



2012

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Recommended Citation

Parent, Chad J.; Hernandez, Fidel; Wester, David B.; and Bryant, Fred C. (2012) "Temporal and Spatial Trends of Northern Bobwhite Survival and Nest Success," *National Quail Symposium Proceedings*: Vol. 7 , Article 85.

Available at: <http://trace.tennessee.edu/nqsp/vol7/iss1/85>

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TEMPORAL AND SPATIAL TRENDS OF NORTHERN BOBWHITE SURVIVAL AND NEST SUCCESS

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ABSTRACT

The northern bobwhite (*Colinus virginianus*) has been declining in abundance across North America for many years. It is unknown, however, if other population variables also exhibit this downward trajectory. We conducted a retrospective-analysis of annual survival and nest success based on a literature review of 64 studies and compared these estimates temporally and spatially. We hypothesized that increased management efforts influenced bobwhite survival in the 1990s. Evidence from linear splining indicated survival trends changed in 1994. Thus, we compared trends across 3 periods: before 1994, after 1994, and overall. Mean (\pm SD) annual survival was $13.9 \pm 9.4\%$ across 31 studies from 1970 to 2007. Annual survival decreased -0.534% per year during 1970–1994 and stabilized thereafter. This stabilization in survival occurred along latitudinal and longitudinal gradients in which survival decreased at the northern and western periphery of the bobwhite range. Our linear splining models did not support the hypothesis that trends in nest success changed in the 1990s; thus, we only compared trends across the overall, 1924–2008 range of studies. Mean nest success across 33 studies was $44.4 \pm 15.2\%$ during this interval and increased slightly across the 1924–2008 range of studies. We observed latitudinal gradients in nest success. Nest success was lowest at the northern periphery of the bobwhite range; it decreased -0.90% per degree of latitude. Annual survival stabilized after 1994 despite monotonic declines in bobwhite abundance since at least the 1960s. Range-wide survival and nest success trends may not parallel trends in abundance, particularly after 1990, which suggests biologists may not fully understand the range-wide population ecology of bobwhites. This lends support for the need to monitor other aspects of the bobwhites range-wide population dynamics as supplements to range-wide abundance.

Citation: Parent, C. J., F. Hernández, D. B. Wester, and F. C. Bryant. 2012. Temporal and spatial trends of northern bobwhite survival and nest success. *Proceedings of the National Quail Symposium* 7:173–183.

Key words: abundance, *Colinus virginianus*, habitat management, meta-analysis, nest success, northern bobwhite

INTRODUCTION

The foundation of most formal management programs includes collection of abundance data (Williams et al. 2002). Understanding the direction and magnitude of annual changes in abundance is essential for management because it helps biologists make decisions that sustain population size and harvest intensities. Northern bobwhite population abundance has been declining range-wide at a rate of 3.8% per year (95% CI = ± 0.3) from 1966 to 2011 based on Breeding Bird Survey (BBS) data (Sauer et al. 2011). Surprisingly, it was not until the early 1990s that biologists fully appreciated the magnitude of the decline. Brennan (1991) was one of the first to describe the decline in the literature, and his cautions, along with others, were a harbinger for new management and research priorities directed at mitigating the downward

trajectory. However, we are not aware of any studies that attempt to link the research and management attention generated in the 1990s to measures of population demographics. It is unclear if bobwhite populations responded to these management efforts. It is also unknown if active habitat management for bobwhites was disproportionately greater in the 1990s.

Northern bobwhite abundance estimates repeated in time and space (e.g., BBS annual roadside counts) should be reasonable indicators of the population status if estimates are derived from a sufficiently large sample (Lancia et al. 2005). Using abundance alone to gauge the health of bobwhite populations only portrays a portion of the available information on their population; especially given recent range-wide declines in bobwhite habitat (Peterson et al. 2002) and abundance (Sauer et al. 2011). The concept of usable space provides a framework to understand bobwhite habitats. Guthery (1997) proposed the long-term mean abundance of bobwhites varied in

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proportion to the amount of usable space. Bobwhite habitat is declining at accelerated rates across their range—a reduction in usable space—and declines in abundance are axiomatic.

However, it is unclear if other measures of bobwhite populations, such as demography, also share this decline. Measures of demographic parameters might include survival, nest success, clutch size, age ratios, or age at maturity; however, range-wide trends for these parameters are rarely evaluated.

We conducted a retrospective-analysis of 2 population parameters commonly reported for bobwhite populations: annual survival and nest success. Our objectives were to evaluate spatial and temporal trends in these variables, understand the direction and magnitude of change in these variables across the bobwhite's range (specifically between 1991 and 2001), and evaluate the suitability of using these variables as supplements to abundance for range-wide population monitoring.

