

Demographic Sensitivity of Population Change in Northern Bobwhite

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ABSTRACT The northern bobwhite (*Colinus virginianus*) is an economically important gamebird that is currently undergoing widespread population declines. Despite considerable research on the population ecology of bobwhites, there have been few attempts to model population dynamics of bobwhites to determine the contributions of different demographic parameters to variance of the finite rate of population change (λ). We conducted a literature review and compiled 405 estimates of 9 demographic parameters from 49 field studies of bobwhites. To identify demographic parameters that might be important for management, we used life-stage simulation analyses (LSA) to examine sensitivity of λ to simulated variation in 9 demographic parameters for female bobwhites. In a baseline LSA based on uniform distributions bounded by the range of estimates for each demographic parameter, bobwhite populations were predicted to decline ($\lambda = 0.56$) and winter survival of adults made the greatest contribution to variance of λ ($r^2 = 0.453$), followed by summer survival of adults ($r^2 = 0.163$), and survival of chicks ($r^2 = 0.120$). Population change was not sensitive to total clutch laid, nest survival, egg hatchability, or 3 parameters associated with the number of nesting attempts ($r^2 < 0.06$). Our conclusions were robust to alternative simulation scenarios, and parameter rankings changed only if we adjusted the lower bounds of winter survival upwards. Bobwhite populations were not viable with survival rates reported from most field studies. Survival rates may be depressed below sustainable levels by environmental conditions or possibly by impacts of capture and telemetry methods. Overall, our simulation results indicate that management practices that improve seasonal survival rates will have the greatest potential benefit for recovery of declining populations of bobwhites. (JOURNAL OF WILDLIFE MANAGEMENT 72(4):970-982; 2008)

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Understanding the sensitivity of population change to changes in demographic parameters is a central goal of wildlife ecology, and a range of quantitative methods can be used to identify parameters that might be useful targets for population recovery, management, or control. Two types of stochastic population models in widespread use include the parametric matrix method (Caswell 2001, Fieberg and Ellner 2001) and life-stage simulation analyses (LSA; Wisdom and Mills 1997, Wisdom et al. 2000). The 2 types of models differ in their diagnostic metrics, in quality of demographic data that are required for modeling, and their use as a tool in wildlife ecology. Parametric matrix models are based on matrix algebra and use derivatives based on absolute (sensitivity) or proportional (elasticity) changes to identify matrix elements or demographic parameters with the greatest effect on finite rates of population growth (λ). In contrast, LSA methods use randomization and coefficients of determination (r^2 values) to identify demographic parameters that make the greatest contributions to simulated variation in λ .

The parametric matrix method requires knowledge of probability distributions for each demographic parameter to bootstrap confidence intervals for matrix properties (Fieberg and Ellner 2001). In analyses of vertebrate demography, fecundity and survival might be modeled as draws from normal and beta distributions, respectively (Cross and Beissinger 2001, Sandercock et al. 2005, Tirpak et al. 2006). One practical advantage of the LSA method is that models can be developed with less information. If the

probability distribution of a demographic parameter is unknown, the parameter can be modeled as draws from a uniform distribution that is bounded by a range of possible values. Other probability distributions can be used with both approaches, but simulations have shown that choice of probability distribution has little effect on qualitative results of stochastic population models (Wisdom et al. 2000, Fieberg and Ellner 2001, Kaye and Pyke 2003). Parametric matrix models have been widely used in wildlife ecology (Oli and Dobson 2003, Stahl and Oli 2006), but applications of LSA have been limited to population studies of a tortoise (Wisdom et al. 2000), 2 species of grouse (Wisdom and Mills 1997, Tirpak et al. 2006), a songbird (Citta and Mills 1999), and 3 species of mammals (Crooks et al. 1998, Cross and Beissinger 2001, Gerber et al. 2004).

The northern bobwhite (*Colinus virginianus*) is an economically and culturally important gamebird that is one of the best-studied wildlife species in North America. Bobwhites are currently of management concern because of widespread population declines caused by habitat loss (Brennan 1991, Guthery et al. 2000, Williams et al. 2004a, Veech 2006). Population studies of bobwhites played a key role in the early development of wildlife ecology (Stoddard 1931, Leopold 1933, Errington and Hamerstrom 1935, Errington 1945), and numerous field studies have examined impacts of management on the demography of bobwhites, including components of fecundity (DeVos and Mueller 1993, Burger et al. 1995b, Cox et al. 2005), survival (Curtis et al. 1988, Robinette and Doerr 1993, Madison et al. 2002,

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Williams et al. 2004b), or both (Taylor et al. 1999, Carter et al. 2002, Hughes et al. 2005). Nevertheless, there have been few attempts to model demographic sensitivity of population change in northern bobwhites, as has been conducted for other galliforms (Wisdom and Mills 1997, Bro et al. 2000, Sandercock et al. 2005, Hannon and Martin 2006, Tirpak et al. 2006). Previous population models for bobwhites have been based on simulated population numbers (Roseberry 1979), time-series analyses of count data (Thogmartin et al. 2002, Williams et al. 2003a), and structured models based on age ratios (Guthery 1997, Guthery et al. 2000, Folk et al. 2007). Unstructured population models facilitate modeling of density-dependence and environmental stochasticity but do not examine impacts of underlying demographic parameters on population dynamics. Age ratios are widely used in wildlife ecology but require restrictive assumptions, including equal sampling effort among age classes, stable age distributions, and knowledge of rates of population change (Conn et al. 2005, Sandercock 2006).

We conducted a literature review to locate estimates of demographic parameters from published field studies of northern bobwhites. Past research on bobwhites has been extensive and we expected parameter estimates to vary with breeding latitude, environmental conditions, and exposure to harvest (Guthery 1997, Guthery et al. 2000, Cox et al. 2005, Hernández et al. 2005, Folk et al. 2007). To account for variation and uncertainty in demographic parameters and to explore different combinations of parameter estimates, we used life-stage simulation analyses to model population viability of bobwhites. Our 3 objectives were to 1) compile estimates of demographic parameters for northern bobwhites, 2) develop a population model that captures the essential elements of the biology of this species, and 3) identify which demographic parameters make the greatest contributions to variance of the finite rate of population change (λ) in declining populations.

METHODS

Demographic Parameters

We conducted a comprehensive search for published estimates of demographic parameters from field studies of northern bobwhites under natural conditions. We searched wildlife ecology literature by using 7 search terms (bobwhite, brood, clutch, fecundity, quail, nest, and survival) in major electronic databases including *Biblioline*, *Biological Abstracts*, and *Web of Science*. In addition, we consulted published volumes of *Proceedings of National Quail Symposium* and articles cited by relevant studies. We restricted our compilation to articles published in peer-reviewed journals or books and did not include agency reports or graduate theses. We compiled annual estimates of demographic parameters and treated estimates as independent if they were presented separately for different years, study plots, or management treatments. We used data from females if a study reported sex-specific differences in demographic parameters, otherwise we used estimates based on a pooled sample of both sexes.

We compiled published estimates of 9 independent demographic parameters for bobwhite populations: 3 components of fecundity, 3 parameters related to production of nesting attempts, and 3 survival rates. All estimates were annual averages calculated for independent samples of nests, broods, or marked birds.

