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DEMOGRAPHIC ANALYSIS OF A DECLINING NORTHERN BOBWHITE POPULATION IN SOUTHWESTERN OHIO

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ABSTRACT

Northern bobwhite (*Colinus virginianus*) populations continue to decline throughout much of their range, especially in the Midwestern United States. Land use and habitat changes are understood to be the primary cause of decline, and it is unclear how vital rates affect growth of regional populations. We estimated relative abundance and population vital rates of bobwhites on 8 private land sites in southwestern Ohio during 2008–2011. Life stage simulation analyses were used to model the influence of 9 demographic parameters on population growth rates (λ). All but one vital rate, chick survival, were modeled with empirical data randomly selected from normal distributions estimated (mean $\pm$ SD) from our study population. The median value of λ after 1,000 simulations was 0.248 (inter-quartile range = 0.113-0.428). Non-breeding season survival was the dominant vital rate, explaining 50.4% of variation in λ, followed by nest success ($r^2 = 0.163$), and breeding season survival of adults ($r^2 = 0.083$). Chick survival, egg success, and clutch size individually explained in order 1.4 to 4.6% of variation in λ when modeled with survival estimates. Renesting, double-brooding, and male incubation individually explained $< 1\%$ of the variation in λ. Total fecundity modeled as the sum across individual vital rate components explained 36.9% of variation in λ. Non-breeding season survival was the most limiting population vital rate, but age ratios of fall-captured birds and simulated fecundity values indicated partial limitation by recruitment. Population stability ($\lambda = 1$) could be achieved by increasing non-breeding survival from 10.9 to 36.9%. Higher rates of nest success, the second most limiting vital rate, would not stabilize population growth unless survival rates also increased. Bobwhite conservation strategies should emphasize habitat enhancements designed to increase survival rates and useable space during the non-breeding season in Ohio and possibly other Midwestern states.

INTRODUCTION

Northern bobwhites are currently hunted in only 16 Ohio counties under harvest regulations that are among the most restrictive of any state. The species still engenders broad interest from Ohio citizens, especially among landowners who participate in private lands wildlife habitat development programs. The adage *if you build it they will come* raises expectations that often result in disappointment after landowners create habitat or adopt wildlife-friendly practices on their properties. The history of northern bobwhites in Ohio reflects what has occurred elsewhere in the upper Midwestern United States. State-wide call-count indices have declined 76% since 1984 as the species' range has contracted to a 20-county area of southwestern Ohio (Spinola and Gates 2008). Christmas Bird Counts document a 3.7% annual rate of decline in relative abundance during 1960–2010 (Fig. 1A). Most remembered are the dramatic declines associated with severe winters in 1977 and 1978 and failure of populations to recover despite implementation of wildlife habitat conservation provisions in Federal Farm Bills enacted since 1985. Ohio Division of Wildlife indices based on spring whistle-count surveys document a 2.2% annual decline from 1985 to present (Fig. 1B).

Previous studies demonstrated bobwhite populations in northern portions of the species' range are limited more by survival than reproductive rates compared to southern populations (Guthery et al. 2000, Folk et al. 2007). Loss of early succession habitats and intensified agricultural practices that favor corn-soybean-wheat crop rotations on

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(A)

(B)