METHODS

Data Collection

Population Demographics.—Our literature search included the following data bases: Academic Search Premier, BioOne, JSTOR, and SCOPUS. We searched the literature for 4 common parameters used to measure bobwhite populations: clutch size, nest success, survival, and probability of renesting. We also searched for articles in the National Quail Symposia (Church and Dailey 1993, Brennan et al. 2000, DeMaso et al. 2002, Cederbaum et al. 2009). Our search included: clutch size and bobwhite, Kaplan-Meier and bobwhite, nest success and bobwhite, population dynamics and bobwhite, and survival rate and bobwhite. We also used search strings of the same measures of population, but replaced 'bobwhite' with 'northern bobwhite' and 'quail'. We relegated our search to title, abstract, and key words, and excluded queries in other search fields. Additional studies were located using the literature cited sections of retrieved publications.

We selected 2 parameters for further evaluation, survival rate and nest success, because these parameters were reported frequently in the literature. We omitted papers containing research on non-native bobwhites (i.e., translocated or captive-raised birds) with the exception of those that contained control groups of native, resident bobwhites. We also omitted papers that were early publications of larger studies. We used the terminal publication containing all the data. For example, the work by Parry et al. (1997) and Townsend et al. (1999) on the Packsaddle Wildlife Management Area in western Oklahoma from 1991 to 2001 is summarized by Cox et al. (2004, 2005) in a later, and more comprehensive publication. We omitted papers that did not use telemetry or recapture methodologies to collect survival data. These papers generally used direct observation to collect data on survival, and the estimates produced from these studies were variable. For example, one of the earliest survival studies was by Errington (1945) and reported survival estimates between 0.001 and 0.732; this variability would

have undue influence on the location of the intercept in regression analyses and could lead to biases in slope estimates. We reduced our analysis to 64 papers using these criteria (Tables 1, 2).

We defined nest success as the proportion of nests with ≥ 1 egg/hatch, or an estimate produced from the Mayfield method. We treated nest success estimates for each study area as independent estimates. We used a pooled estimate for analysis when papers reported pooled estimates of nest success across study areas. We converted daily survival rates to apparent estimates of nest success assuming a 23-day incubation period.

We collected the pooled estimates of survival for age, sex, or study area for analysis when authors reported pooled estimates. We collected only 1 of the reported survival rates with a preference for female and adult survival estimates if inferential statistics precluded the pooling of data based on sex or age. For example, if a paper reported adult and juvenile survival rates were similar, but female survival rates were significantly different from males, we collected the estimate of survival for females pooled across age. We chose female survival estimates because we assume population change is most sensitive to female survival. This convention was also used by Sandercock et al. (2008) in their bobwhite meta-analysis. We treated each study area as a unique, independent estimate of survival if inferential statistics precluded the pooling of study areas. We standardized the survival rate to an annual estimate of survival using the equation:

$$\hat{S}_a = S_p^{365/t}$$

where \hat{S}_a represents the annual survival estimate, S_p represents the reported survival rate, and t represents the time interval (days) associated with a reported survival rate. This extrapolation was not done for studies which reported annual survival rates.

Some authors did not provide exact dates that survival monitoring started and stopped (e.g., 'we conducted this study from Oct to Mar'). Thus, it is unclear when in October survival monitoring began, and when in March monitoring ceased. We assigned the start and stop date as the mid-point of the beginning and ending month, respectively. Thus, the interval for the survival estimate in the example would have been 15 October to 15 March. We calculated survival rates from mortality estimates by subtracting the mortality rate from 1.0 for studies that reported mortality.

Some papers did not report independent estimates of survival or nest success for each year of study, and presented 1 averaged estimate across the entire study (e.g., Taylor et al. 1999, Staller et al. 2005). We collected the reported estimate and applied it to the median year of the study to control for lack of independence. Using Staller et al. (2005) as an example, they reported an average nest success of 0.44 from 1999 to 2001. Thus, in our analysis, we treated this as a single estimate of nest success (0.44) and associated it with the year 2000.

Habitat Management Trends.—The National Quail Symposia has united researchers, biologists, managers,

Table 1. Published studies on survival of northern bobwhite in North America, 1970–2007.