1. Total clutch laid (*TCL*) was the number of eggs laid per nesting attempt.
2. Nest survival (*NEST*) was the probability that nests survived the laying and incubation periods to successfully hatch. Most published estimates were presented as the proportion of nests that hatched young, but apparent nest survival overestimates nest survival because it fails to account for exposure prior to nest discovery. Only a few studies reported extrapolated nest survival based on daily survival rates calculated with Mayfield (1975) methods or nest survival models (e.g., Burger et al. 1995b).
3. Hatchability (*HATCH*) was the proportion of eggs that hatched and produced chicks that left the nest, conditional upon survival of the nest until hatching. Values of *HATCH* <1 included losses to partial clutch predation and eggs that failed to hatch.
4. Renesting (*RENEST*) was the probability of a female producing a replacement clutch if her first clutch was destroyed before hatching.
5. Double-brooding (*SECOND*) was the probability of a female producing a second nesting attempt if her first clutch successfully hatched and the young survived until independence at 30 days. Triple-brooding has been documented in some bobwhite populations but we did not include this parameter because it is a rare strategy that contributes little to seasonal fecundity (Guthery and Kuvlesky 1998).
6. Male nesting (*MALE*) was the ratio of the number of male-incubated nests per female-incubated nesting attempts.
7. Chick survival (S_c) was the proportion of chicks hatched that survived until independence at 30 days. We selected 30 days as a threshold because chick survival is low before young develop wing feathers (14 days) and are capable of thermogenesis (28 days; Lusk et al. 2005). Broods are usually deserted by the attending parents after about a month, although timing of abandonment may vary among populations (17–39 days; Sermons and Speake 1987, Suchy and Munkel 1993, DeMaso et al. 1997). Posthatching brood amalgamation can bias estimates of chick survival based on brood counts but is relatively rare in bobwhites (Faircloth et al. 2005).
8. Summer survival (S_s) was the survival of bobwhites for the 6-month period from 1 April to 30 September. We included estimates of survival based on covey counts (e.g., Robel and Kemp 1997) but recognize that these estimates may be biased if bobwhites disperse among social groups (Williams et al. 2003b). Estimates of summer survival were reported for a 6-month period in 60% of published studies, but other authors used periods of different duration. We adjusted all estimates to a 6-month period for use in our

Table 1. A generalized breeding season for northern bobwhites in the United States. We subdivided the 6-month breeding season into biweekly periods to account for seasonal variation in timing of nest initiation for reproductive strategies that included renesting, double-brooding, and male-incubated nests.

Nesting attempt	Apr		May		Jun		Jul		Aug		Sep	
	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0
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							
Second reneest (f_4)						Interval	Laying	Incubation		Chick survival		Fledgling survival
M nest (f_5)			Interval	Laying	Incubation		Chick survival		Fledgling survival			
M reneest (f_6)					Interval	Laying	Incubation		Chick survival		Fledgling survival	

population model by calculating summer survival as $\hat{S}_s = \hat{S}_{obs}^{183/per}$, where \hat{S}_{obs} was the observed survival reported by the authors and *per* was the period of exposure in days.

- Winter survival (S_w) was the survival of bobwhites for the 6-month period from 1 October to 31 March. Estimates of winter survival were reported for a 6-month period in 50% of available studies. Using the same procedure as in summer survival, we adjusted estimates of winter survival to a 6-month period for the remaining studies.

Population Model

We developed a female-based population model based on reproductive strategies of bobwhite described by Curtis et al. (1993), Burger et al. (1995b), and Guthery and Kuvlesky (1998), including reneesting, double-brooding, and male-incubated nests. We assumed that all females started breeding as yearlings and produced ≥ 1 clutch per year. Rates of nesting among radiomarked bobwhites are sometimes < 1 (Curtis et al. 1993, Burger et al. 1995b, Cox et al. 2005), but we were unable to distinguish between variation in breeding propensity (Harveson et al. 2004, Hernández et al. 2007) and possible nest failure before nests were located by observers (Suchy and Munkel 1993, McPherson et al. 2003). We assumed that all components of fecundity were independent of the age and sex of the attending parent, type of nesting attempt, and seasonal timing of clutch initiation (Burger et al. 1995b, Cox et al. 2005, Hernández et al. 2007). We split the year into 2 equal 6-month periods and further subdivided the 6-month summer breeding season into biweekly periods (Table 1). We based our analyses on a compilation of demographic parameters from the literature, and we were unable to model possible effects of density-dependence or life-history tradeoffs among different parameters.

We calculated rates of population change for bobwhites in 4 steps. First, we calculated number of female young produced per nesting attempt that survived to independence at 30 days (*YOUNG*) as:

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

where 0.5 is the proportion of young that are female (based on a 1:1 sex ratio at hatching; Lusk et al. 2005).

Second, we calculated productivity for 6 types of nesting attempts (f_i). Nesting attempts included first nests incu-

bated by females (f_1), second nests laid after successful hatching of a first clutch and incubated by females (f_2), reneests laid after loss of a first nest and incubated by females (f_3), second reneests laid after loss of first reneests and incubated by females (f_4), first nests incubated by males (f_5), and reneests laid after loss of a first male clutch and incubated by males (f_6). The formulae for nesting productivity for nesting attempts f_1 to f_6 were:

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

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

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

$$f_4 = [(1 - NEST) \times RENEST]^2 \times YOUNG \times S_s^{0.5/6}$$

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

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

where the exponents on the 6-month estimate of summer survival (S_s) account for the period of exposure between independence at 30 days and the end of the summer breeding season (Table 1). For example, broods from female-incubated first nests (f_1) would be independent by the start of the sixth biweekly period and would have to survive 3.5 months until the end of the 6-month breeding season.

Third, we calculated seasonal fecundity (F) as the sum of fledglings produced from the 6 types of nesting attempts (f_i):

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

Last, we calculated finite rate of population change (λ) as:

$$\lambda = (S_s \times S_w) + (F \times S_w)$$

where the first term is the proportion of birds that survive between consecutive breeding seasons, calculated as the product of survival in the 6-month summer (S_s , 1 Apr–31 Sep) and winter periods (S_w , 1 Oct–31 Mar), and the second term is population gains due to reproduction, calculated as the product of seasonal fecundity and winter survival of juveniles.