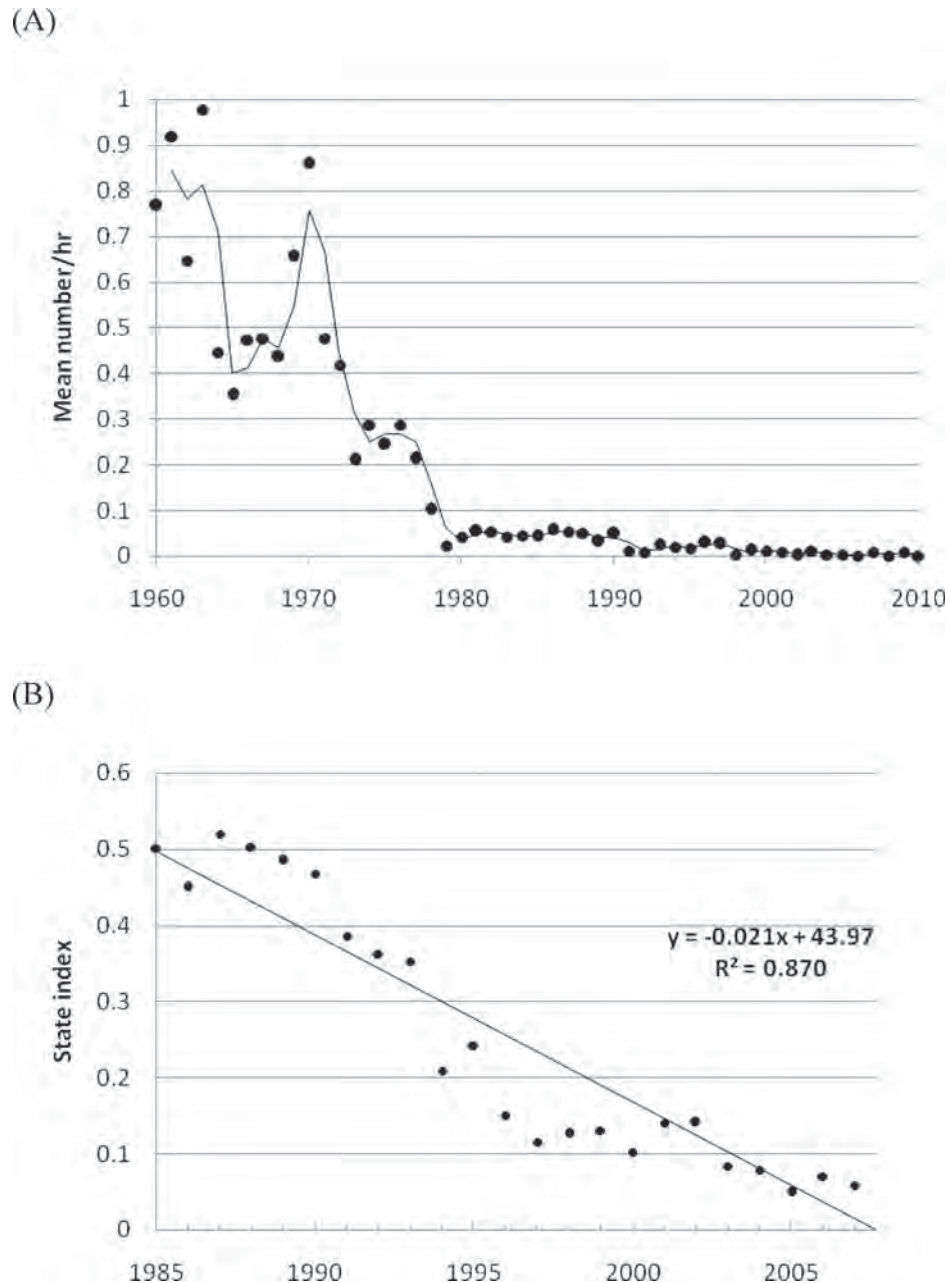$$y = -0.021x + 43.97$$
$$R^2 = 0.870$$

Fig. 1.   Northern bobwhite population indices in Ohio from Christmas Bird Counts during 1960–2010 (A) and spring whistle-count surveys conducted by the Ohio Division of Wildlife during 1984–2009 (B).

large fields over farming practices that included small-grain, row crop, and perennial forage crops on small land parcels have negatively impacted northern bobwhites in the upper Midwest (Brennan 1991). Maturation and canopy closure of farmland woodlots and associated development of hard edges (no ecotones) between forests and row croplands has been overlooked in design and implementation of private land conservation practices in the Midwest despite awareness of the effect of forest maturation on northern bobwhites.

Sandercock et al. (2008) investigated sensitivity of bobwhite population growth rates to variation in vital rates (survival and fecundity components) from across the

bobwhite's range, but there is little information on how vital rates affect growth for extant populations (e.g., DeMaso et al. 2011) particularly in the upper Midwestern U.S. These analyses can help inform strategies to focus conservation on the most population growth-limiting vital rates. We initiated an investigation of population-habitat relationships of northern bobwhites on private lands in southwestern Ohio to gain a better understanding of factors that affect population growth in agricultural landscapes in the current core of the species' geographic range within the state. Our objectives were to: (1) investigate bobwhite abundance on study sites with apparently suitable habitat, (2) estimate key population

vital rates (e.g., breeding and non-breeding survival, components of fecundity), (3) examine the influence of vital rates on population growth rates, and (4) identify conservation strategies to maintain and increase bobwhite populations in Ohio.

STUDY AREA

The study area was in southwestern Ohio (39° 04′ 59″ N, 83° 39′ 10″ W) where the core density of bobwhites in Ohio currently occurs (Spinola and Gates 2008). Weather conditions varied during the study and were generally more severe than long-term averages for winter temperature and snowfall (Janke and Gates 2012). Timing and severity of weather varied among years with relatively mild weather and short duration of snow cover in 2008–2009. Winter 2009–2010 was mild during December-January but a 22-day period of deep snow accumulation and cold temperatures occurred in February. Winter 2010–2011 had consistent snow cover with depths that did not exceed 25 cm during December-January and little snow accumulation in February. Our study sites were open to hunting (28 days, 4 bird bag) but received little hunting pressure and harvest mortality was low (Janke and Gates 2012).

We selected 8 study sites in Adams, Brown, Clinton, and Highland counties. All sites were in private ownership, although a state wildlife management area was adjacent to one study site. Agriculture was the predominant land use on each site with 38–72% row crop (mostly soybeans and corn). Pasture and haylands, defined as herbaceous land cover that were annually grazed or mowed, accounted for 2 to 23% of study sites. Early succession herbaceous vegetation covered 9 to 21% of each site and included fields enrolled in the Conservation Reserve Program (CRP), old fields, fencerows, and agricultural drainage ditches. Early succession grass fields were mostly dominated by fescue (*Festuca* spp.) but some had native warm-season grasses. Early succession woody vegetation (3.1–6.5%) was mostly associated with fencerows, streams, or drainage ditches. Forests accounted for 8–29% of the study sites. Janke and Gates (2012) described the species composition of these land cover types in greater detail.

METHODS

Potential study sites were identified from 2001 National Land Cover Data (NLCD; Homer et al. 2004) merged with an ArcGIS shapefile of lands enrolled in CRP, including parcels enrolled in conservation practices 1, 2, 4, 8, 10, 21, 25, 29, 31, and 33. We overlaid a 5-km^2 (presumptive study site size) hexagonal grid on the merged NLCD/CRP habitat coverage. Proportions of grassland/herbaceous, shrub, agricultural, and developed lands were calculated for each hexagon with the spatial analyst tool in ArcMap. We identified all hexagons with > 10% grassland/herbaceous and shrub cover (presumptive bobwhite habitat) and calculated ratios of agriculture to forest land cover for each hexagon. Hexagons with less

than half as much agriculture as forest were eliminated from consideration. The landscape matrix was classified as agricultural if the ratio of agriculture to forest was > 2 and as mixed agriculture-forest if the agriculture: forest ratio was 0.5-2.0. We counted adjacent hexagons with > 10% bobwhite habitat for each hexagon classified as agriculture or mixed agriculture-forest. Potential study sites were randomly selected within strata and examined with aerial photographs and on-site reconnaissance. Hexagons that did not meet classification criteria, or when landowner permission was not available or were otherwise unsuitable were replaced by the next hexagon from the randomized list until the sample matrix was filled (2 sites per stratum).