Citation	Study duration ^a	Study interval	Sample size ^b	Type ^c	State
Burger et al. 1995b	3	1989–91	297	RT	MO
Carter et al. 2002	2	1994–95	131	RT	TX
Cox et al. 2004	10	1991–2000	2,012	RT	OK
DeVos and Mueller 1993	2	1985–86	134	RT	FL
DeVos and Speake 1995	3	1990–92	206	RT	AL
Dixon et al. 1996	1	1991	71	RT	SC
Folk 2006	3	2002–04	319	RT	AL
Guthery et al. 2004	3	2000–02	67	RT	TX
Haines et al. 2004	2	2001–02	63	RT	TX
Hernández et al. 2003	3	1997–99	88	RT	TX
Hernández et al. 2005	2	1999, 2002	102	RT	TX
Holt et al. 2009	2	2000–01	118	RT	MS
Hughes et al. 2005	2	1997–98	64	RT	GA
Liu et al. 2000	3	1990–92	13	RT	TX
Lohr et al. 2011	3	2006–08	154	RT	NJ
Madison et al. 2002	3	1994–96	61	RT	KS
Palmer and Wellendorf 2007	5	1999–2003	3,149	Band	FL
Pollock et al. 1989	14	1970–83	560 ^d	Band	FL
Puckett et al. 1995	2	1993–94	218	RT	NC
Robinette and Doerr 1993	2	1987–88	43	RT	NC
Seckinger et al. 2008	4	1998–2001	200	RT	TN
Sisson et al. 2000	3	1993–95	133	RT	GA
Suchy and Munkel 2000	4	1984–87	39	RT	IA
Taylor et al. 1999	3	1991–94	46	RT	KS
Taylor et al. 2000	4	1993–97	52	RT	MS
Terhune et al. 2006	2	1997–98	107	RT	GA
Terhune et al. 2007	6	1997–2002	3,190	Band	GA
Terhune et al. 2009	3	1999–2001	166	RT	GA
Townsend et al. 1999	4	1992–95	877	RT	OK
Williams et al. 2000	3	1993–96	157	RT	KS
Williams et al. 2004	3	1997–99	167	RT	KS

^a Years.

^b Units equal radio-marked or banded bobwhites.

^c RT = radiotelemetry study, Band = band recovery study.

^d Study reported an average of 560 banded birds/year.

and hunters since 1972. The accompanying *Proceedings* are repositories of information concerning vogue issues related to northern bobwhite. The *Proceedings* are primarily comprised of field studies pertaining to various aspects of bobwhite habitat management and population biology. Papers in the *Proceedings* that document field studies contain descriptions of the study area where the research occurred, and it is conventional to describe past and present management activities on the area. We believe the total number of unique study areas with active management represent a coarse index for bobwhite management effort during the range of years the National Quail Symposia occurred (hereafter, Quail I, Quail II, etc.).

We reviewed Quail I through VI and identified field studies that were actively managing habitat for bobwhite. We defined a field study as one in which the primary data were collected serially at established areas to answer a research question or hypothesis. We excluded the following: papers based on opinion (e.g., invited papers), literature reviews, papers containing meta- and retrospective analyses of secondary data, and papers describing

research conducted on other quail species. We ascertained if active bobwhite habitat management was occurring at a study area based on explicit, unambiguous descriptions from the authors. We recorded the proportion of field studies from each *Proceedings* that occurred on habitat actively managed for bobwhites. We pooled the field studies in which active management was occurring, recorded the total number of discreet study areas by study interval, and summed by year (Fig. 1). We intentionally excluded non-discrete study areas to account for pseudoreplication that might result from multiple studies at the same location (e.g., Tall Timbers Research Station in Florida). We pooled nest success and survival data by year and explored correlations with the management index.

Data Analysis

We analyzed the data using a linear mixed-model (with random intercepts and random slopes) to evaluate survival and nest success trajectories through time and across space; AICc comparisons were used to select

Table 2. Published studies on nest success of northern bobwhite in North America, 1924–2008.

Citation	Study duration ^a	Study interval	Sample size ^b	Type ^c	State
Burger et al. 1995a	3	1990–92	159	RT	MO
Carter et al. 2002	2	1994–95	81	RT	TX
Collins et al. 2009	2	2006–07	21	RT	NJ
Cox et al. 2005	10	1991–2000	331	RT	OK
DeVos and Mueller 1993	2	1985–86	134	RT	FL
Errington and Errington 1933	1	1931	69	DO	WI
Folk 2006	3	2002–04	319	RT	AL
Hernández et al. 2001	1	1998	50	RT	TX
Hernández et al. 2003	2	1997–98	15	RT	TX
Hernández et al. 2005	2	1999, 2002	37	RT	TX
Hernández et al. 2007	5	2000–05	148	RT	TX
Hughes et al. 2005	2	1997–98	472	RT	GA
Klimstra and Roseberry 1975	15	1952–66	863	DO	IL
Labrum 2007	1	2006	17	RT	AR
Lehmann 1946	2	1942–43	51	DO	TX
Lehmann 1984	10	1936–39, 1942–43, 1949–52	532	DO	TX
Lusk et al. 2006	2	2001–02	26	RT	TX
Parmalee 1955	1	1951	59	DO	TX
Parsons et al. 2000	3	1990–92	26	RT	TX
Potter et al. 2011	2	2003–05	67	RT	IA
Puckett et al. 1995	2	1993–94	16	RT	NC
Rader et al. 2007	3	2003–05	127	RT	TX
Rolland et al. 2010	6	2003–08	310	RT	FL
Simpson 1973	5	1967–71	680	DO	GA
Singh et al. 2010	5	2002–07	365	RT	FL
Staller et al. 2002	2	1999–2000	30	RT	FL
Staller et al. 2005	3	1999–2001	139	RT	FL
Stoddard 1931	4	1924–27	602	DO	FL
Suchy and Munkel 1993	4	1984–88	16	RT	IA
Taylor et al. 1999	3	1992–94	33	RT	KS
Terhune et al. 2006	2	1997–98	71	RT	GA
Terhune et al. 2009	3	1999–2001	165	RT	GA
Wellendorf and Palmer 2009	3	2003–05	176	RT	FL

^a Years.