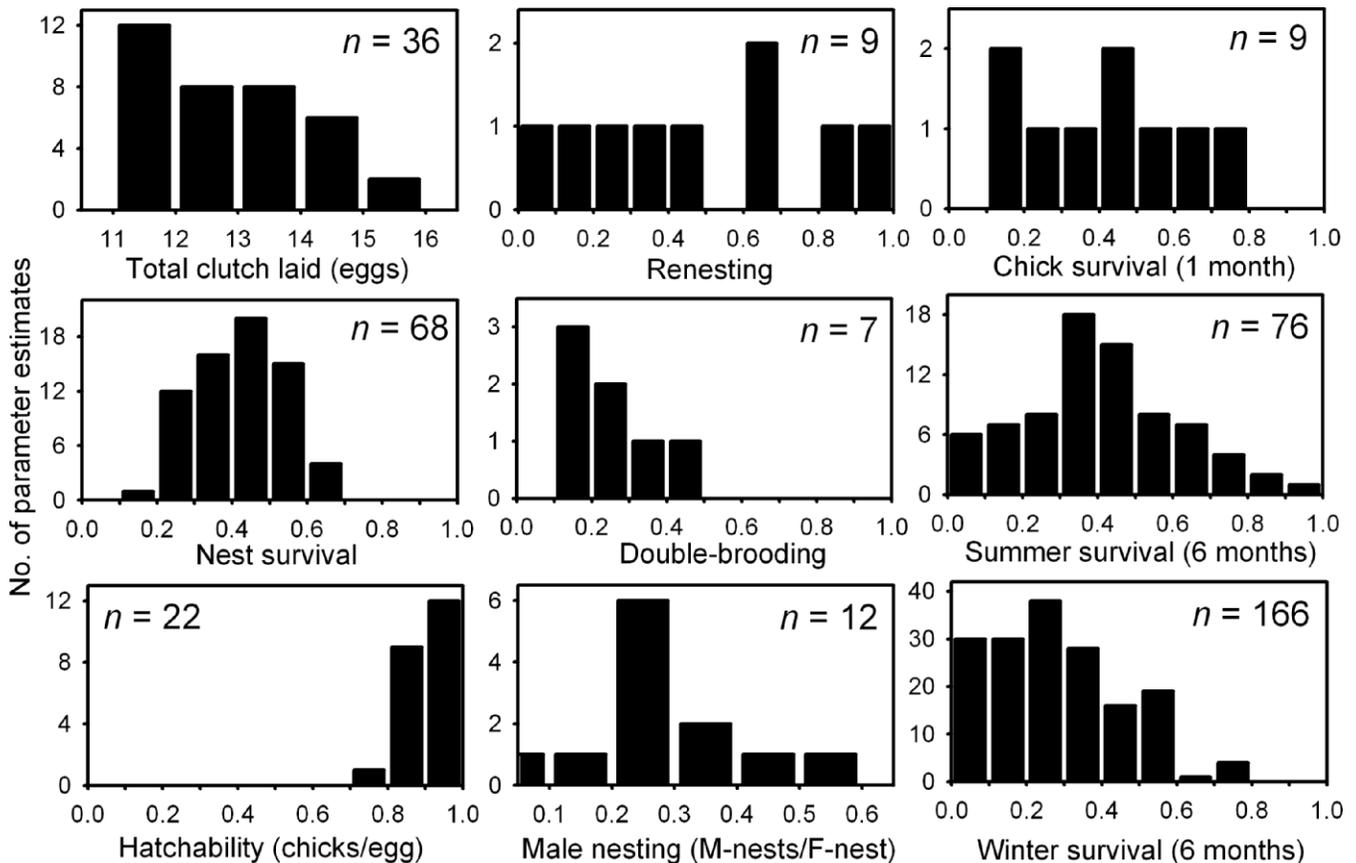


Figure 1. Estimates of 9 demographic parameters from field studies of northern bobwhites in the United States, based on articles published between 1955 and 2007 ($n = 405$ estimates from 49 articles).

Life-Stage Simulation Analysis

We used LSA to examine contributions of the 9 demographic parameters to simulated variation in λ (Wisdom et al. 2000). We conducted all simulations using algorithms of Program Matlab (ver. 6.1; The Mathworks, Inc., Natick, MA). We drew a random set of 9 parameters, combined them to calculate λ with the formulae presented in the 4 steps above, and then repeated these steps for $n = 1,000$ iterations. We treated parameters as independent and did not utilize a covariance structure or a function with density-dependence to select random draws (Wisdom et al. 2000). We conducted linear regression analyses with procedures of Program SAS (Proc REG; SAS Institute Inc., Cary, NC) and used coefficients of determination to calculate amounts of variation in λ explained by simulated variation in each of the 9 demographic parameters.

In our baseline LSA analysis, we took random draws for the demographic parameters from uniform probability distributions bounded by the full 100% range of estimates for each demographic parameter. Our baseline analysis is identical to past studies based on LSA methods (e.g., Citta and Mills 1999, Cross and Beissinger 2001, Gerber et al. 2004), but we conducted additional simulation scenarios to explore the sensitivity of our conclusions. To explore the possible effect of outliers, we repeated the LSA analysis using draws from uniform distributions bounded by the 50% (interquartile) and 80% range of the parameter

estimates. To compare results for different types of probability distributions, we also conducted an LSA analysis using empirical distributions of each demographic parameter based on estimates compiled from the literature (see Results). Our baseline scenario identified winter and summer survival as explaining the greatest amounts of variation in λ . The lower bounds for these 2 parameters were based on field studies of radiomarked birds ($S < 0.02$) and were much lower than minimum estimates of seasonal survival based on bobwhites that were banded only ($S = 0.32-0.40$; Pollock et al. 1989, Palmer and Wellendorf 2007, Terhune et al. 2007). In our last set of scenarios, we used the same conditions as our baseline scenario, except that we adjusted the lower bounds of summer survival from 0.1 to 0.4 by 0.1 and then repeated the same adjustments with winter survival. To compare simulation scenarios, we scaled the coefficients of determination for the 9 demographic parameters to sum to 100%.

RESULTS

We located 405 estimates of 9 demographic parameters from 49 field studies of free-living populations of northern bobwhites (Fig. 1). Our compilation included estimates of 6 components of fecundity (Table 2) and 3 survival rates (Tables 3-5) from populations exposed to different environmental conditions and levels of harvest at sites throughout the continental range of the species. The most frequently

Table 2. Annual estimates of 6 components of fecundity from field studies of northern bobwhites in the United States, based on articles published between 1955 and 2007 ($n = 154$ estimates from 25 articles).