We gained access to 8 sites that met our selection criteria in Highland, Brown, Clinton, and Adams counties. Permission was not unanimously granted within each study site and we adjusted site boundaries to create a core of contiguous properties that provided 70–100% access to the total area of each study site. Study-site boundaries were adjusted (net expansion) each year as we learned more about local distribution and movements of bobwhites, and availability of suitable habitats. The selection process produced a representative sample of sites that appeared to be most suitable for occupancy by bobwhites within the core of the species' range in Ohio.

We located coveys on all study sites with covey-call surveys (Wellendorf et al. 2004) conducted at systematically-placed survey points during October-December 2008–2011. Covey-call surveys were followed by intensive searches with pointing dogs and track searches when snow cover was present. We also conducted whistle-count surveys (Norton et al. 1961) at systematically-placed survey points distributed across 8 study sites during 2008–2009 and 4 study sites during 2009–2011. Covey-call surveys and dog searches were more regularly and intensively conducted on 4 study sites where we consistently found and radiomarked coveys. Intensive dog searches, snow tracking, and continuous presence of field personnel on 4 study sites helped detect all resident bobwhite coveys present on those 4 sites. Whistle-count detections were compared among years with linear-mixed models using study site as a random effect (Pinheiro et al. 2012). Covey densities were compared between years using paired *t*-tests (R Development Core Team 2012).

We captured, leg-banded, and radiomarked bobwhites on the 4 intensive study sites during the non-breeding season (Oct-Mar). Bobwhites were captured using baited funnel traps (Stoddard 1931) and targeted mist-netting (Wiley et al. 2012) during October-March 2009–2011. We attached an aluminum leg band and recorded age, sex, and body mass of each bird (Rosene 1969). A sample of captured birds weighing > 165 g were marked with 6.6-g (≤ 4% body mass) necklace-style radio transmitters equipped with an 8-hr mortality sensor (Advanced Telemetry Systems, Isanti, MN, USA). All birds were released at capture sites within 30 min. Trapping, handling, and marking techniques were reviewed and approved by the Animal Care and Use Committee at Ohio State University (protocol #2007A0228). Our goal was to place and maintain radio transmitters on 2–4 birds in each

Table 1. Vital rates used in life-stage simulation analyses of northern bobwhite population growth rates in southwestern Ohio, 2009–2010 and 2010–2011.

Vital rate	Estimate ± SD	Range
Incubated clutch size	14.4 ± 2.4	6.9–21.62
Egg success	0.912 ± 0.166	0.466–1.000
Nest success	0.307 ± 0.161	0.000–0.739
Renesting rate	0.647 ± 0.116	0.334–0.994
Double brooding rate	0.250 ± 0.125	0.000–0.626
Proportion of nests incubated by males	0.432 ± 0.094	0.100–0.737
Chick survival	0.842[a]	0.740–0.943[b]
Summer survival (adults)	0.286 ± 0.131	0.000–0.730
Fall-winter survival (adults and juveniles)	0.109 ± 0.069	0.000–0.310

[a] Suchy and Munkel (2000), adjusted from a 38- to a 30-day interval.
[b] Sampled from a uniform distribution because there was no estimate of SD in original estimate.

covey on all sites throughout the non-breeding season. New birds were radiomarked in each covey to replace transmitters lost after death or transmitter failure. This provided a cohort of radio-marked birds as they entered the breeding season, supplemented by opportunistic capture and radiomarking of individuals after covey brea-up in spring.

Nests ($n = 52$) were found by locating radio-marked birds during the breeding season. Nests were marked with flagging placed > 5 m from the nest and attendance was monitored by locating radio-marked birds every 1–2 days. We avoided flushing birds from nests when possible and then only to count the number of incubated and hatched eggs or to identify gender of the incubating adult. Nests were checked when radio-marked birds were off-nest for > 2 days.

Nest fate was ascertained by examining shell fragments or from association of radio-marked adults with chicks after hatching. We estimated nest success using the logistic exposure method (Schaffer 2004). We used only nests ($n = 40$) found with at least 1 egg and excluded nests that were abandoned or depredated < 1 day after discovery to minimize bias caused by investigator-caused nest failure.

Five additional nesting productivity parameters, including total clutch size, egg success, renesting rate, double brooding rate, and male nesting rate also were estimated. Renesting rate was the proportion of radio-marked females that initiated new clutches after failed nesting attempts, while double-brooding rate was the proportion of radio-marked females that initiated new nests after successful nests. Egg success was the proportion of eggs that hatched from successful clutches. Male nesting rate was the ratio of the probability of finding a radio-marked male to that of finding a radio-marked female incubating a nest. Probability of incubation was calculated with a modified version of Trent and Rongstad's (1974) survival estimator as described in Collins et al. (2009). We treated the ratio (male: female) of sex-specific incubation probabilities equivalent to the ratio of male to female incubated nests as reported by Sandercock et al. (2008).

Radio-marked birds were tracked ≥ 6 days/week by homing and triangulation (White and Garrott 1990) from short distances (< 25 m). We located transmitters after detecting mortality signals and assigned the fate of individuals from field signs at recovery sites (Einarsen 1956) or transmitter condition. Survival rates were estimated from radio-tracking histories of radio-marked birds using the Kaplan-Meier estimator adjusted for staggered entry (Pollock et al. 1989). We pooled age and sex classes to estimate breeding season survival rates during April-September 2010–2011 ($n = 99$) and non-breeding season survival rates during October-March 2009–2011 ($n = 256$). We lacked empirical data on chick survival between hatching and fledging and substituted a published estimate from Suchy and Munkel (2000) in Iowa. These authors estimated chick survival over a 38-day period which we rescaled to a 30-day pre-fledging period.