^b Units equal nests.

^c RT = radiotelemetry study, DO = direct observation.

variance-covariance structures. One of the features of this approach is that it allows for the possibility that relationships between survival and nest success, respectively, and time might vary from study to study—in some studies, the slope might be positive, whereas in others it might be negative. The same is true for randomly varying intercepts. Several years of data were collected for many of the studies included in the analyses and it is possible this has induced some correlation structure in our data that should be recognized and modeled. This approach recognizes and models the repeated measures nature of the data. We tested the hypothesis that annual survival and nest success, respectively, reversed their negative trends by using a version of a linear spline model commonly called a ‘piece-wise’ or ‘broken-stick’ model (Fitzmaurice et al. 2004) with 1 knot. The location of the knot was identified by comparing AICc values of models with knots sequentially from 1991 through 2001.

Our analyses included studies from 14 states. The number of studies by state ranged from 1 to 6 for survival, and 1 to 7 for nest success (Fig. 2). Annual survival and

nest success were the response variables, and year, latitude, and longitude were the explanatory variables. We did not include other explanatory variables that may influence quail populations (e.g., precipitation) because we were only interested in evaluating long-term survival and nest success trajectories over time and space. We performed standard regression diagnostics to ensure assumptions of regression were not violated. Regression analyses were performed using SAS (1989–2007).

Spatial autocorrelation is common in ecology when response variables deal with animal population parameters such as abundance because nearby points in space are likely more correlated than expected by chance (Lichstein et al. 2002). We tested for spatial autocorrelation by comparing 2 models, 1 that did not include latitude and longitude, and 1 that included latitude and longitude and a spherical correlation structure whose parameters were based on a semi-variogram (Pinheiro and Bates 2004). The likelihood ratio test (P) associated with a comparison of these 2 models ($df = 2$, $P = 0.67$) indicated a model which assumed spatial independence was adequate.

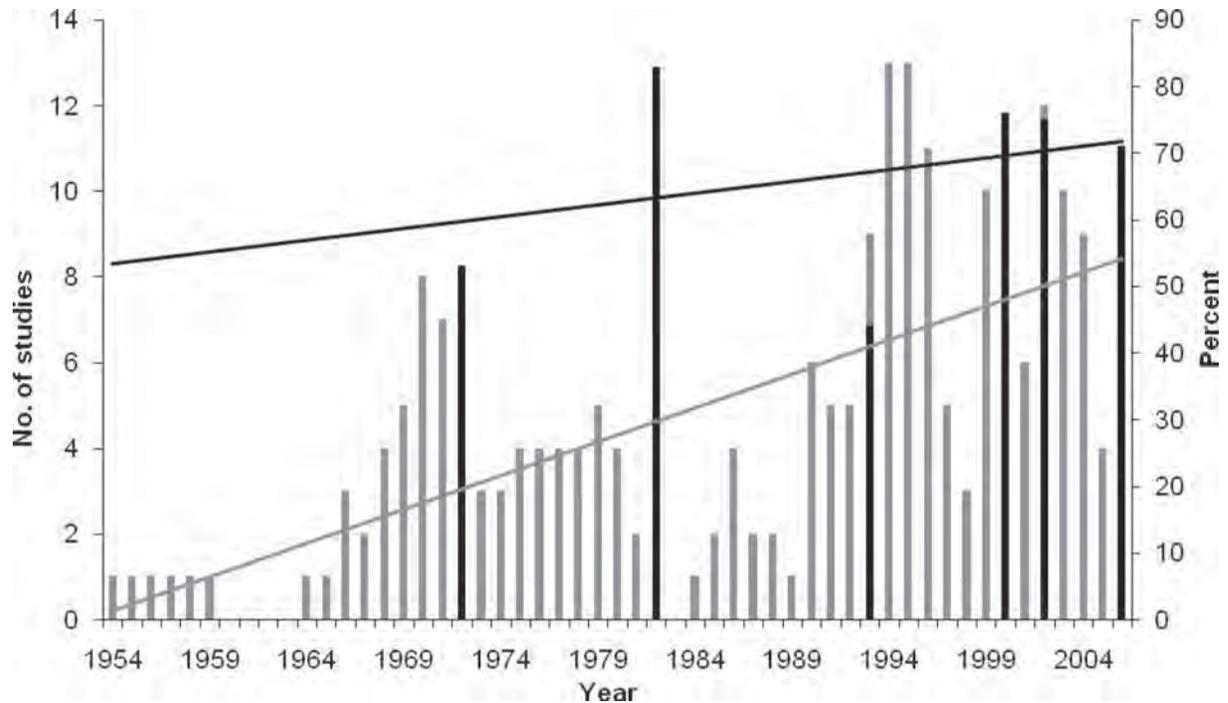


Fig. 1. Eighty-eight field studies on northern bobwhite were identified from the first 6 National Quail Symposia to index active habitat management at bobwhite research study areas. Study durations were recorded and the number of discrete study areas (gray) totaled across years. The proportion of field studies performing active habitat management for bobwhite was recorded for each symposium (black).