Parameter	Parameter estimate			Sample size					Source
	Median	Min.	Max.	Median	Min.	Max.	<i>N</i>	State	
Clutch size (<i>TCL</i>)	14.0	11.4	14.9	26	12	54	12	IL	Roseberry and Klimstra 1984
	13.9	11.5	15.6	17	12	22	6	MO	Burger et al. 1995 ^b
	13.6			161			1	OK	Cox et al. 2005
	12.9			59			1	TX	Parmalee 1955
	12.8			54			1	FL	DeVos and Mueller 1993
	12.0			52	34	69	2	TX	Hernández et al. 2005
	11.9	11.8	12.2	66	25	92	4	TX	Hernández et al. 2007
	11.7			28			1	NC	Puckett et al. 1995
	11.7			21			1	MS	Taylor and Burger 1997
	11.5	11.2	13.4	27	20	53	7	TN	Dimmick 1974
Nest survival (<i>NEST</i>)	0.63	0.56	0.70	59	37	81	2	TX	Hernández et al. 2005
	0.63			59			1	TX	Parmalee 1955
	0.61	0.55	0.67	26	18	33	2	KS	Taylor et al. 1999
	0.55	0.33	0.65	19	13	26	4	IA	Suchy and Munkel 1993
	0.54			53			1	NC	Palmer et al. 1998
	0.50	0.38	0.58	24	10	47	3	TX	Hernández et al. 2003
	0.50	0.43	0.58	26	17	39	4	GA	Terhune et al. 2006
	0.49	0.41	0.59	65	13	81	4	TX	Hernández et al. 2007
	0.48			331			1	OK	Cox et al. 2005
	0.48			50			1	TX	Hernández et al. 2001
	0.44	0.26	0.54	19	11	26	8	MO	Burger et al. 1995 ^b
	0.45	0.36	0.54	26	25	26	2	FL	DeVos and Mueller 1993
	0.44	0.33	0.55	52	30	74	2	FL/GA	Staller et al. 2002
	0.44	0.42	0.46	99	59	139	2	FL/GA	Staller et al. 2005
	0.41	0.33	0.49				2	GA	Hughes et al. 2005
	0.41	0.23	0.50	9	7	20	7	TN	Dimmick 1974
	0.39	0.27	0.50	27	16	37	2	NC	Puckett et al. 1995
	0.38			21			1	TX	Carter et al. 2002
	0.33	0.27	0.39	30	26	33	2	TX	Lusk et al. 2006
	0.32			41			1	TX	Parsons et al. 2000
Hatchability (<i>HATCH</i>)	0.31	0.21	0.53	53	18	124	13	IL	Roseberry and Klimstra 1984
	0.25	0.19	0.27	9	5	9	3	MS	Taylor and Burger 1997
	0.95			35			1	TX	Mueller et al. 1999
	0.94	0.87	0.96	28	16	39	9	IL	Roseberry and Klimstra 1984
	0.93			121			1	NC	Puckett et al. 1995
	0.92			14			1	FL	DeVos and Mueller 1993
	0.92			20			1	TX	Parmalee 1955
	0.90			161			1	OK	Cox et al. 2005
	0.88	0.87	0.88	26	18	33	2	KS	Taylor et al. 1999
	0.86	0.82	0.90	36	13	63	4	TX	Hernández et al. 2007
	0.85	0.80	0.90	35	24	45	2	TX	Hernández et al. 2005
	0.69	0.69	1.00	13	12	13	3	MO	Burger et al. 1995 ^b
	0.54	0.20	0.87				2	TX	Hernández et al. 2005
0.37			30			1	NC	Puckett et al. 1995	
0.25	0	0.50	11	11	18	3	MS	Taylor and Burger 1997	
P of second clutch (<i>SECOND</i>)	0.31	0.28	0.34	25	18	32	2	GA	Terhune et al. 2006
	0.25			16			1	AL	Sermons and Speake 1987
	0.26	0.15	0.42	12	10	13	3	MO	Burger et al. 1995 ^b
	0.18			38			1	IA	Suchy and Munkel 1993
	0.39	0.26	0.51	56	43	60	3	MO	Burger et al. 1995 ^b
M nesting rate (<i>MALE</i>)	0.34	0.27	0.41	36	24	47	2	FL/NC	Curtis et al. 1993
	0.29	0.18	0.38	19	13	26	4	IA	Suchy and Munkel 1993
	0.28			23			1	MS	Taylor and Burger 1997
	0.24			92			1	OK	Cox et al. 2005
	0.06			53			1	NC	Puckett et al. 1995

reported components of bobwhite demography included probabilities of winter survival, summer survival, and nest survival ($n > 60$ estimates), although clutch size and egg hatchability were also well-documented ($n = 20$ – 40 estimates). Parameters related to production of nesting attempts and chick survival had the fewest estimates available ($n < 15$).

Relative to other small-bodied birds, northern bobwhites have high reproductive potential with a large clutch size (*TCL*: median [med.] = 12.8 eggs, range = 11.2–15.6, $n = 36$ estimates) and high rates of egg hatchability (*HATCH*: med. = 0.92 chicks/egg, 0.80–0.96, $n = 22$). In addition, bobwhites can increase seasonal reproductive output with a range of different reproductive strategies, including rene-

Table 3. Estimates of chick survival to 30 days (\hat{S}_c) from field studies of northern bobwhites in the United States, based on articles published between 1993 and 2005 ($n = 9$ estimates from 6 articles).

Chick survival (\hat{S}_c) ^a			Obs survival (\hat{S}_{obs})			Period (days)	Sample size			<i>n</i>	Type ^b	Sex	State	Source
Median	Min.	Max.	Median	Min.	Max.		Median	Min.	Max.					
0.72			0.52			59	19			1	T	MF	IA	Suchy and Munkel 2000b
0.66			0.68			28	5			1	C	MF	NC	Puckett et al. 1995
0.45	0.38	0.59	0.36	0.29	0.51	39	20	17	22	3	C	MF	OK	DeMaso et al. 1997
0.29			0.29			30	22			1	C	MF	FL	DeVos and Mueller 1993
0.28	0.14	0.41	0.40	0.25	0.54	21	22	18	25	2	C	MF	TX	Mueller et al. 1999
0.19			0.19			30	67			1	T	MF	OK	Lusk et al. 2005

^a We calculated chick survival as $\hat{S}_c = \hat{S}_{obs}^{30/per}$, where \hat{S}_{obs} was the observed survival reported by the authors, and *per* was the period of exposure in days.

^b Type of estimate: C = brood counts, T = telemetry.

ing after clutch failure (*RENEST*: med. = 0.50, 0.0–1.00, $n = 9$), double-brooding after success of a brood from a first nest (*SECOND*: med. = 0.25, 0.15–0.42, $n = 7$), and uniparental incubation by males (*MALE*: med. = 0.28 M-incubated nests/F-incubated nest, 0.06–0.51, $n = 12$). However, maximum rates of reproductive output are reduced by variation in nest survival (*NEST*: med. = 0.42, 0.19–0.70, $n = 68$) and chick survival after hatching (S_c : med. = 0.41, 0.14–0.72, $n = 9$). Moreover, bobwhites are short-lived birds with low probabilities of survival during the 6-month summer (S_s : med. = 0.39, 0.01–0.92, $n = 76$) and winter periods (S_w : med. = 0.26, 0.01–0.73, $n = 166$).

In our baseline LSA analysis, we used random draws from uniform distributions bounded by the full 100% range of field estimates for each of the 9 demographic parameters. Median rate of population change was $\lambda = 0.56$ (95% CI = 0.03–2.29) and most random sets of parameters (76.0%, $n = 1,000$ iterations) resulted in declining populations ($\lambda < 1$). Simulated variation in the winter survival made the greatest

contribution to variance in λ ($r^2 = 0.453$), followed by summer survival of adults ($r^2 = 0.163$), and survival of chicks ($r^2 = 0.120$; Fig. 2). Rate of population change was not sensitive to 3 demographic parameters associated with reproductive output ($r^2 < 0.06$, clutch size, nest survival, hatchability) or to 3 parameters that determined number of nesting attempts ($r^2 < 0.04$, probabilities of reneating and double-brooding, M nesting rate). Coefficients of determination were not correlated with the absolute range (max.–min.) of variation in the 9 demographic parameters (all parameters: $r = -0.14$, $P = 0.73$, $n = 9$; probabilities only: $r = 0.40$, $P = 0.38$, $n = 7$).