We conducted life-stage simulations of population growth and fecundity following Sandercock et al. (2008) using 9 demographic parameters (Table 1). Simulations were conducted with R (R Development Core Team 2012). We specified mean and standard deviation of each parameter and sampled from normal distributions with 1,000 iterations. We calculated standard deviations for chick survival and renesting, double-brooding, and male nesting rates using the equation for simple proportions. Suchy and Munkel (2000) did not report standard deviation of their chick survival estimate and we sampled this vital rate from a uniform distribution bounded by 95% confidence intervals (proportion) approximated after adjusting the upper and lower limits for a 30-day period. Post-fledging survival of juveniles was assumed to be the same as for adults between fledging and covey formation. We solved univariate equations from regressions of vital rates on simulated population growth rates for $\lambda = 1$ to identify the magnitude of change necessary to achieve stable populations.

RESULTS

Relative Abundance

Mean detection rates of whistling males were highest on 3 of 4 intensive study sites (Wildcat, Fee, and Thurner) during springs 2008–2011 (Fig. 2). Lower detection rates (< 0.5 calls/survey point) occurred on the other 5 sites.
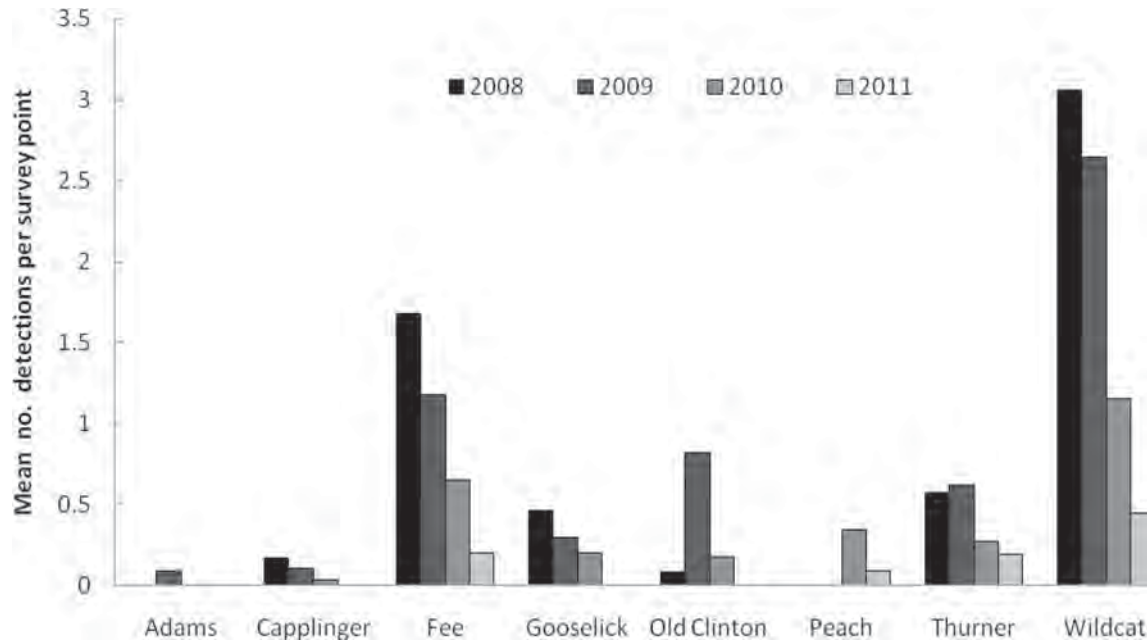
GATES ET AL.

Fig. 2. Mean number of detections/survey point of whistling-male northern bobwhites on 8 study sites in southwestern Ohio, April-June 2008–2011.

We found few or no coveys with covey-call surveys or dog searches on 4 sites (Adams, Capplinger, Gooselick, Old Clinton) during 2008–2010. Call surveys and covey searches were discontinued at these locations in 2011. Whistle-detection rates (calls/survey point) declined ($b =$ 0.349, SE $= 0.093$, $P = 0.002$) on all study sites, including the 4 intensive survey sites during 2008–2011 ($b = 0.543$, SE $= 0.112$, $P = 0.001$).

Mean annual covey densities on the intensively-searched study sites ranged from 0.25 to 1.6 coveys/km^2 during 2009–2011. There was no change (paired $t =$ 0.479, df $= 3$, $P = 0.6647$) in covey densities between 2009–2010 ($0.85 + 0.83$, 95% C.I.) and 2010–2011 ($0.76 + 0.74$, 95% C.I.).

Vital Rates

We monitored 52 nest attempts during summers 2010–2011. Forty of these nests were located after egg-laying and survived > 1 day after discovery. Incubated

clutch size (Table 2) was ascertained from 37 nests. Egg success (Table 2) was calculated for 20 nests with known incubated clutch sizes and clutch size at hatch ($n = 295$ eggs). Nests were monitored over 756 exposure days during 2010 ($n = 16$) and 2011 ($n = 24$). Daily nest survival rate (years combined) was 0.973 (SE $= 0.563$), resulting in a nest success rate of 30.7% assuming our mean observed incubated clutch size (Table 1), 1.2 eggs laid/day, and a 21-day incubation period.

