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A MID-ATLANTIC AND A NATIONAL POPULATION MODEL OF NORTHERN BOBWHITE DEMOGRAPHIC SENSITIVITY

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ABSTRACT

Numerous field studies have estimated fecundity and survival rates for northern bobwhites (*Colinus virginianus*), but a synthetic population model based on life-stage simulation analysis (LSA) was only recently developed to examine demographic sensitivity of the finite rate of population change. We compare local demographic parameters of bobwhite versus a national compilation to identify limiting demographic factors for improved regional habitat planning and management. The national compilation provided a useful overview but combined parameters across populations at different latitudes and under different management regimes. We parameterized our LSA model to examine the sensitivity of the finite rate of growth (λ) to simulated variation in 9 demographic parameters primarily estimated from field studies for one population in regional decline in New Jersey. Our model results predicted population declines in New Jersey ($\lambda = 0.55$) comparable to the national estimate ($\lambda = 0.54$), but notable differences occurred in sensitivity of demographic variables. The national model predicted winter survival of adults made the greatest contribution to variance of λ ($r^2 = 0.42$) followed by summer survival of adults ($r^2 = 0.13$), and survival of chicks ($r^2 = 0.11$). Our regional model for New Jersey also predicted winter and summer survival of adults would make the greatest contribution to variance of λ ($r^2 = 0.33$ and $r^2 = 0.13$). The New Jersey model, in contrast to the national model, showed that annual variation in components of fecundity had a large effect on $\text{Var}(\lambda)$: including clutch size ($r^2 = 0.18$ vs. national $r^2 = 0.01$), nest success ($r^2 = 0.20$ vs. national $r^2 = 0.06$), and the number of young produced per nest that survived 30 days ($r^2 = 0.53$ vs. national $r^2 = 0.16$). Slopes of linear regression between simulated variation in each demographic variable against λ were similar between the national and regional models. The slope for number of young produced per nest that survived 30 days with one exception was lower in the New Jersey data indicating more young are required to realize a stationary population. Our simulation results suggest management practices that improve winter survival or the number of young surviving 30 days will have the greatest potential to increase bobwhite population growth rate in New Jersey. Future linkage of models of demographic performance to experimental habitat manipulations will aid regional scientific planning to improve necessary habitat management.

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Key words: *Colinus virginianus*, fecundity, life-stage simulation analysis, New Jersey, northern bobwhite, population model, survival

INTRODUCTION

The northern bobwhite is an upland gamebird of conservation concern because of widespread population declines primarily caused by habitat loss and degradation (Brennan 1991, Guthery et al. 2000, Williams et al. 2004, Veech 2006). Population roadside counts from the Breeding Bird Survey (BBS) indicate a range-wide decline of 3.9%/year between 1980 and 2007 (Sauer et al. 2011), despite being a short-lived species with high reproductive

potential (Sandercock et al. 2008). Some of the most marked declines in bobwhite populations are occurring at the northern periphery of the species' range, including the upper Mid-Atlantic states with an average decline of 8.8%/year (Fig. 1). It is unknown which population vital rates or stages of the annual life cycle are most limiting and how they account for recent population declines.

Numerous northern bobwhite field studies have estimated vital rates (compiled by Sandercock et al. 2008), and early population models used simulations, time-series, and structured models based on age ratios to model population dynamics (Roseberry 1979, Guthery

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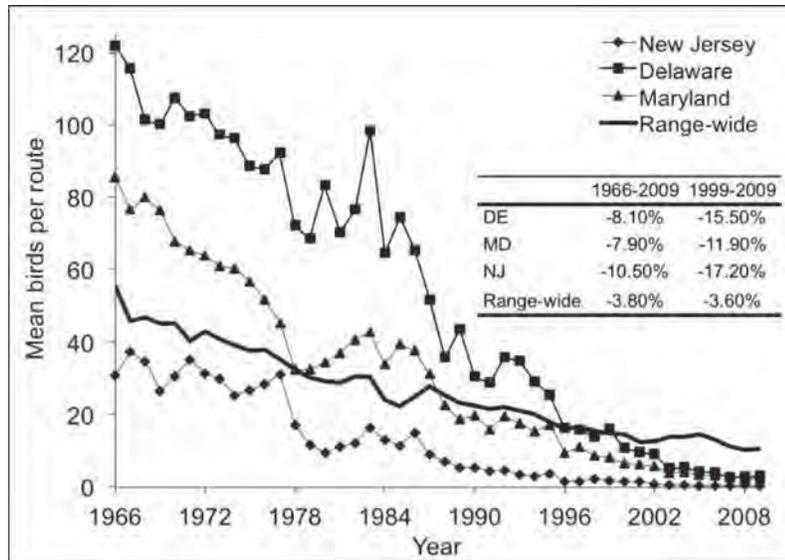


Fig. 1. Population trends of northern bobwhite in 3 Mid-Atlantic states and range-wide as estimated from the Breeding Bird Survey (1966–2009).