Linear regression equations for the relationships between λ and probabilities of chick survival, summer survival, and winter survival (Fig. 2) were: $\hat{\lambda} = 0.197 + 1.195(CHICK)$, $\hat{\lambda} = 0.267 + 0.931(\hat{S}_s)$, and $\hat{\lambda} = -0.010 + 1.933(\hat{S}_w)$. Given simulated variation in the other 8 of 9 demographic parameters in the population model, the regression equations indicate that adjustment of one parameter would

Table 4. Seasonal estimates of summer survival (\hat{S}_s) for the 6-month period between 1 April and 31 September from field studies of northern bobwhites in the United States, based on articles published between 1984 and 2007 ($n = 76$ estimates from 15 articles).

Summer survival (\hat{S}_s) ^a			Obs survival (\hat{S}_{obs})			Period			Sample size			<i>n</i>	Type ^b	Sex	State	Source
Median	Min.	Max.	Median	Min.	Max.	Start	End	Days	Median	Min.	Max.					
0.63	0.46	0.92	0.57	0.38	0.90	19 Mar	3 Nov	229	130	72	212	17	C	MF	IL	Roseberry and Klimstra 1984
0.47	0.33	0.53	0.47	0.33	0.53	1 Apr	30 Sep	182	70	33	116	4	T	MF	GA	Hughes et al. 2005
0.47			0.47			1 Apr	30 Sep	183	72			1	T	F	FL	Curtis et al. 1988
0.44	0.14	0.76	0.44	0.14	0.76	1 Apr	30 Sep	182				14	R	MF	GA	Terhune et al. 2007
0.36	0.17	0.55	0.69	0.55	0.82	24 Jun	25 Aug	62	27			2	T	F	FL	DeVos and Mueller 1993
0.36	0.31	0.41	0.36	0.31	0.41	1 Mar	31 Aug	184	160	146	173	2	T	MF	TX	Hernández et al. 2005
0.35	0.24	0.62	0.35	0.24	0.62	1 Apr	30 Sep	182	47	25	66	8	T	MF	IA	Suchy and Munkel 2000a
0.35	0.28	0.41	0.35	0.28	0.41	1 Apr	29 Sep	181	87	79	95	2	T	MF	NC	Puckett et al. 1995
0.34	0.33	0.38	0.34	0.33	0.38	1 Apr	30 Sep	182	54	52	58	3	T	F	MO	Burger et al. 1995a
0.34	0.16	0.50	0.35	0.17	0.51	1 Apr	27 Sep	179	45	26	52	4	T	MF	MS	Taylor et al. 2000
0.34	0.31	0.43	0.29	0.26	0.38	2 Feb	2 Sep	212	60	31	90	4	T	MF	GA	Terhune et al. 2006
0.25			0.25			1 Apr	30 Sep	183	22			1	T	MF	NC	Curtis et al. 1988
0.21	0.07	0.34	0.56	0.42	0.70	10 Apr	9 Jun	60	71			2	T	MF	AL	DeVos and Speake 1995
0.17	0.12	0.21	0.31	0.26	0.36	24 Apr	20 Aug	118	39	32	46	2	T	F	KS	Taylor et al. 1999
0.16			0.29			1 May	1 Sep	123	58			1	T	MF	TX	Carter et al. 2002
0.10	0.01	0.54	0.39	0.14	0.77	27 Apr	14 Jul	>62	54	13	71	9	T	MF	TX	Liu et al. 2000

^a We calculated summer survival as $\hat{S}_s = \hat{S}_{obs}^{183/per}$, where \hat{S}_{obs} was the observed survival reported by the authors, and *per* was the period of exposure in days.

^b Type of estimate: C = brood counts, R = recapture, T = telemetry.

Table 5. Seasonal estimates of winter survival ($\hat{\delta}_w$) for the 6-month period between 1 October and 31 March from field studies of northern bobwhites in the United States, based on articles published between 1984 and 2007 ($n = 166$ estimates from 21 articles).

Winter survival ($\hat{\delta}_w$) ^a			Obs survival ($\hat{\delta}_{obs}$)			Period			Sample size			<i>n</i>	Type ^b	Sex	State	Source
Median	Min.	Max.	Median	Min.	Max.	Start	End	Days	Median	Min.	Max.					
0.52	0.24	0.73	0.52	0.24	0.73	1 Oct	31 Mar	181				14	R	MF	GA	Terhune et al. 2007
0.51	0.41	0.60	0.52	0.42	0.61	1 Sep	28 Feb	180	23	21	26	4	T	MF	TX	Haines et al. 2007
0.50			0.50			1 Oct	31 Mar	183	52			1	T	F	FL	Curtis et al. 1988
0.45	0.30	0.60	0.45	0.30	0.60	1 Sep	28 Feb	181	87	71	102	2	T	MF	TX	Hernández et al. 2005
0.44	0.25	0.58	0.44	0.25	0.58	1 Oct	31 Mar	181	62	31	86	4	T	MF	GA	Hughes et al. 2005
0.41	0.12	0.58	0.61	0.31	0.74	19 Nov	28 Feb	101	19	15	26	4	T	MF	NC	Robinette and Doerr 1993
0.37	0.03	0.64	0.62	0.18	0.80	27 Dec	27 Mar	90				36	C	MF	KS	Robel and Kemp 1997
0.30	0.12	0.42	0.31	0.13	0.43	15 Nov	9 May	175	62	52	74	6	T	MF	GA	Sisson et al. 2000 ^b
0.29	0.25	0.33	0.67	0.64	0.70	31 Jan	1 Apr	60	87	56	118	2	T	MF	GA	Mueller et al. 1988
0.29	0.25	0.42	0.35	0.32	0.48	1 Nov	4 Apr	154	63	52	74	3	T	MF	GA	Sisson et al. 2000 ^a
0.28	0.16	0.71	0.28	0.16	0.71	1 Oct	31 Mar	184	38	25	67	5	T	MF	TX	Guthery et al. 2004 ^b
0.23	0.11	0.55	0.34	0.19	0.64	5 Nov	20 Mar	135	361	176	655	27	C	MF	IL	Roseberry and Klimstra 1984
0.22	0.12	0.39	0.22	0.12	0.40	1 Oct	31 Mar	181	59	17	92	8	T	MF	IA	Suchy and Munkel 2000 ^a
0.19	0.14	0.20	0.35	0.29	0.36	24 Nov	20 Mar	116	21	15	35	3	T	MF	SC	Dixon et al. 1996
0.19			0.19			1 Oct	31 Mar	183	30			1	T	F	NC	Curtis et al. 1988
0.15	0.08	0.22	0.38	0.29	0.47	1 Nov	31 Jan	91	79	66	91	2	T	MF	KS	Williams et al. 2000
0.14	0	0.38	0.14	0	0.39	1 Nov	30 Apr	180	43	23	68	11	T	MF	OK	Cox et al. 2004
0.12	0.10	0.19	0.13	0.10	0.20	1 Oct	31 Mar	181	128	120	141	3	T	F	MO	Burger et al. 1995 ^a
0.12	0.01	0.23	0.18	0.03	0.31	1 Nov	31 Mar	150	200	168	294	8	T	MF	OK	Townsend et al. 1999
0.09	0.01	0.34	0.37	0.13	0.64	1 Dec	15 Feb	76	53	23	153	10	RT	MF	OK	Parry et al. 1997
0.08	0.03	0.33	0.30	0.20	0.61	9 Nov	31 Jan	83	66	46	90	6	T	MF	KS	Williams et al. 2004 ^b
0.04	0.02	0.14	0.07	0.04	0.19	15 Oct	15 Mar	151	80	49	107	6	T	MF	KS	Madison et al. 2002

^a We calculated winter survival as $\hat{\delta}_w = \hat{\delta}_{obs}^{183/per}$, where $\hat{\delta}_{obs}$ was the observed survival reported by the authors, and *per* was the period of exposure in days.