We monitored radio-marked birds over 4,011 radio-days (males) and 3,848 radio-days (females) during the nesting season. We ascertained gender of incubating birds for 38 nest attempts; 28 nests (73.6%) were incubated by females, 9 (23.6%) were incubated by males, and 1 (2.6%) was incubated by both sexes. Nine of 53 (15.1%) radio-marked males incubated nests, compared to 28 of 43 (65.1%) radio-marked females that were found incubating nests. The ratio of probability of finding a radio-marked male incubating a nest (0.291) to that of a radio-marked

Table 2. Regressions of northern bobwhite vital rates on estimates of population growth rates calculated from life-stage simulation analyses following Sandercock et al. (2008). Vital rates were randomly selected ($n = 1,000$) from normal distributions with mean and standard deviations based on data collected on northern bobwhites in southwestern Ohio during 2009–2011 (Table 1).

| Vital rate	Intercept	Regression coefficient (b)	SE(b)	r^2
Non-breeding survival	0.001	2.710	0.085	0.504
Breeding survival	0.144	0.531	0.056	0.083
Chick survival	−0.127	0.504	0.130	0.015
Clutch size	−0.011	0.021	0.003	0.046
Egg success	0.046	0.284	0.061	0.021
Nest success	0.095	0.643	0.046	0.163
Male nest rate	0.250	0.108	0.080	0.002
Renesting rate	0.216	0.124	0.067	0.003
Double clutch rate	0.288	0.036	0.063	<0.001
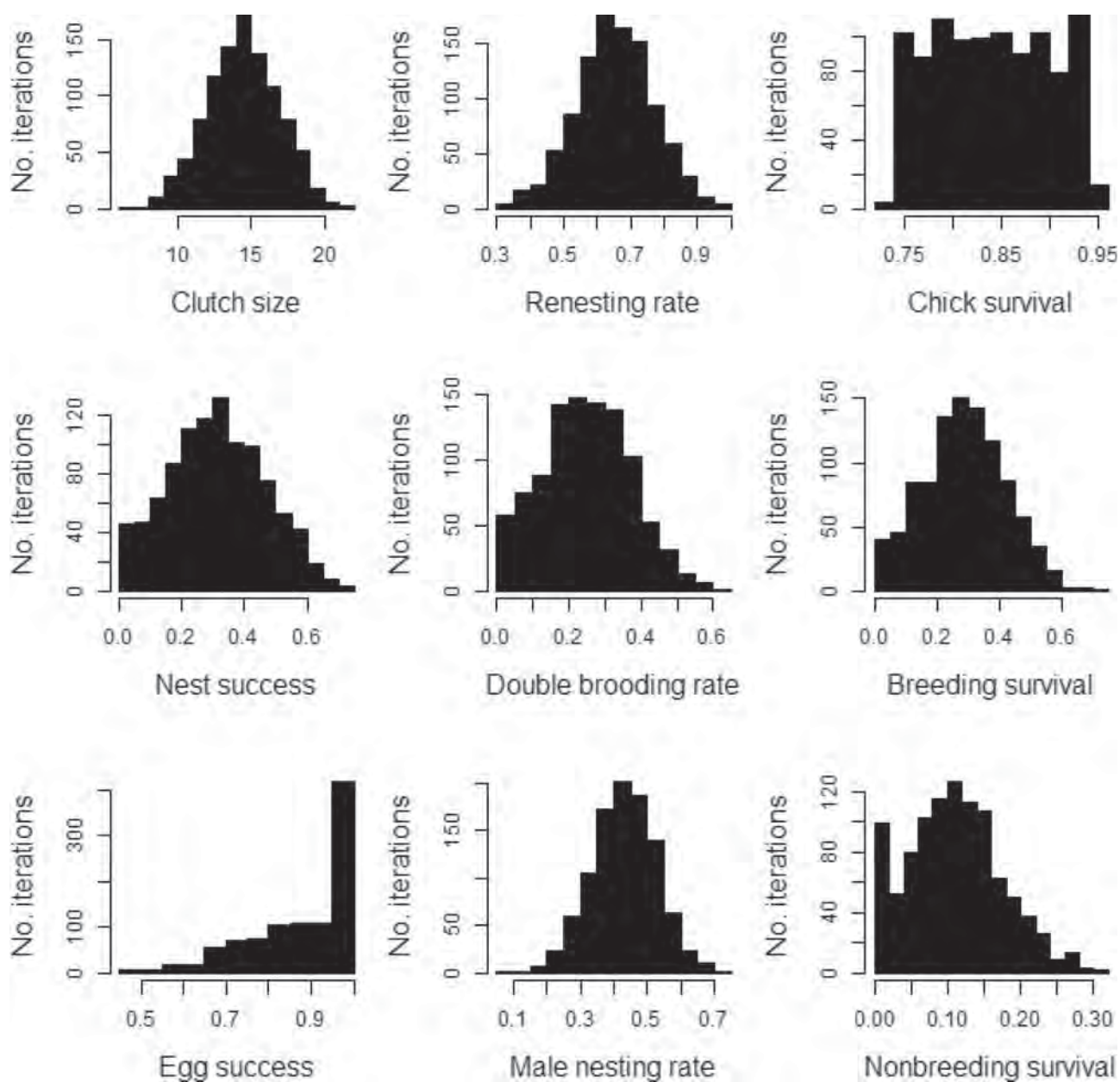
Fig. 3.   Values of vital rates randomly selected from normal or uniform (chick survival only) distributions of 9 vital rates for life-stage simulations of population growth rates of northern bobwhites in southwestern Ohio.

female was 0.432 (95% CI = 0.361-0.517). We estimated that 43% of nests were incubated by males assuming that nests were not incubated by both sexes and that all females made > 1 nest attempt (Table 1). Eleven of 17 (64.7%) females initiated new nests after losing a clutch and 3 of 12 (25.0%) females initiated new nests after successful clutches (Table 1).