1997, Guthery et al. 2000, Thogmartin et al. 2002, Williams et al. 2003). However, it was not until recently (Sandercock et al. 2008), that a structured population model was developed. That model was an important first step because it provided a framework for investigating the impacts of underlying demographic parameters on population growth of northern bobwhites. We developed a model based on life-stage simulation analysis (LSA; Wisdom and Mills 1997, Wisdom et al. 2000), which uses randomization and coefficients of determination (r^2 values) to identify demographic parameters that make the greatest contributions to simulated variation in finite rates of population growth (λ). One advantage of LSA is that exploratory models can be built with limited demographic data. For example, if probability distributions of parameters are unknown, LSA models can be built using uniform distributions bounded by the range of possible values.

We used life-stage simulation analyses to develop a regional model of the demography of bobwhite in New Jersey with the goals to: (1) compare local/regional dynamics to a national model as a baseline, and (2) identify limiting local/regional demographic factors to improve habitat planning and management. Field data were collected during a 3-year study in a declining peripheral population of bobwhite in New Jersey (Collins et al. 2009, Lohr et al. 2011). We improve the national model to guide regional management because 8 of 9 demographic estimates were taken from one population exposed to a common set of ecological conditions. Our demographic model provides an example of the effectiveness of life-stage simulation analysis for local/regional bobwhite populations to guide future management in other regions of the country.

STUDY AREA

This 3-year field study was conducted within a ~ 125 - km^2 area without fixed study area boundaries in west-

central Cumberland County, New Jersey (focal area) during the 6-month bobwhite breeding season (1 May–30 Sep, 2006–2008) and nonbreeding season (1 Oct–30 Apr, 2006–2009). The focal area is within the Outer Coastal Plain physiographic region, bordering Delaware Bay. Land use in the focal area was 39.1% forest; 24.9% wetland; 20.0% agriculture, hayland, or pasture; 5.9% developed; 5.4% early successional habitat (including old fields, grasslands, and shrubland habitats); and 4.7% other land use (orchards and nurseries, extractive mining, and barren land) (NJDEP 2008). Forest overstorey species were predominantly oaks (*Quercus* spp.) and Virginia pine (*Pinus virginiana*); common understory and edge species were multiflora rose (*Rosa multiflora*), greenbriar (*Smilax* spp.), Russian olive (*Elaeagnus angustifolia*), and mountain laurel (*Kalmia latifolia*). Common grasses were broom sedge (*Andropogon virginicus*), big bluestem (*A. gerardi*), and orchard grass (*Dactylis glomerata*). The focal area was predominantly private land, but included $\sim 1.5 \text{ km}^2$ of managed grassland and savannah on the Buckshutem Wildlife Management Area.

METHODS

Field Collection of Parameter Estimates

We captured bobwhites year round using funnel traps (Stoddard 1931) baited with corn and red millet. Funnel traps were placed in locations with dense overhead vegetation to reduce risk of detection by avian predators. We also captured bobwhites by night-lighting when weather and roosting vegetation allowed (Labisky 1968), and by mist nesting with audio lures in summer. Captured birds were classified to age and gender (Rosene 1969), fitted with an individually-numbered aluminum leg band, and weighed to the nearest gram. We fit birds that weighed $\geq 150 \text{ g}$ with a 6-g necklace-mounted radio

transmitter (Burger et al. 1995). Bobwhites weighing ≤ 150 g were not radiomarked to avoid stress from radio transmitters weighing $\geq 5\%$ of an individual's body mass (Samuel and Fuller 1994). We collected the first primary on each wing if no flight feathers were missing for future genetic and stable isotope analysis. We released all bobwhites at location of capture. The Institutional Animal Care and Use Committee at the University of Delaware approved the capture and handling procedures used in this study (IACUC Approval #1142).

Individual bobwhites were allowed to acclimate to radio transmitters for 7 days before being included in survival analysis to reduce potential bias (Tsai et al. 1999). We located all bobwhites 4 to 7 times per week using handheld VHF and H-antennas for the 3-year period between 1 May 2006 and 30 April 2008 until mortality, radio loss, radio failure, or end of study season. Bobwhites were censored (9 of 152 = 6%) because of unknown fate, radio loss, or survival beyond the end of the study season. The midpoint between the last known location and the day the radio stopped moving or was not found was used as the censor date if exact dates of radio loss or disappearance were unknown, and fate was coded as survived. We visually confirmed potential mortalities following 3 consecutive locations at the same point in the first year of the study. Radio transmitters contained a mortality sensor that doubled the transmitter's pulse rate after 12 hrs of inactivity in the second year, allowing for more prompt investigation of mortality events. We recorded likely mortality causes as avian predation, mammalian predation, hunter harvest, study related mortality, unknown source, or other based on evidence present at the mortality site. We used the midpoint between the last day known alive and the date the bird was found dead, when exact mortality dates were not known, as the mortality date. We calculated 6-month summer and winter survival rates with Kaplan-Meier staggered-entry additions (Kaplan and Meier 1958, Pollock et al. 1989) in S-Plus 8.0 (Insightful Co., Seattle, WA, USA).