^b Type of estimate: C = brood counts, R = recapture, T = telemetry.

require a 1-month chick survival rate ≥ 0.67 , a 6-month summer survival rate ≥ 0.79 , or a 6-month winter survival rate ≥ 0.52 to realize a stationary rate of population change ($\lambda = 1$).

Our baseline LSA indicated that variation in winter survival explained most of the simulated variation in λ (Fig. 3A), and this result was robust to a series of alternative scenarios. Winter survival still had the highest coefficient of determination if we used 50% or 80% confidence intervals of our parameter estimates to bound the uniform distributions (Figs. 3B, C) or if we used draws from the actual empirical distributions for each demographic parameter (i.e., Fig. 1) in the LSA (Fig. 3D). Moreover, coefficients of determination for winter survival increased from 54% to 64% if we adjusted the lower bound of summer survival from a baseline value of 0.01 (Fig. 3A) up through the range of 0.1 to 0.4 (Figs. 3E–H). In the first 8 scenarios (Figs. 3A–H), median rates of population change were consistently < 0.8 . In agreement with these results, the relative contributions of the different parameters to simulated variation in λ only changed if we adjusted the lower bound of our estimates of winter survival. Adjusting the lower bound of winter survival from 0.01 up to 0.4 (Figs. 3A, I–L) increased median rates of population change from $\lambda = 0.56$ to 0.95. Accordingly, the coefficient of determination for winter survival decreased from 54% to 11%, whereas coefficients of determination for summer and chick survival increased from 19% to 40%, and 14% to 27%, respectively.

DISCUSSION

Our compilation of demographic rates and life-stage simulation analysis for northern bobwhites resulted in 3 major findings. First, bobwhite demography was characterized by high reproductive potential and low seasonal survival. The demographic parameters with the greatest range of variation included clutch size, probability of reneating, and 3 survival rates. Second, most estimates of λ were < 1 , suggesting that a subset of the demographic parameters in our population model were either biased low or depressed below sustainable levels. Last, simulated variation in winter survival, summer survival, and chick survival explained the greatest amount of variance in λ among declining populations of bobwhites.

Variation and Bias in Demographic Parameters

Variation in demographic parameters of northern bobwhites was caused by spatial and temporal variation in environmental conditions and possibly by methodological differences among field studies. Northern populations exposed to cold winters tend to have higher fecundity and lower annual survival compared to southern populations (Guthery 1997, Folk et al. 2007). Guthery (1997) suggested that the mean demographics of northern bobwhites may have a narrow range of variation, and we found limited variation in egg hatchability, probability of double-brooding, and male nesting rates. However, clutch size and probabilities of nest survival, reneating, chick survival, and summer and winter survival of adults were highly variable both within and

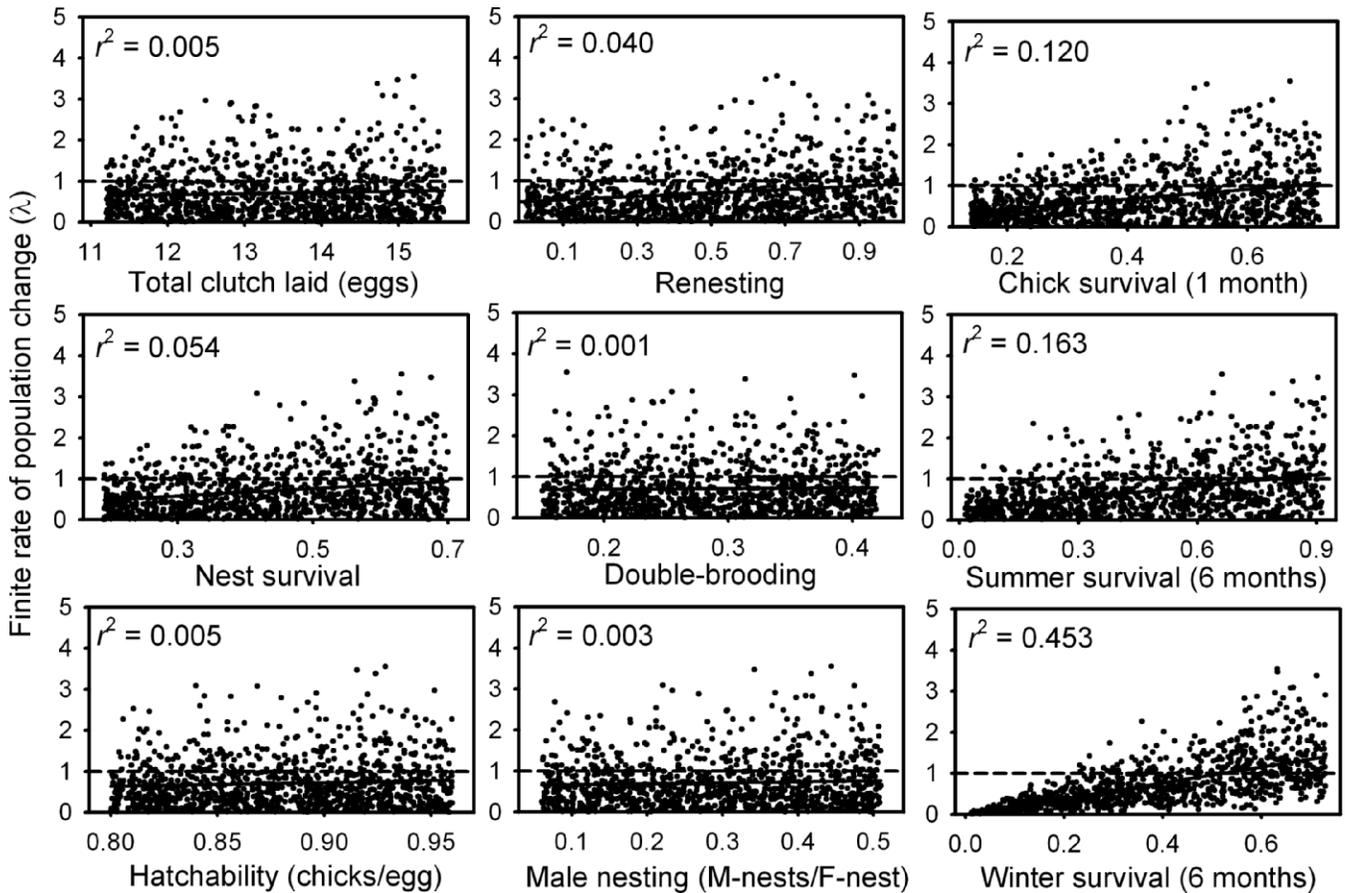


Figure 2. Regression of the finite rate of population change (λ) in response to simulated variation in 9 demographic parameters for northern bobwhites in the United States, based on articles published between 1955 and 2007.

among different field studies. One advantage of the LSA modeling approach was that it allowed us to explore the potential range in the mean demographic parameters and reproductive strategies of northern bobwhites.