Kaplan-Meier estimates of breeding season survival were 0.528 (95% CI = 0.348-0.800) in 2010 compared to 0.202 (95% CI = 0.107-0.381) in 2011. The pooled estimate of breeding season survival was 0.286 (95% CI = 0.177-0.462). Non-breeding season survival was 0.057 (95% CI = 0.028-0.117) in 2009–2010 compared to 0.118 (95% CI = 0.068-0.205) in 2010–2011. The pooled

estimate of non-breeding season survival was 0.107 (95% CI = 0.073-0.164).

Life Stage Simulations of Population Growth Rate and Fecundity

Life stage simulations of fecundity and population growth rates were based on 8 of 9 vital rates estimated from radiotelemetry data for adults and juveniles during October-March 2009–2010 and adults during April-September 2010–2011 (Table 1; Fig. 3). The median population growth rate from 1,000 combinations of vital rates was 0.296 (0.113-1.694 inter-quartile range). Non-breeding season survival of adults and juveniles was the most dominant vital rate affecting population growth rate
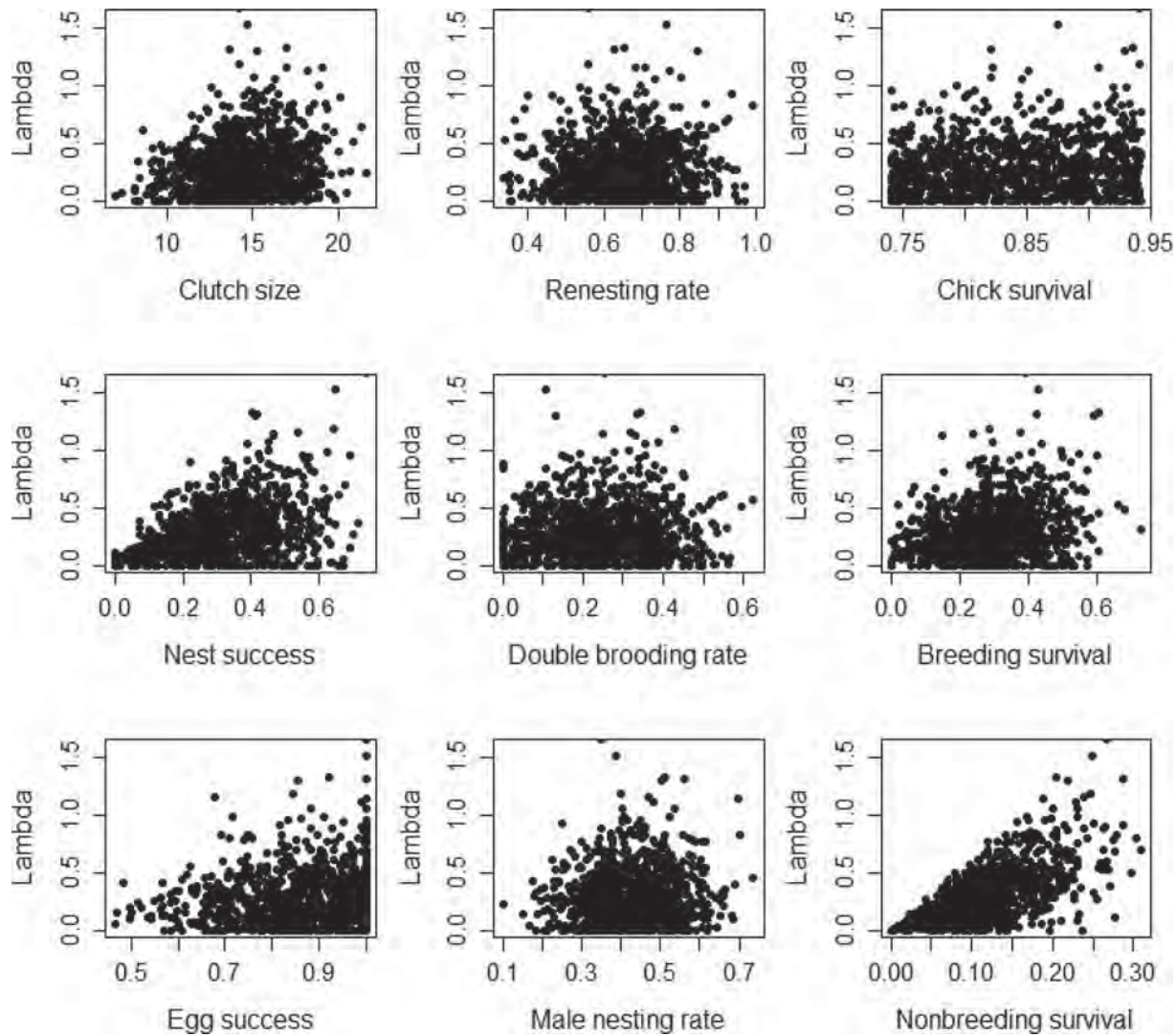
Fig. 4. Simulated growth rates for 9 vital rates used for life-stage analyses of population growth rates of northern bobwhites in southwestern Ohio.

in our simulations, followed by nest success and spring-summer survival (Table 2; Fig 4). Chick survival, egg success, and clutch size in order accounted for 2–5% of variation in λ. Components of nesting propensity were inconsequential in our simulations ($r^2 < 1\%$).

Total fecundity from all sources explained 36.9% of variation in λ. Total fecundity was most strongly influenced by variation in nest success, followed by

clutch size, and egg success (Table 3; Fig. 5). Vital rates of nesting propensity were inconsequential ($r^2 < 1\%$). Mean simulated fecundity was lower (2.41 juvenile females/adult female) than we observed in fall-capture age ratios (3.2 juveniles/adult).