We identified potential bobwhite nests after 2 consecutive identical location estimates of a radio-marked adult (Burger et al. 1995). We placed a flag 10–15 m from the suspected nest site, and visually confirmed the nest location once the incubating adult was away from the site (Burger et al. 1995, Taylor et al. 1999). We attempted not to flush suspected incubating adults to minimize nest abandonment. We recorded the number of eggs and the location of the nest with a handheld Global Positioning System unit in UTM coordinates if a nest was discovered before the nesting attempt was completed. We monitored the status of each nest 4–7 times/week by locating the incubating adult. We visually inspected nests each time the incubating adult was away from the nest and recorded whether nests were depredated, eggs had hatched, or were undisturbed. We considered undisturbed nests where incubation did not resume within 7 days as naturally abandoned. We considered nests abandoned due to observer disturbance if abandonment occurred immediately after the accidental flush of an incubating bobwhite. We defined successful nests as those hatching ≥ 1 egg

(Taylor et al. 1999). We considered predated and naturally abandoned nests as failed.

We estimated nest daily survival rates (NEST) using the Mayfield method (Mayfield 1961) for a 24-day incubation period (Burger et al. 1995). We documented 5 other reproductive parameters including: (1) mean size of total clutch laid for all nests (TCL), (2) mean hatching success of eggs in nests that survived incubation (HATCH), (3) re-nesting probability (RENEST), (4) double-clutch attempts (SECOND), and (5) male nesting rates (MALE) by the simple proportion of radio-marked birds incubating a nest. We attempted to capture chicks to radiomark and estimate survival, but our efforts were unsuccessful; thus, we used a national average value for chick survival (S_c) for model formulation (Sandercock et al. 2008).

Population Model

We developed a female-based population model (following Sandercock et al. 2008) based on known bobwhite breeding behaviors that included: (1) all females nest as yearlings, (2) all females produce of at least one clutch, (3) re-nesting, (4) double-brooding, (5) male-incubated nests, and that (6) all components of fecundity are independent of the age and gender of the attending parent, type of nesting attempt, and seasonal timing of clutch initiation (Burger et al. 1995, Cox et al. 2005, Hernández et al. 2007). We split the year into 2 equal 6-month periods to include summer (S_s , 1 Apr to 31 Sep) and winter survival (S_w , 1 Oct to 31 Mar), and assumed seasonal survival to be density independent.

We first calculated the number of female young produced per nesting attempt that survived to independence at 30 days (*YOUNG*) to estimate yearly λ as:

$$YOUNG = TCL \times NEST \times HATCH \times 0.5 \times S_c,$$

where TCL is the total clutch laid, NEST is nest success, HATCH is the proportion of eggs that hatch, 0.5 is the proportion of young that are female (based on a 1:1 sex ratio at hatching; Lusk et al. 2005), and S_c is chick survival from hatch to independence at 30 days. Second, we calculated productivity for 6 different types of nesting attempts (f_i) (Table 1). Nesting attempts included: first nests incubated by females (f_1), second nests laid after successful hatching of a first clutch (SECOND) and incubated by females (f_2), renests laid after loss of a first nest (RENEST) and incubated by females (f_3), second renests laid after loss of first renests and incubated by females (f_4), first nests incubated by males (MALE) (f_5), and renests after loss of first male clutch and incubated by males (f_6). The formulae for nesting productivity for nesting attempts f_1 to f_6 were:

$$f_1 = YOUNG \times S_s^{3.5/6},$$

$$f_2 = NEST \times SECOND \times YOUNG \times S_s^{1/6},$$

$$f_3 = (1 - NEST) \times RENESEST \times YOUNG \times S_s^{2/6},$$

Table 1. Generalized breeding season for northern bobwhites based on reproductive strategies that include reneesting, double-brooding, and male-incubated nests. The 6-month breeding season is subdivided into 12 biweekly periods to account for seasonal variation in timing of nest initiation.