Spatial autocorrelation analyses were performed using R (Version 2.12.0; R Foundation for Statistical Computing, Vienna, Austria).

We used a Geographic Information System (GIS; ArcMAP 10; ESRI 1999–2010, Redlands, CA, USA) to identify the approximate geographic center of study areas based on study area descriptions when study area coordinates were not reported. We mapped survival and nest success studies to help conceptualize the distribution of these studies across the bobwhites' range (Fig. 2).

RESULTS

We reviewed 64 studies: 31 reported survival (Table 1) and 33 reported nest success (Table 2). Average (\pm SD) study duration was 3.5 ± 2.6 years for survival studies and 3.6 ± 3.1 years for nest success studies. Most studies were distributed in the southern and southeastern portions of the bobwhite range (Fig. 2).

Mean (\pm SD) annual survival for northern bobwhites was $13.9 \pm 9.4\%$ across 31 studies from 1970 to 2007; annual survival during this time period did not change. However, our linear spline model identified 2 periods with different survival rates. This analysis identified 1994 as the year when declining annual survival ceased (Fig. 3). Annual survival decreased from 1970 to 1994 at a rate of 0.534% per year ($95\% \text{ CI} = \pm 0.60\%$, $t = -1.83$, $df = 24$, $P = 0.08$). An annual decline in survival was not detected after 1994, and our results indicate survival stabilized during this interval (slope = 0.71% , $\text{CI} = \pm 1.67\%$, $t =$

0.91 , $df = 14.6$, $P = 0.38$). Average survival before ($13.1 \pm 9.4\%$) and after ($14.4 \pm 9.1\%$) 1994 supported these trends.

Annual survival rates were highest in the southeastern portion of the bobwhites range, followed by the southwestern and midwestern portions. We modeled survival as a function of time, latitude, and longitude. The relationship between annual survival and latitude and longitude was consistently negative before and after 1994, and we present pooled results from the 1970–2007 range of studies. Our analysis indicated annual survival decreased more rapidly with increases in latitude (-1.49% per degree of latitude; $95\% \text{ CI} = \pm 0.24\%$, $t_{42} = -12.71$, $P < 0.0001$) than with changes in longitude (-0.20% per degree of longitude; $95\% \text{ CI} = \pm 0.20\%$, $t_{42} = -1.97$, $P = 0.0553$). This suggests annual bobwhite survival is lowest at the northern and western edges of the species' range. There was no indication that spatial dependence was occurring according to likelihood ratio tests comparing models with and without a correlation structure based on a semi-variogram. Thus, we did not account for spatial autocorrelation in our regression models.

Average nest success for northern bobwhites was $44.4 \pm 15.2\%$ across the 33 studies from 1924 to 2008. We attempted to fit a knot to our nest success data between 1991 and 2001 with our linear spline model, but a knot could not be located. This indicated trends in nest success did not change significantly between 1991 and 2001. Thus, it is only appropriate to present results from the 1924–2008 range of studies. Nest success increased from