Most of the estimates of λ from our life-stage simulation analysis were <1 , suggesting that several of our 9 demographic parameters were either biased low or depressed below sustainable levels. We set breeding propensity at unity in our model but this parameter would have been biased high if females failed to nest, which occurs in dry years in semiarid environments (Harveson et al. 2004, Hernández et al. 2007). It is unlikely that total clutch laid or hatchability were biased because both parameters are readily measured from direct inspection of the clutch. Probability of nest survival was likely to be biased high because most authors have reported apparent nesting success, which does not control for exposure and losses prior to nest discovery. Estimated number of nesting attempts could have been biased low if nests were destroyed before discovery by observers. Estimates of probabilities of renesting and double-brooding and the rate of male nests per female nest had the fewest parameter estimates and were not well-characterized.

Field estimates of summer and winter survival could have been lower than sustainable levels for 3 reasons. First, the physiological stress of handling northern bobwhites for

banding and radiomarking may increase mortality rates over short-term periods (Pollock et al. 1989, Abbott et al. 2005). Second, population studies of northern bobwhites frequently use radiotelemetry to investigate demographic parameters, but attachment methods or transmitters may reduce survival of radiomarked birds (Osborne et al. 1997, Cox et al. 2004, Guthery and Lusk 2004). Losses of radiomarked birds could potentially reduce chick survival if attending parents are killed before the young are independent. Last, our compilation of survival rates likely included estimates from bobwhite populations in decline. Survival rates depressed below sustainable levels by environmental conditions may explain why median estimates of λ were frequently <1 in our modeling scenarios.

What level of annual survival is necessary to ensure population viability for northern bobwhites? Our regressions of simulated variation in demographic parameters indicated that λ would be stationary if $S_s > 0.79$ or if $S_w > 0.52$, which would correspond to an annual survival rate of 0.41. An estimate of 0.41 is low but is comparable to the lower range of estimates of annual survival reported for some species of grouse (0.3–0.5; Wisdom and Mills 1997, Sandercock et al. 2005) and small-bodied songbirds (0.4–0.6; Martin 1995, Sandercock and Jaramillo 2002, Stahl and Oli 2006). Survival estimates in our compilation were primarily based on radiomarked birds, and most estimates

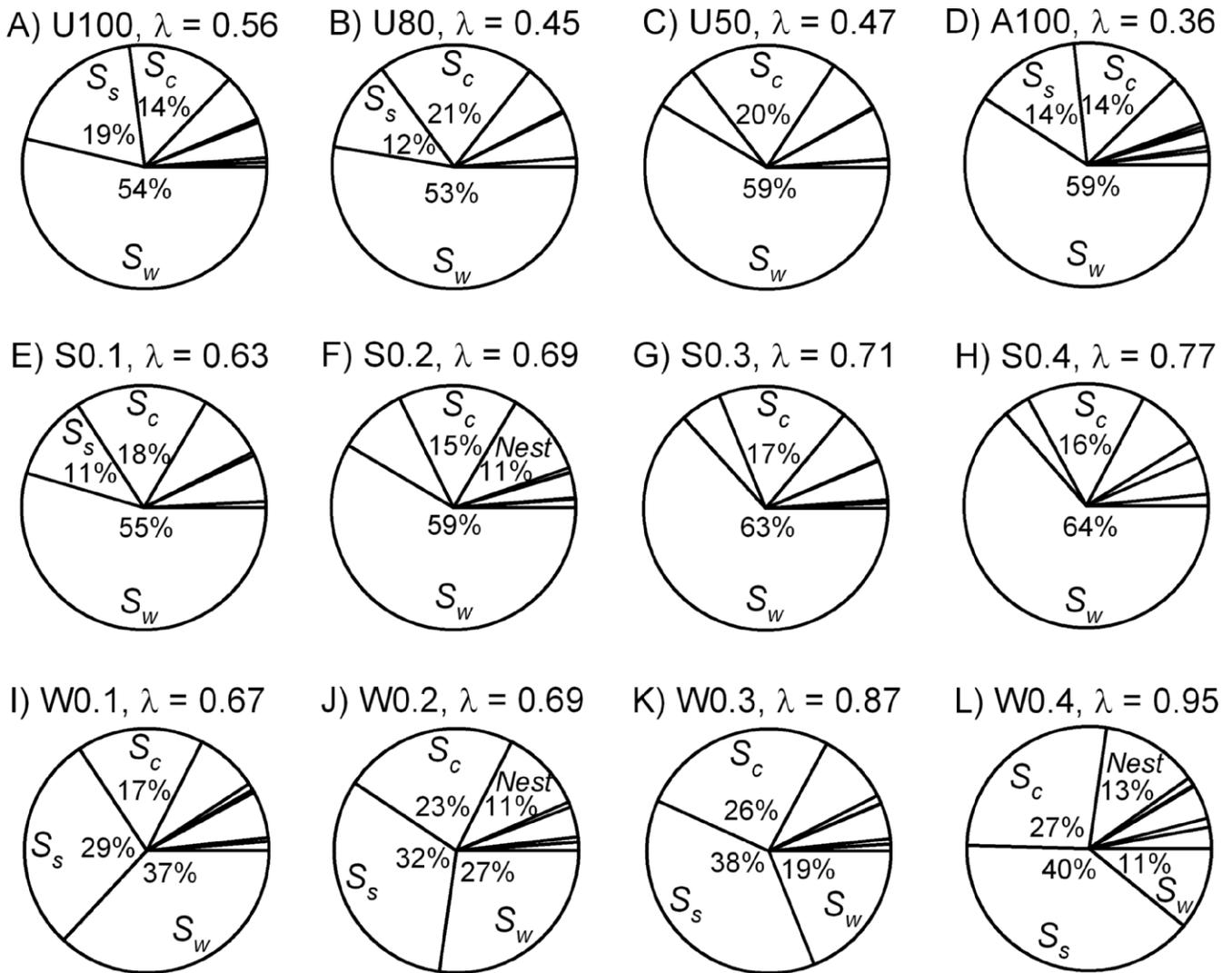


Figure 3. Median rates of population change (λ) and percentage of variance in λ explained by 9 demographic parameters under 12 simulation scenarios in life-stage simulation analyses (LSA) for northern bobwhites in the United States, based on articles published between 1955 and 2007. In a baseline scenario, we took random draws from uniform distributions bounded by the full 100% range of estimates for each demographic parameter (A: U100). We then used draws from uniform distributions bounded by 80% or 50% confidence intervals of the parameter estimates (B–C: U80–U50), and draws from the actual empirical distributions of each parameter (D: A100). Last, we adjusted the lower bound of summer survival from 0.1 to 0.4 by 0.1 (E–H: S0.1–S0.4), and then repeated the same adjustments for winter survival (I–L: W0.1–W0.4). We report coefficients of determination for winter survival (S_w), summer survival (S_s), chick survival (S_c), and nest survival ($Nest$) if the parameter explained $\geq 10\%$ of the simulated variance in λ ($n = 1,000$ bootstrap iterations in each scenario).