| | Apr | | May | | Jun | | Jul | | Aug | | Sep | |
|--------------------------|--------|------------|----------------|--------|--------------------|----------------|------------|--------------------|----------------|--------------------|--------------------|----|
| Nesting attempt | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| First nest (f_1) | Laying | Incubation | Chick survival | | Fledgling survival | | | | | | | |
| Second nest (f_2) | | | | | | Laying | Incubation | Chick survival | | Fledgling survival | | |
| First reneest (f_3) | | | Interval | Laying | Incubation | Chick survival | | Fledgling survival | | | | |
| Second reneest (f_4) | | | | | | Interval | Laying | Incubation | Chick survival | | Fledgling survival | |
| Male nest (f_5) | | | Interval | Laying | Incubation | Chick survival | | Fledgling survival | | | | |
| Male reneest (f_6) | | | | | Interval | Laying | Incubation | Chick survival | | Fledgling survival | | |

$$f_4 = (1 - NEST) \times RENEST \times (1 - NEST) \times RENEST \\ \times YOUNG \times S_S^{0.5/6},$$

$$f_5 = MALE \times YOUNG \times S_S^{2/6},$$

$$f_6 = (1 - NEST) \times RENEST \times MALE \times YOUNG \times S_S^{1/6},$$

where the exponents on the 6-month estimate of summer survival (S_S) account for the number of months of 6 months that each of the 6 different types of productivity survived between independence at 30 days and the end of the summer breeding season. We summed components of productivity using these 6 estimates to estimate seasonal fecundity per breeding female (F):

$$F = \sum_{i=1}^6 f_i$$

and estimated the finite rate of population change (λ) as:

$$\lambda = (S_S \times S_w) + (F \times S_w),$$

where lambda was the sum of surviving adults and surviving juveniles.

Life-stage Simulation Analysis

We used LSA to examine contributions of the 9 demographic parameters to simulated variation in λ (Wisdom et al. 2000). All simulations were conducted using algorithms implemented in Program R (R Development Core Team 2005). We drew a random set of 9 parameters from uniform probability distributions bounded by the full 100% range of field estimates for each demographic parameter. We combined them to calculate λ with the formulae presented in the population model, and repeated these steps for $n = 1,000$ iterations. We treated parameters as independent and did not use a covariance structure or a function with density-dependence to select random draws (Wisdom et al. 2000). We used linear regression and coefficients of determination

(r^2) to calculate the amount of variation in λ explained by simulated variation in each of the 9 demographic parameters. We also reran the national model using parameter distributions in Sandercock et al. (2008) and compared regression parameter estimates (β) for each demographic variable between the New Jersey model and National model to identify areas of biological difference (paired t -test, Clogg et al. 1995). We recognize the robustness of the t -test is compromised because the distributions are based on a uniform distribution instead of a normal distribution.

RESULTS

We captured and radiomarked 152 bobwhites including 86 during the breeding seasons of 2006 and 2007. We censored 6 that survived ≤ 7 days leaving 80 (35 juv M, 11 ad M, 25 juv F, 9 ad F) to estimate breeding season survival. We captured 66 bobwhites during the winter seasons of 2006–2007 and 2007–2008. We censored 5 that survived ≤ 7 days after capture leaving 61 bobwhites (18 juv M, 12 ad M, 18 juv F, 13 ad F) to estimate winter survival. Estimated survival during the 6-month breeding season was 0.267 (95% CI = 0.172–0.417, Table 2). Survival during the 6-month non-breeding season was higher at 0.308 (95% CI = 0.210–0.453). Annual survival pooled across years was 0.063 (95% CI = 0.029–0.136). We used the 95% CI for each season as the uniform distribution boundary of possible survival rates in the LSA.

We located 23 bobwhite nests (16 in 2006, 7 in 2007) by tracking radio-marked birds during the breeding season. Ten nests hatched over both years, 10 were depredated, 1 was abandoned (incubating adult was killed away from the nest site), and 2 nests were abandoned due to observer disturbance. Interval survival (NEST) (based on 340 monitoring days and a daily survival rate = 0.967 [95% CI = 0.948–0.987]) for the 24-day incubation period was 0.454 (95% CI = 0.282–0.728; Table 2). Mean clutch size (TCL) was 14.2 (range = 10–19). Hatching success of eggs (HATCH) in successful nests that survived incuba-

Table 2. Demographic rates estimated from New Jersey (2006–2009) compared to national median values (Sandercock et al. 2008). Predicted LSA λ estimates based on demographic rates are shown at the bottom.

| Demographic parameter | New Jersey Mean (range or 95% CI) | Range-wide Median (range) |
|--|--------------------------------------|------------------------------|
| Total clutch laid (eggs) | 14.2 (10–19) | 12.8 (11.2–15.6) |
| Renesting | 0.44 (0.33–0.67) | 0.50 (0.0–1.00) |
| Nest survival | 0.454 (95% CI = 0.282–0.728) | 0.42 (0.19–0.70) |
| Double-brooding | – | 0.25 (0.15–0.42) |
| Hatching rate (chicks/egg) | 0.96 (0.86–1.00) | 0.92 (0.80–0.96) |
| Male nesting (M-nest/F-nest) | 0.27 (0.25–0.27) | 0.28 (0.06–0.51) |
| Chick survival (1 mo) | – | 0.41 (0.14–0.72) |
| Total young survived 30 days per nesting attempt | 1.27 (0.35–3.67) | 1.01 (0.12–3.77) |
| Summer survival (6 mo) | 0.267 (95% CI = 0.172–0.417) | 0.39 (0.01–0.92) |
| Winter survival (6 mo) | 0.308 (95% CI = 0.210–0.453) | 0.26 (0.01–0.73) |
| λ (Median and 95% CI) | 0.548 (0.263–1.124) | 0.543 (0.034–2.175) |