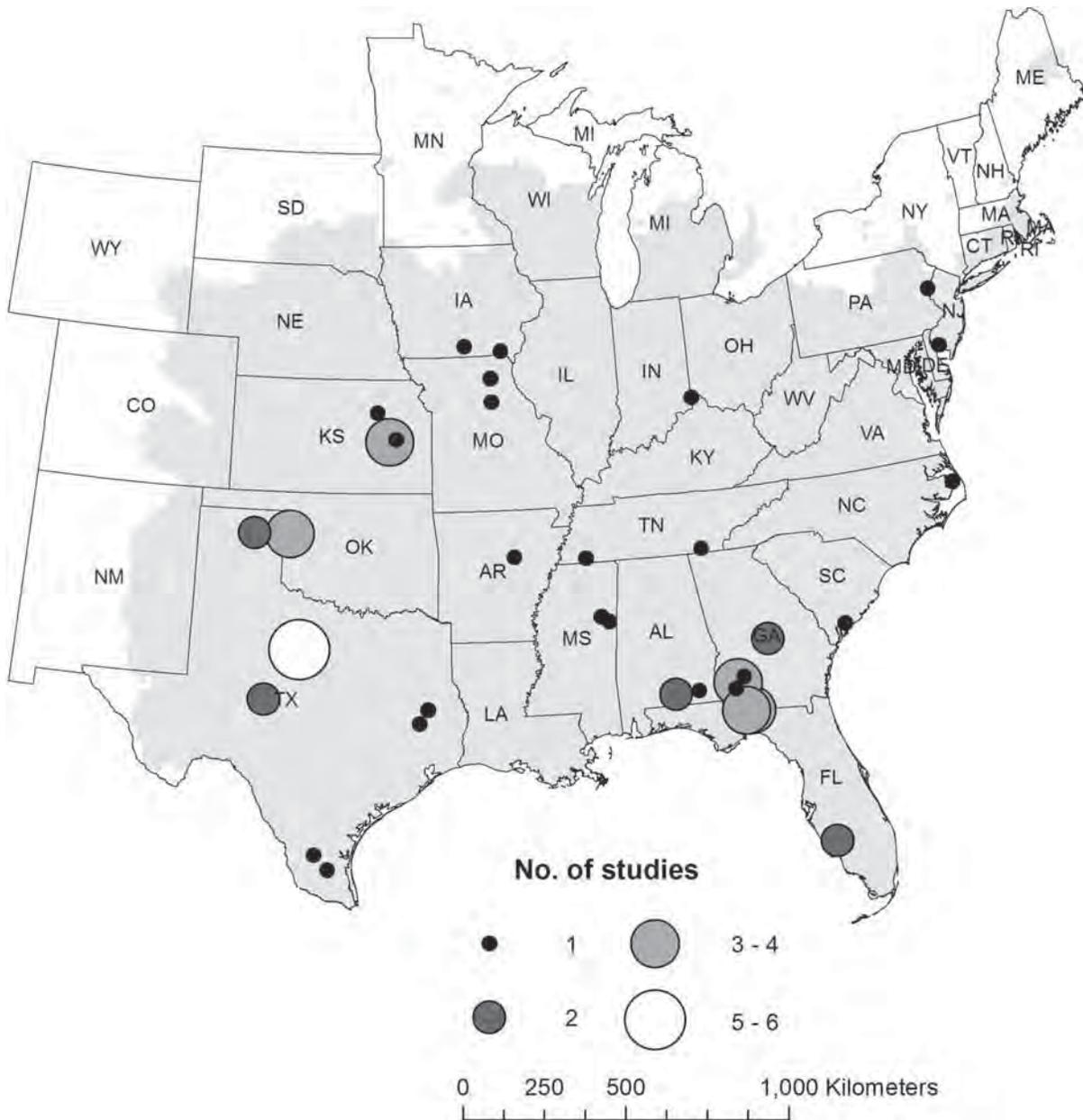


Fig. 2. Distribution of northern bobwhite survival ($n=31$ studies from 1970 to 2007) and nest success ($n=33$ studies from 1924 to 2008) across their range in eastern North America. Regions shaded gray represent the 2010 bobwhite range based on Sauer et al. (2011).

1924 to 2008; these trends were statistically significant (slope = 0.15%, 95% CI = $\pm 0.10\%$, $t_{97} = 2.55$, $P = 0.012$), but probably not biologically significant. There was some geographic variation in nest success. Our modeling of time, latitude, and longitude indicated nest success decreased significantly with increases in latitude (-0.90% per degree of latitude; 95% CI = $\pm 0.80\%$, $t_{41} = -2.26$, $P = 0.0293$); thus, nest success was lower at the northern edge of the bobwhite range.

We identified 88 field studies in Quail I through VI. The proportion of field studies from each *Proceedings* performing active habitat management for bobwhites was on a positive trend with the greatest proportion occurring during Quail II (Fig. 1; Quail I = 10 of 19 studies, Quail II

= 5 of 6, Quail III = 4 of 9, Quail IV = 16 of 21, Quail V = 9 of 12, Quail VI = 15 of 21). The number of discrete study areas performing active habitat management increased over time and ranged from 2 to 13 (Fig. 1). Survival and nest success were not well correlated with the number of discrete study areas performing active management (survival, $r = -0.04$; nest success, $r = 0.44$).

DISCUSSION

Survival

Annual survival rates stabilized and increased by 0.71% per year after 1994. We hypothesized that