Solving univariate equations relating vital rates to λ (Table 2) indicates a stable population could be attained if fall-winter survival of adults and juveniles was raised

Table 3. Regressions of northern bobwhite nesting productivity vital rates on estimates of fecundity rates calculated from life-stage simulation analyses following Sandercock et al. (2008). Vital rates were randomly selected ($n = 1,000$) from normal distributions with mean and standard deviations based on data collected on northern bobwhites in southwestern Ohio during 2009–2011 (Table 1) .

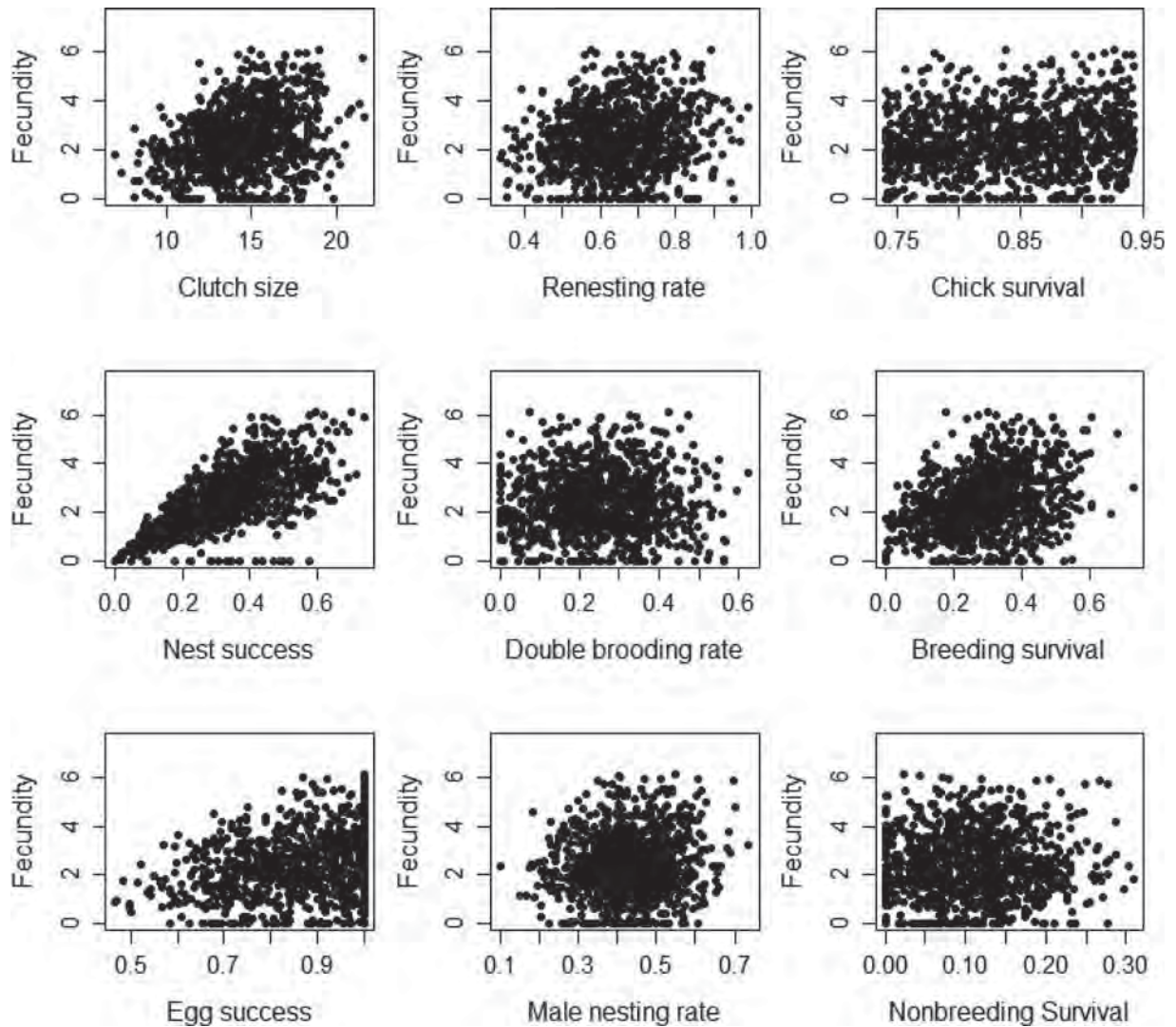| Vital rate	Intercept	Regression coefficient (b)	SE(b)	r^2
Clutch size	0.134	0.158	0.016	0.089
Egg success	0.053	2.679	0.319	0.066
Nest success	0.466	6.210	0.182	0.538
Male nest rate	1.769	1.490	0.426	0.012
Renesting rate	1.068	2.055	0.352	0.033
Double clutch rate	2.360	0.197	0.355	<0.001

Fig. 5. Total fecundity for 9 vital rates used for life-stage simulation analyses of population growth rates of northern bobwhites in southwestern Ohio.

from 10.9% (observed) to 36.9%. Population stability was not attainable with any biologically reasonable (e.g., total clutch size = 47) or mathematically possible (e.g., chick survival rate = 2.24) increase in any single vital rate. Raising nest success alone to the highest value we simulated (Table 1) would raise λ to only 0.571.

DISCUSSION

Study sites were selected to include only areas with sufficient habitat and densities of bobwhites to investigate habitat relationships and estimate population vital rates. We expected to find viable populations of bobwhites on the majority if not all study sites within the core of the geographic range of bobwhites in Ohio. We did not estimate covey or breeding bird densities on all study sites but only 2 (Wildcat and Fee) sustained populations that could be considered sufficient to provide hunting opportunity (DeMaso et al. 2011). Our findings

indicate a highly patchy distribution of bobwhites within the core of the species' range in Ohio. Isolated areas with suitable habitat and microhabitat conditions appear to support metapopulations of bobwhites within a regional population that is steadily declining in southwestern Ohio.