tion was 96.1 (range = 86–100%). Nine females had a failed first nest attempt, and 4 (44.4%) renested (RENEST, inter-year variation = 33.3–66.6%). The ratio of the number of male-incubated nests per female-incubated nesting attempt (MALE) was 0.267 (range = 0.25–0.273). No females were observed to initiate a second nest (SECOND) after fledgling young from a successful first nest (0 of 5; 0.0%). Lack of second broods could be a function of high latitude in New Jersey, but we conservatively assumed the possibility of second nesting could occur using the national average (range = 0.15–0.42). We were unable to estimate chick survival S_c and used the national average to parameterize this variable (range = 0.29–0.53).

The median rate of population change for our New Jersey population was $\lambda = 0.548$ (95%CI = 0.263–1.124) which was comparable to the national median rate of population change at $\lambda = 0.543$ (95% CI: 0.034–2.175; Table 1). Simulated variation in the New Jersey winter survival, like the national model, made the greatest contribution to variance in λ ($r^2 = 0.331$; Fig. 2), although it was lower than the national model ($r^2 = 0.420$; Fig. 3). However, the estimates of the slopes of the two linear regressions were not different (New Jersey = 1.82 vs. national = 1.95, $t_1 = 0.914$, $P = 0.361$). A 1% change in winter survival would produce a change in λ of 1.8% for regional and national models. The New Jersey model predicted 56.1% overwinter survival would be required to produce $\lambda = 1$ while the national model predicted 53.5% survival would be required. Summer survival of New Jersey adults ($r^2 = 0.185$) was also similar to the national model ($r^2 = 0.127$), and regression slope parameter estimates did not differ (New Jersey = 1.16 vs. national = 0.97, $t_1 = 0.443$, $P = 0.658$). A 1% change in summer survival would produce a λ change of 1.1% in the New Jersey model and 1.8% in the national model. The New Jersey model predicted 65.5% summer survival would be required to produce $\lambda = 1$ while the national model predicted 75.4% survival would be required.

The rate of population change was not sensitive to hatching success, probability of renesting, or male-

incubated nests per female nest in either the New Jersey and national models ($r^2 < 0.01$) and showed no difference in regression parameter estimates ($t_1 < 0.934$, $P > 0.350$). National values were used for chick survival ($r^2 = 0.13$), and second nesting ($r^2 = 0.001$) and we did not compare regression betas. The var (λ) for bobwhite in New Jersey, unlike the national model, showed strong responses to clutch size ($r^2 = 0.175$; national $r^2 = 0.005$) and nest success ($r^2 = 0.201$; national $r^2 = 0.063$) (Figs. 2, 3). Neither parameter showed differences in the predicted regression slopes (Clutch Size: New Jersey = 0.04 vs. national = 0.04, $t_1 = 0.047$, $P = 0.963$ and Nest Success: New Jersey = 0.79 vs. national = 0.92, $t_1 = 0.897$, $P = 0.370$, respectively). A 1-egg change in clutch size would produce a 3.6% change in λ in the New Jersey model compared to 3.3% in the national model. The New Jersey model predicted a clutch size of 26 would be required to produce $\lambda = 1$ while the national model predicted a clutch size of 22. A 1% change in nest success would produce a λ change of 0.8% in the New Jersey model and 0.9% in the national model. The New Jersey model predicted 103.4% nest success would be required to produce $\lambda = 1$ whereas the national model predicted 76.0% nest success would be required.

The coefficients of variation were most different in clutch size and nest success, and we combined all nesting variables required to equal the number of YOUNG produced (TLC, NEST, HATCH, and S_c) and compared the model fit between the New Jersey and national models. The estimated coefficient of determination for the New Jersey data was strong ($r^2 = 0.525$; Fig. 2) compared to the national model ($r^2 = 0.160$; Fig. 3), but also indicated a lower slope in the regression lines (New Jersey = 0.315 vs. national = 0.380, $t_1 = 3.928$, $P < 0.001$). Addition of one female young produced per nesting attempt that survived to independence at 30 days would produce a 31.5% change in λ in the New Jersey model compared to 38.0% in the national model. The New Jersey model predicted 2.74 female young produced per nesting attempt that survived to independence at 30 days would be required to produce $\lambda = 1$ while the national model predicted 1.90 female young.