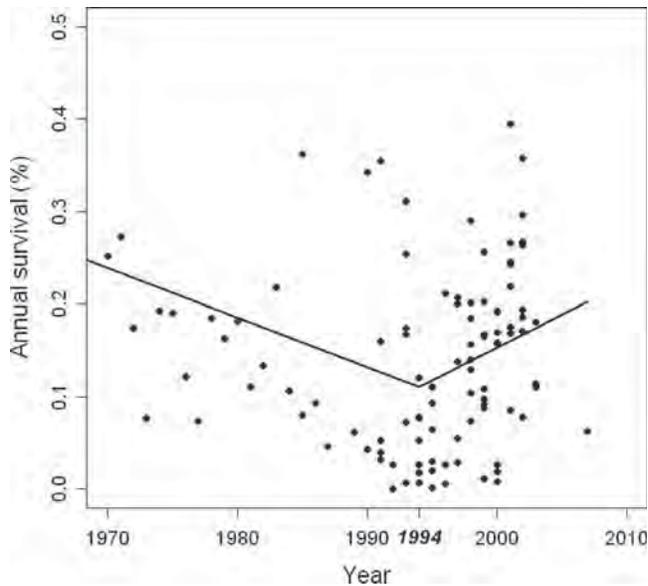


Fig. 3. Annual survival of northern bobwhite in North America from 1970 to 2007. A linear spline model indicated range-wide survival of bobwhites decreased at a rate of 0.53% per year until it stabilized in 1994.

increased management attention beginning in the 1990s was responsible for the stabilization in survival we observed. The mechanism for this relationship was probably the creation of more, high quality habitat that provides bobwhites with essential habitat needs (i.e., forage, nesting cover, escape cover, thermal cover). However, this is not supported by our results; annual survival was not well correlated with our management index. This contrasts with simulations by Sandercock et al. (2008). They conclude that seasonal survival, winter survival in particular, is responsible for a majority of variation in the finite rate of population change, and suggest management practices that improve seasonal survival rates should benefit declining populations. They provide an empirical basis for a relationship between survival and habitat management. Our findings differ from those of Sandercock et al. (2008) and it is possible that differences in how survival was extrapolated created the dissimilarity in results. We note the difference in survival before and after 1994 only differed by 1.3%; such a small effect size is not likely to be explained by management.

It is possible that our management index does not adequately reflect trends in bobwhite management, but these trends appear to reflect recent conclusions about the direction of quail management in the literature (Brennan et al. 2008). The life history of bobwhites makes comparing relationships between survival and habitat management difficult. Bobwhites senesce at a rate of 44% (Guthery 2002). Thus, despite a quail manager's best effort, a large portion of the bobwhite population dies each year as a result of their life history. These difficulties are compounded when abiotic and biotic mortality factors are included. Guthery (2002) suggested it is difficult to

augment survival through management as one source of mortality is readily replaced by another.

Our results indicated bobwhite survival decreased at the northern and western edges of their range. This is consistent with literature for spatial variation in survival between northern and southern latitudes (Guthery et al. 2000, Folk et al. 2007a). Presently, there is no evidence in the literature of spatial variation in demographic parameters along longitudes. Guthery et al. (2000) modeled populations in northern and southern latitudes and postulated annual survival is depressed in northern populations by winter weather catastrophes and density-dependent processes. In contrast, annual survival of southern bobwhite populations is depressed by summer weather catastrophes (e.g., drought) and harvest. Folk et al. (2007b), in a retrospective analysis of 2 bobwhite populations at the northern (Wisconsin) and southern (Alabama) extent of their range, concluded non-breeding season survival of young bobwhites was responsible for most changes in population growth in Wisconsin, while fertility was most responsible for changes in Alabama.

One possible mechanism that could be responsible for longitudinal differences in survival from west to east is the diversity of climates given that northern bobwhite abundance's are sensitive to weather variables such as precipitation (Lusk et al. 2002) and drought (Bridges et al. 2001). For example, semi-arid regions of south and west Texas and Oklahoma prone to drought are known for their boom-and-bust population cycles (Hernández and Peterson 2007). Invariably, the effects of drought would extend to survival, and reduce survival rates at the western edge of the bobwhites' range. A second mechanism likely includes changing trends in land use. Increases in average farm size and brush cover on rangelands were much more pervasive from 1978 to 1997 at the western edge of the bobwhites range (Peterson et al. 2002). These changes result in reductions of habitat and, by extension, usable space and population abundance. Changes in land use are also creating habitat loss in the eastern portion of the bobwhites' range. Birds with grassland and grass-shrub affinities like the northern bobwhite are more sensitive to land-use changes when they occur in grasslands at the edge of their range (Johnson and Igl 2001, Brennan and Kuvlesky 2005). The potential for spatial and temporal dependence exists because our analysis used data from studies that were repeated in space and time. We did not detect spatial autocorrelation in our data, and temporal correlation was addressed with a repeated measures analysis that accounted for both between- and within-study effects. Many of the studies that our data included did not take these precautions.

There are potential biases with the data we used to analyze survival trends. This places limitations on our analyses and warrants cautious interpretation of our conclusions on survival trends. We identify 2 possible sources of bias: estimates of survival derived from radiotelemetry studies and our extrapolation of survival intervals to annual survival estimates.