were below our threshold values for summer ($S_s < 0.79$, 100% of $n = 45$ estimates from 13 telemetry studies) and winter survival ($\hat{S}_w < 0.52$, 92% of $n = 89$ estimates and 18 studies). Published estimates of annual survival for radio-marked bobwhites are among the lowest rates of survival reported for any species of bird (0.05, Burger et al. 1995a; 0.06, Curtis et al. 1988; 0.07, Cox et al. 2004), and are lower than estimates based on banded bobwhites (0.17, Pollock et al. 1989; 0.18, Terhune et al. 2007; 0.24, Palmer and Wellendorf 2007). Nevertheless, 3 field studies based on large samples of marked birds and rigorous mark–recapture modeling have failed to detect a negative effect of radios on bobwhite survival (Parry et al. 1997, Palmer and Wellendorf 2007, Terhune et al. 2007). At least 2 of the 3 studies were conducted at high-quality sites intensively managed for

bobwhite production, and radios may be more of a handicap for birds in marginal habitats. Overall, our compilation of estimates and population modeling indicates that survival rates are the demographic parameters most likely to be biased low or naturally depressed in wild populations of bobwhites. If telemetry estimates prove to be unbiased, then environmental factors affecting variation in winter and summer survival could be the demographic mechanism underlying ongoing population declines.

Sensitivity of Demographic Parameters

The major result of our LSA analysis was that under conditions of population decline, winter, summer, and chick survival made the greatest contributions to variance of rates of population change for bobwhites. This result was robust to a range of modeling scenarios, and the relative

contributions of different rates changed only if we increased the lower bounds of winter survival to match estimates from banded birds. Our observations are consistent with demographic theory for populations with discrete generations; changes in survival are expected to have the greatest effect on λ in declining populations (Meats 1971). Comparisons across a range of species are not yet possible because LSA analyses have been applied to only 2 other galliforms. Nonbreeding survival of adults accounted for the greatest amount of variance in λ for ruffed grouse (*Bonasa umbellus*; Tirpak et al. 2006), whereas a composite estimate of realized fecundity made the greatest contribution to the variance of λ in greater prairie-chickens (*Tympanuchus cupido*; Wisdom and Mills 1997, Wisdom et al. 2000).

Sensitivity analyses for gamebirds have been based on both deterministic or stochastic matrix models. A naïve expectation for northern bobwhites is that λ might be most sensitive to variation in the components of reproduction because bobwhites are a species with high reproductive potential, early maturity, and low adult survival (Sandercock 2006, Stahl and Oli 2006). Identification of survival rates as having the greatest effect on variance of λ is consistent with elasticity values from matrix models developed for bobwhites and other galliforms. Survival of chicks until independence, juvenile survival, and winter survival of adults have been identified as the demographic parameters with the highest elasticity values and greatest potential impact on λ in northern bobwhites (Folk et al. 2007), 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). We found that parameters related to the components of fecundity and production of nesting attempts made essentially no contribution to the variance of λ for bobwhites, which is consistent with previous reports that double-brooding has limited benefit for increasing productivity of bobwhites (Guthery and Kuvlesky 1998) and that reneesting has little effect on rates of population change in gray partridge (*Perdix perdix*; Bro et al. 2000).

If winter survival is important, development of improved management practices for northern bobwhites would benefit from a better understanding of the interactions among habitat structure, food, and relative losses to natural mortality and hunter harvest. Bobwhites prefer to use habitats with extensive woody cover, presumably because predation risk is reduced (Williams et al. 2000, Guthery et al. 2001). Provision of supplementary food in feeders or food plots may increase winter survival if bobwhites are better able to cope with inclement weather with additional food or body reserves (Robel and Kemp 1997, Doerr and Silvy 2006). However, potential benefits of improved cover and supplemental feeding could be negated by higher mortality rates if hunters or natural predators concentrate their effort near food plots or habitats preferred by bobwhites (Roseberry 1979, Williams et al. 2000, Madison et al. 2002, Haines et al. 2004, Hardin et al. 2005). Exposure to harvest

may also increase natural mortality if bobwhites incur greater predation risk after disturbance by hunters or during movements from small to larger coveys (Curtis et al. 1988, Robinette and Doerr 1993, Williams et al. 2003*b*).

One key issue that arises in trying to understand effects of hunter activity on winter survival is whether harvest mortality is additive or compensatory to natural mortality, especially in declining populations. A long-standing paradigm in management of northern bobwhites is that most harvest mortality is compensatory (Errington and Hamerstrom 1935, Errington 1945). Hunting may not be a limiting factor for some populations of northern bobwhites (Suchy and Munkel 2000*a*), but recent studies have frequently reported that harvest mortality is additive to natural mortality, especially if harvest occurs in late winter (Curtis et al. 1988, Pollock et al. 1989, Robinette and Doerr 1993, Burger et al. 1995*a*, Williams et al. 2004*b*) and if hunter efficiency increases when bobwhite numbers are declining (Guthery et al. 2004*a*). Additive harvest mortality may be a general feature of gamebird populations, including wild turkey, ruffed grouse, and willow ptarmigan (*Lagopus lagopus*; Small et al. 1991, Pack et al. 1999, Pedersen et al. 2004).

MANAGEMENT IMPLICATIONS

Our life-stage simulation analyses are best viewed as an exploratory analysis based on the best current demographic information for northern bobwhites. Our population model could be improved with new data on demographic parameters or reproductive strategies or by a better understanding of effects of density-dependence and life-history tradeoffs in bobwhite demography. One knowledge gap for northern bobwhites is whether survival rates are biased low as an artifact of field methods and effects of handling and radios on survival should be evaluated with additional controlled field experiments. Given the contributions of survival rates to variance of population change in declining populations, quail management would benefit from a better mechanistic understanding of the environmental factors that drive spatial and temporal variation in winter survival. Most losses are due to predation or harvest. Future research should identify predators responsible for winter losses and investigate their numerical and functional responses (Mueller et al. 1988, Rollins and Carroll 2001). A second avenue of research should be investigations of effects of quail abundance and harvest regulations on hunter behavior and harvest (Peterson and Perez 2000, Hardin et al. 2005). Current seasons and bag limits are often liberal because harvest mortality is assumed to be compensatory and regulations are set to maximize recreational opportunities (Williams et al. 2004*a*). Reductions in late-season harvest might minimize hunting mortality when effects are likely to be additive (Peterson 2001, Guthery et al. 2004*b*). Finally, management practices may be most cost-effective at increasing rates of population change if they improve survival rates in concert with other demographic parameters.

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