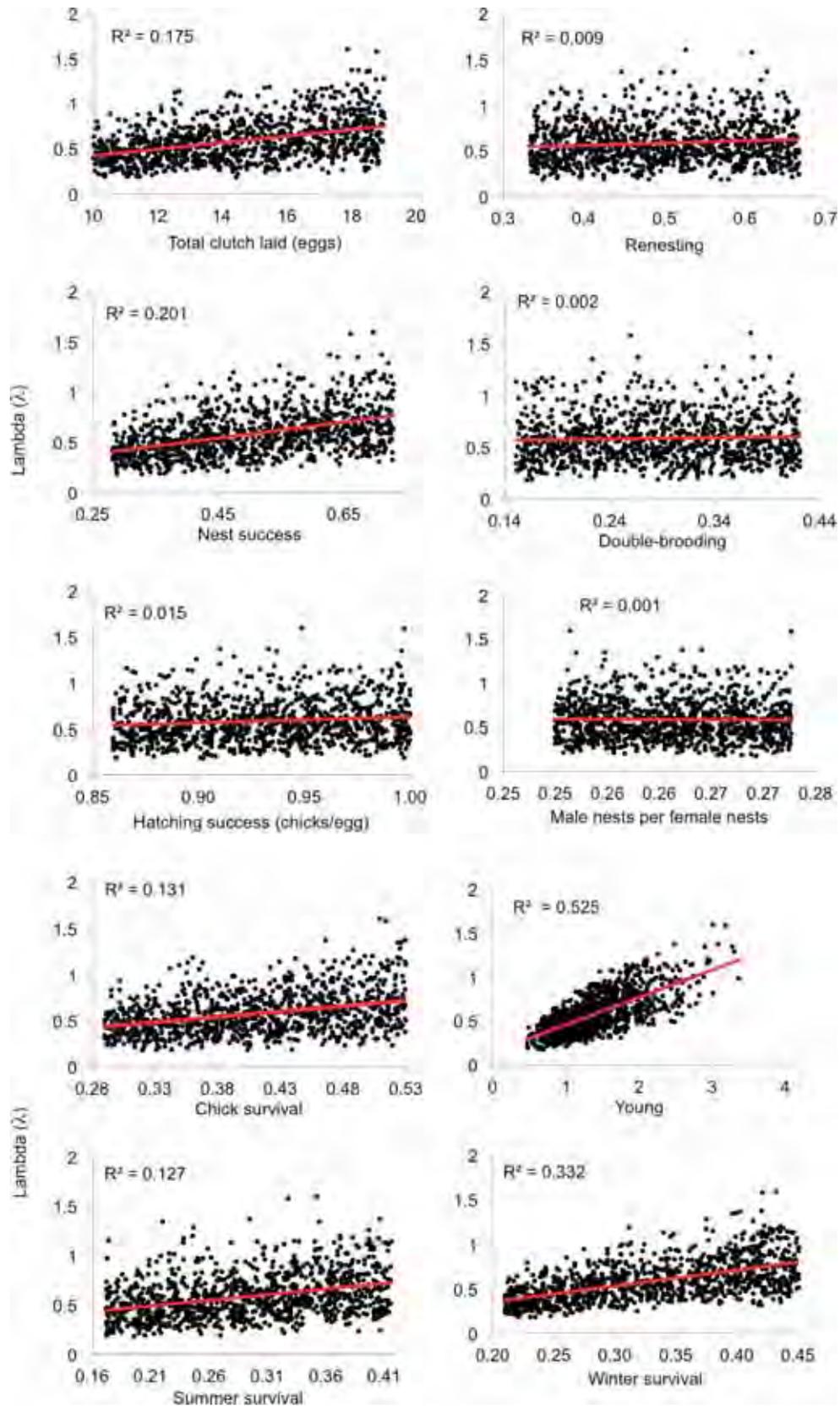


Fig. 2. Life-stage simulation analysis of the finite rate of population change (λ) in response to simulated variation in 10 demographic parameters for northern bobwhites in New Jersey (2006–2009). Coefficients of determination (R^2) indicate the proportion of simulated variance in λ explained by variation in the demographic parameters. Eight demographic parameters were bounded by the minimum and maximum values observed under field conditions. Estimates were drawn from uniform distributions and combined to calculate λ ($n = 1,000$ bootstrap iterations). National values (Sandercock et al. 2008) were used for chick survival and the probability of second nesting attempts.