Our estimates of non-breeding and breeding season survival were lower than reported from across the range of bobwhites (Burger et al, 1995a, Sandercock et al. 2008, DeMaso et al. 2011). Nesting productivity and nesting propensity vital rates can be considered within the normal range of values reported from other studies (Burger et al. 1995b, Sandercock et al. 2008, DeMaso et al. 2011). Our life-stage simulations based on empirical information from southwestern Ohio support Guthery et al. (2000), Folk et al. (2007), and Sandercock et al. (2008) in that non-breeding season survival was the most important vital rate affecting growth rates in our population. Renesting, double-brooding, and male incubation have been considered sources of enhanced nesting productivity (Burger et

al. 1995b, Guthery and Kuvlesky 1998), but there is little evidence these vital rates affect population growth rate compared to other vital rates, especially survival and to a lesser extent nesting productivity.

The dominance of non-breeding survival in our life-stage simulations with 6 separate breeding vital rates seemed to diminish the influence of reproduction on population growth. Total fecundity had an intermediate univariate contribution to λ ($r^2 = 0.369$), compared to non-breeding ($r^2 = 0.504$) and breeding ($r^2 = 0.083$) season survival rates. This may have been an artifact of the mathematical structure of our life-stage simulations, failure to account for underlying covariance among vital rates, or over-simplicity of univariate regressions of λ on individual vital rates that do not account for complementary effects of variation in factors that affect total fecundity. These issues merit further consideration in future life-stage simulations.

Sandercock et al.'s (2008) life-stage simulations used vital rates sampled from uniform distributions informed by studies across the bobwhite's range. Our simulations were based almost entirely on empirical values observed during 2009–2011 in southwestern Ohio. Simulated vital rates were sampled from normal distributions that should better reflect stochastic annual variation compared to uniform distributions where all possible simulated values are equally probable. Our estimates of non-breeding season survival, nesting success, and other vital rates were from only 2 consecutive years that did not adequately represent the full range of effects of annual variation in weather conditions on population vital rates. Timing, depth, and duration of snow cover varied between years but we observed similar rates of non-breeding season survival (Janke and Gates 2012). Both years were characterized by several snow events that are less frequent in mild winters when non-breeding season survival may be higher than we observed. The breeding season also was extremely wet in 2011 when we observed a lower survival rate (0.202) compared to 2010 (0.528), but nest success did not differ between years.

Our life-stage simulations of population growth rate indicated the vital rates we measured, particularly non-breeding survival, were well below that required to sustain bobwhite populations in southwestern Ohio. Only 1.2% of simulated values for λ exceeded 1, the threshold value for population growth. This is consistent with the continual downward trend in regional population indices (Spinola and Gates 2008) from whistle-counts conducted by Ohio Division of Wildlife (Fig. 1B) that we also observed on our study sites (Fig. 2). Lohr et al. (2011) similarly concluded that survival rates were unsustainably low in a declining population of bobwhites at the northern periphery of the species' range.

Two consecutive years of low survival associated with above-average snow cover (Janke and Gates 2012) caused alarmingly low λ values in our simulations. We hypothesize that growth of this population was limited primarily by weather-mediated predation during winter. Simulated and observed (capture age ratio) fecundity rates were similar to those Roseberry et al. (1979) observed in a declining population that occupied deteriorating habitat in southern Illinois. Age ratios of < 4 juveniles/adult are considered low and generally inadequate to support viable populations (Roseberry and Klimstra 1984, Guthery et al. 2000). Fecundity rates were within the normal range of variation for northern bobwhites but were inadequate to sustain the population after severe winters or to produce surplus individuals that could colonize vacant or low-density habitats.

Covey densities did not differ between 2009-10 and 2010-11 despite low non-breeding survival during 2009–2010 and declining whistle-counts on the 4 intensive study areas. Negative population growth rates suggest our study sites were population sinks but we cannot explain how bobwhite populations were sustained on our intensive study sites except to hypothesize they are supplemented by ingress of birds from out-lying areas during the 'fall shuffle' (Murphy and Baskett 1952, Townsend et al. 2003), or that some birds disperse beyond the study areas to nest during spring and summer and then return with young in fall. This population does not appear to be dispersal-limited, as bobwhites dispersed up to 11.5 km in spring (Liberati and Gates 2012) but we know of no source populations near our study sites.

MANAGEMENT IMPLICATIONS

The future of northern bobwhites in Ohio hinges primarily on raising non-breeding season survival rates to levels that sustain population growth and range expansion to fill vacant habitats. Sandercock et al. (2008) also concluded that management to improve seasonal survival rates has the greatest potential for recovery of declining bobwhite populations. Our life-stage simulations were encouraging in that non-breeding season survival would need to increase by 26% to achieve population stability. Northern bobwhites on our study areas were highly dependent on early succession woody habitats, edges of early succession herbaceous fields, or woodlot edges that provided protective cover near winter food sources (Janke 2011, Janke and Gates 2013). Survival declined through winter and mortality rates were associated with depth, duration, and timing of snow cover during December-February (Janke 2011, Janke and Gates 2012). Improving protective cover near food sources (crop and warm-season grass fields) would increase useable space (Guthery 1997) and could raise non-breeding season survival rates to levels that support population recovery and range expansion in Ohio and perhaps other areas in the Midwestern U.S. We advocate greater emphasis on managing succession of woody cover along field, grassland, and woodlot edges that are heavily used during winter (Janke and Gates 2013). Continued effort to conserve early succession herbaceous habitats is still necessary to sustain nesting and perhaps raise nest success and summer survival rates of adults and fledged young before coveys form in October. Improving breeding season vital rates would augment efforts to raise population growth rates by improving non-breeding season survival.

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