relative to known demographics such as natural mortality and harvest rate may help to establish hunting regulations or adjust bag limits. We observed, for instance, that for every hour of hunting during the first 9 years (1998 – 2006), 4.2 birds were harvested compared to only 3.0 birds harvested per hour of hunting during the last 9 years, suggesting hunt success was lower during 2007 – 2015. Numerous factors could explain this decline in hunt success such as inexperienced hunters, variable climate or variable scenting conditions, or changes in vegetation density. Although hunting effort (total hours hunted per year) remained high from year to year, we observed a lower proportion of banded birds harvested later (2007 – 2015) in the study due to a change in hunter demographics which may have contributed to lower estimated abundance from SPR during some years. The interplay between hunter effort and hunter success (harvested birds) on SPR abundance estimates merits additional research.

In this study, we demonstrated the utility of SPR models in estimating bobwhite abundance, yet these models could still be improved with additional or different types of auxiliary data. In addition to harvested wing data, many agencies collect auxiliary data on bobwhite such as visual counts (e.g., mail route counts, coveys moved, broods seen), offspring observed per adult bird, band-recovery, mark-recapture or telemetry data rendering this technique broadly applicable across the range of bobwhite. Various auxiliary inputs likely influence demographic estimation and precision differently, substantiating the need to further investigate how sensitive these models are to specific auxiliary data as well as to better understand the limitations to lack of temporally and spatially comprehensive datasets for the period/area of interest. For example, while an agency may procure multiple years of age-at-harvest data from hunter harvested wings, auxiliary data may only be necessary for a subset of those years in order to obtain reliable SPR estimates. Given the successful application of SPR, we recommend its use for bobwhites, particularly on areas too large to conduct covey call counts, and where age-at-harvest and other auxiliary data are available.

MANAGEMENT IMPLICATIONS

Statistical population reconstruction is a relatively easy, low effort technique which takes advantage of data (age-at harvest, hunter effort) already being collected on many public lands; and, SPR provides the added benefit of a measure of precision, unlike some other techniques (e.g., coveys moved or seen per hour hunted). Thus, the use of SPR provides land managers with a credible and defensible means for developing conservative harvest strategies while ensuring long-term population persistence and recreational opportunity (Skalski et al. 2011). Use of wings from harvested birds also involves hunters in research and management through citizen science. As such, and if not already doing so, we urge state agencies to consider collection of harvested wings as a low-cost monitoring tool to help adaptively inform management.

Deliberate collection of auxiliary information over time, will enhance the use of statistical population reconstruction models to inform conservation and management of bobwhites on public and private lands. Careful planning by state wildlife agencies can provide improved estimation of abundance and further aid in making management decisions or setting harvest regulations through use of SPR. The extension of local auxiliary data to be broadly applied to regional areas offers promise but needs to be further tested. Large-scale conservation efforts, such as the National Bobwhite Conservation Initiative (Palmer et al. 2011) and the Coordinated Implementation Plan, could structure data collection to inform target population densities from archived data or develop abundance measures across the range using SPR to evaluate successful habitat management implementation.

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