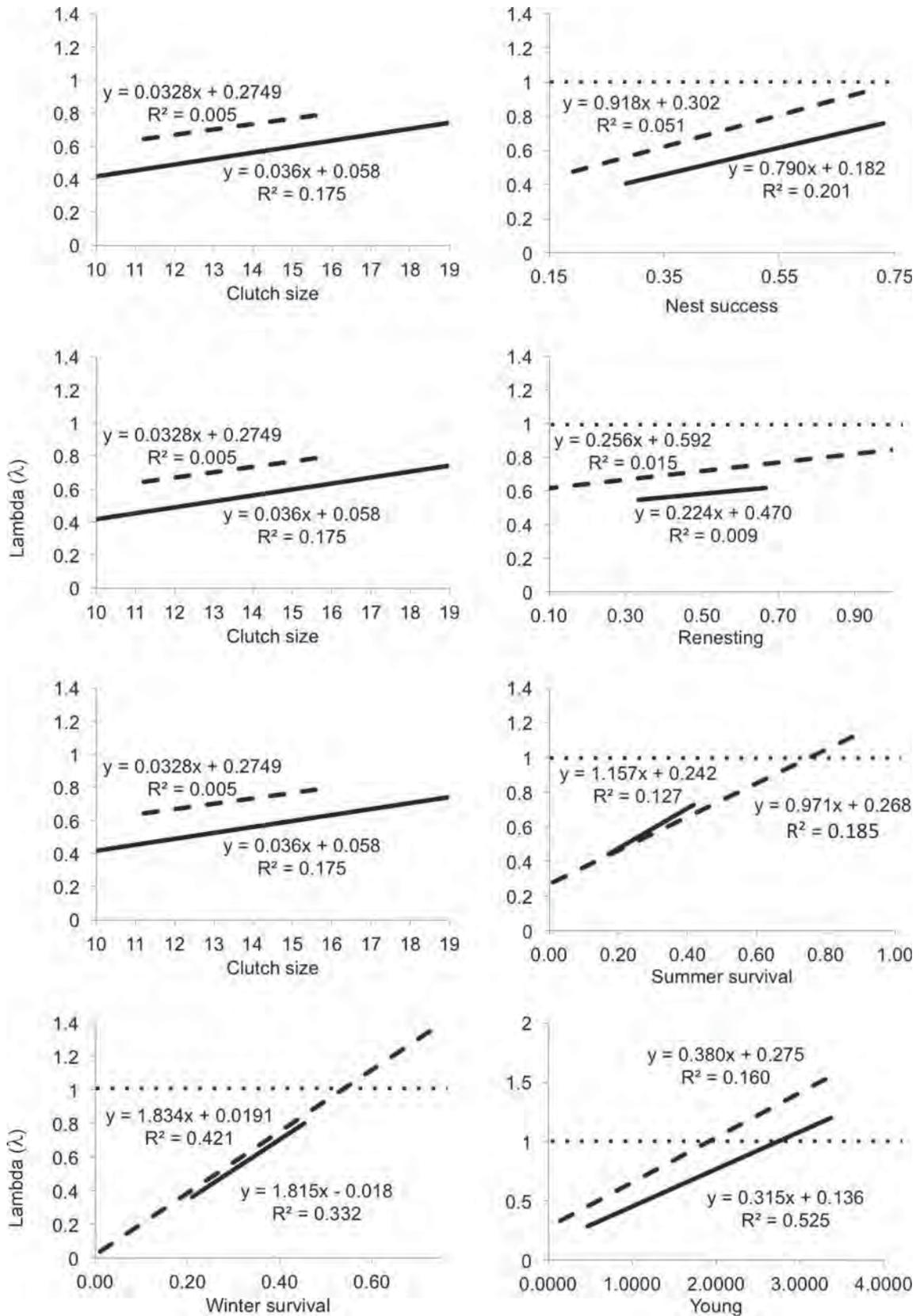


Fig. 3. Estimated regressions of life-stage simulation analysis of the finite rate of population change (λ) in response to simulated variation in 8 demographic parameters for northern bobwhites in New Jersey (solid line, 2006–2009) and national (dotted line, Sandercock et al. 2008). Coefficients of determination (r^2) indicate the proportion of simulated variance in λ explained by variation in the demographic parameters. The national values for chick survival and probability of second nesting attempts were used in the state model but are not compared in this figure.

DISCUSSION

Our demographic analyses for northern bobwhites in New Jersey addressed 2 goals; first to illustrate the use of life-stage simulation analysis for local or regional studies of population viability, and second, to inform regional management of a declining population of bobwhites at the northern periphery of the species' geographic range. Multiple quantitative methods are available for modeling populations, including LSA (Wisdom and Mills 1997, Wisdom et al. 2000, Sandercock et al. 2008) and parametric matrix models (Caswell 2001, Fieberg and Ellner 2001). Parametric matrix models are widely used (Oli and Dobson 2003, Stahl and Oli 2006) and have the advantage of using sensitivity or elasticity analysis to ascertain demographic parameters that most influence λ . However, they require large long-term data sets because a probability distribution must be used to bootstrap confidence intervals (Fieberg and Ellner 2001). In contrast, because modeling relies on randomization and coefficients of determination to identify demographic parameters that most influence λ , LSA does not require *a priori* knowledge of a probability distribution and use of uniform distributions can suffice. Simulations have shown that different probability distributions usually have little effect on qualitative results of stochastic population models (Wisdom et al. 2000, Fieberg and Ellner 2001, Kaye and Pyke 2003, Sandercock et al. 2008). A practical advantage of LSA models is that they can be developed with less information or with data from different sources. The LSA approach proved invaluable in our synthetic national northern bobwhite model for pulling together data from many different sources of varying quality. The LSA method may prove useful for local and regional researchers who wish to model populations with less information collected over limited spatial or temporal scales. Regression beta coefficients in the comparisons of our study were similar between the national meta-analysis and the local study indicating biological relevance can be examined through LSA despite different data sources.