Radiotelemetry became widely used in northern bobwhite field studies beginning in the early 1990s. It was later recognized that radiomarking may handicap

bobwhites resulting in estimates of survival that are biased low (Guthery and Lusk 2004). However, others have shown no effect of radiomarking on bobwhite survival (Terhune et al. 2007) and have drawn attention to the possible flaws in the methodology used by Guthery and Lusk (Folk et al. 2007b). If telemetry bias did exist in the studies we evaluated, the effect of telemetry is likely consistent through time for 2 primary reasons. First, radiomarking is a systematic bias because it affects all individuals similarly. Second, nearly all of the studies we evaluated were based on data collected from radiotelemetry (28 of 31 survival studies, 26 of 33 nest success studies, and collectively, 94% of survival and nest success studies after 1990). Thus, we could adjust survival or nest success upwards to appropriately reflect true estimates but this would not change the trends we observed based on the literature.

Few bobwhite survival studies actually monitor survival of individuals over an entire year. Most studies are conducted over some biologically important interval (e.g., breeding season). Survival rates procured during the monitoring interval can be extrapolated to produce estimates of survival during periods that were not monitored (e.g., annual survival). This technique is useful, but is likely biased because the assumption that factors that influence survival are homogeneous through time is rarely satisfied. For example, an annual survival estimate produced from monitoring conducted in spring (i.e., during breeding season) would be much different from annual survival estimates produced during summer or fall (i.e., during harvest). We are unable to make direct study-to-study comparisons without standardizing survival to an annual estimate due to the variety of monitoring intervals. This introduces bias but is an acceptable tradeoff because it allows conclusions to be drawn from a much larger population of studies.

Nest Success

Average nest success between 1924 and 2008 was 44% across 33 studies in the northern bobwhites' range. We observed an increasing trend in nest success from 1924 to 2008. This may not be a biologically significant relationship at a rate of increase of 0.15% per year. There was weak evidence that nest success increased dramatically in the 1990s, which suggests trends in nest success did not respond to the shift in management practices in the early 1990s. The 84-year range of studies is quite long relative to other variables studied for bobwhites. Nest success during this period was stable and suggests that it is not a variable that managers can directly influence.

Biologists have a good understanding of the variety of habitats bobwhites select as nest sites and possess the knowledge to alter the habitat structure and composition to meet these needs. Despite this, there is evidence to suggest managers cannot manage, or have difficulty managing, habitat to influence nest success. Simpson (1973), in southwest Georgia, reported 86% of successful nests occurred in medium or sparse vegetation densities, and 61% of successful nests had poor concealment (Simpson did not classify density and concealment around

unsuccessful nests). Klimstra and Roseberry (1975) evaluated the relationship between nest success and nest concealment with land-cover type in Illinois. Nest success was numerically greater in more dense vegetation, but was not statistically significant. Lehmann (1984) reported nest concealment in south Texas was not correlated with nest success for 155 nests. Lusk et al. (2006) demonstrated successful nests in north Texas were characterized by higher canopies and more shrub cover than failed nests, but successful nests also had more bare ground. Rader (2006) studied the factors influencing nest-site selection and nest success in south Texas and concluded bobwhites select nest sites based on the structure and composition of vegetation, as opposed to minimizing the potential for nest predation. Rader (2006) concluded that managers can increase available habitat by influencing nest-site availability, but managers cannot influence nest success.

We observed a decrease in nest success at northern latitudes from 1924 to 2008. This was unexpected because we anticipated poorer success in southern latitudes. Guthery et al. (2001) presented a compelling explanation counter to our findings. They provide empirical evidence demonstrating that excessive thermal conditions created by drought and heat waves inhibit quail reproduction across extensive areas. This includes deaths of embryos in eggs and adults, and inducing premature incubation and staggered hatching.

There is a paucity of research on bobwhite life history at range-wide scales. Our results might contrast with the prevailing conclusions in the literature because of biases associated with apparent nest success. Apparent nest success only considers success of a nest after onset of incubation and ignores the assumption that success decreases exponentially over time. This creates the potential for bias and potentially high estimates of nest success. Use of daily survival rates (DSR) to measure nest survival accounts for additional exposure prior to incubation. Our meta-analysis included 6 (Folk 2006; Terhune et al. 2006, 2009; Collins et al. 2009; Rolland 2010; Potter et al. 2011) studies that reported DSR and we converted these to apparent nest success. It is possible that nest success estimates in the 2000s are artificially high if bias exists as a result of converting to a DSR. Thus, the increasing trend in nest success that we observed in reality could be stabilized, or even decreasing.

MANAGEMENT IMPLICATIONS

We examined (1) if there was a need for a more holistic approach to bobwhite population ecology and management, and (2) if there was an alternate portrayal of range-wide northern bobwhite population ecology. Trends in survival and nest success through time do not parallel trends in abundance. Thus, we are left with an incomplete understanding of range-wide population demographics for bobwhites. A range-wide monitoring program that collects information on abundance as well as other aspects of the bobwhites' population ecology could solve this problem. Range-wide monitoring of survival or nest

success could be adequate supplements to range-wide monitoring of abundance based on this meta-analysis.

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