Our model for bobwhite in New Jersey was mostly based on demographic parameter estimates from field studies of a single population, whereas the national model combined estimates from different populations exposed to varying ecological conditions. Results of our regional and national model for bobwhite were comparable. Our analyses indicated winter and summer survival had strong influences on variation in rates of population change in a declining population. Changes in survival often have a strong effect on rates of growth in declining populations (Meats 1971), and similar results have been reported for bobwhites (Folk et al. 2007, Sandercock et al. 2008), wild turkeys (*Meleagris gallopavo*, Alpizar-Jara et al. 2001), 2 species of partridge (Bernard-Laurent and Léonard 2000, Bro et al. 2000), and 9 of 10 species of grouse (Sandercock et al. 2005, Hannon and Martin 2006, Tirpak et al. 2006). Guthery (1997) and Guthery et al. (2000) suggested that northern populations of bobwhites tend to have higher fecundity and lower annual survival compared to southern populations. One interesting difference between the New Jersey and national models was a large

impact of two key components of reproductive effort: total clutch size (New Jersey: $r^2 = 0.175$; national: $r^2 = 0.005$) and nest success (New Jersey: $r^2 = 0.201$; national: $r^2 = 0.051$) on the rates of population change. The observed New Jersey estimates were slightly higher than the national estimates for both vital rates. We found a strong r^2 value associated with winter survival in New Jersey despite predicted latitudinal variation in bobwhite life histories. The predicted survival rate was higher (31%) than that of the national model average (26%) which was dominated by data from southern states.

High reproductive potential may compensate for greater seasonal losses during cold winters in northern populations. We further calculated the number of female young produced per nesting attempt that survived to independence at 30 days (YOUNG) and found the greatest contribution to variance around λ ($r^2 = 0.525$) compared to the national value of $r^2 = 0.160$. A high contribution of fecundity is consistent with Wisdom and Mills (1997) and Wisdom et al. (2000) who found similar impacts of fecundity for greater prairie-chicken (*Tympanuchus cupido*) population growth. Each reproductive parameter actually produced a lower impact on λ despite the higher predictive power in variance explanation. New Jersey would require 2.74 female young per adult female surviving to 30 days to produce population stability whereas the range-wide estimate of YOUNG predicted 1.90 would be sufficient. Despite the greater coefficient of determination of this data in New Jersey, it also deviated sufficiently from the national data for a lower slope and less of an effect on λ .

We have shown using LSA to model local and regional populations with sparse data sets allows for population predictions and estimates. We encourage state and regional researchers who have conducted demographic and ecological studies of bobwhite to combine their data sources to catalogue the 9 demographic variables used in our national LSA model to produce their own regional assessments. Regional land managers may have an opportunity to identify and adjust management efforts to address demographic limitations of population growth through comparison of demographic differences with a baseline $\lambda = 1$ and national results. The National Bobwhite Conservation Initiative (NBTC 2011) has recently increased efforts to improve scientific rigor and develop an information framework. We encourage future researchers to: (1) test the robustness of this methodology with independent measures of λ , and (2) refine local chick survival estimates in New Jersey as well as throughout the bobwhite range. We hope this population model will increase that regional information base in an effort to improve regional management recommendations.

MANAGEMENT IMPLICATIONS

Northern populations of bobwhites should have higher fecundity to compensate for stochasticity in winter survival (Guthery 1997). That high fecundity did not offset high rates of mortality suggests an area for future habitat management with special emphasis on nest

success and chick survival. Grassland and early successional habitats are traditionally viewed as good bobwhite nesting and brood-rearing habitat (Edminster 1954, Roseberry and Klimstra 1984), and can improve survival of breeding adults (Lohr et al. 2011). However, New Jersey is on the low end of a range-wide continuum of bobwhite breeding habitat availability and quality due to extensive urban development and cover in forested habitats. Only 8.7% of our study area was early successional habitat in grassland or shrub-scrub versus 49–80% early successional cover at sites in Kansas and Mississippi (Taylor et al. 1999, Taylor and Burger 2000). Steep declines in BBS numbers in New Jersey are likely related to local extinctions resulting from loss of patchily-distributed habitat associated with grassland and early successional habitat. We recommend local managers examine: (1) opportunities to improve or increase grassland habitat to improve breeding demographic parameters, and (2) increase woody escape cover around grassland habitat to improve winter survival.

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