

Sensitivity Analyses of a Population Projection Model of Ring-Necked Pheasants

WILLIAM R. CLARK,¹ *Department of Ecology, Evolution, and Organismal Biology, Iowa State University, 253 Bessey Hall, Ames, IA 50011, USA*

TODD R. BOGENSCHUTZ, *Iowa Department of Natural Resources, 1436 255th Street, Boone, IA 50036, USA*

DALE H. TESSIN, *Department of Ecology, Evolution, and Organismal Biology, Iowa State University, 253 Bessey Hall, Ames, IA 50011, USA*

ABSTRACT A large literature exists on population dynamics of ring-necked pheasant (*Phasianus colchicus*) in North America, but there has not been an attempt to formulate a matrix model nor a sensitivity analysis of the relationships between vital rates and population finite growth rate (λ) that can be used to guide management. We summarized demographic data available from a 5-year field study in Iowa, USA, collected in Kossuth County (low composition of perennial habitat) and Palo Alto County (high composition of perennial habitat) into a 2-stage (young and adult) matrix projection model. We estimated λ_1 (the dominant eigenvalue of the deterministic matrix), the stable age distribution (w), relative reproductive value vector (v), other demographic parameters, and λ_{iid} , a bootstrap estimate of growth that includes interannual variation in life history parameters. We analyzed the relative importance of vital rates on population growth rate using sensitivity and elasticity of both matrix elements and lower-level parameters such as winter survival and nest success. We first characterized general life history using averaged data from both areas and all years that yielded $\lambda_1 = 1.086$, and a stable stage distribution of $w = \begin{pmatrix} 0.79 \\ 0.21 \end{pmatrix}$. Minimum success of the initial nesting attempt (H_1) that would maintain $\lambda \geq 1$ under average conditions was estimated to be 42%. Changes in λ_1 were most sensitive to survival of chicks during brood rearing (S_B), followed in importance by survival during the subsequent winter (S_W), followed by H_1 . We followed the general analyses with analyses that helped us to focus on the differences in the landscapes of northwest Iowa. λ_{iid} was ≥ 1 in only 9% of simulations of data from Kossuth whereas estimated λ_{iid} was ≥ 1 in 88% of simulations from Palo Alto. Our analyses of the relative importance and interactions between S_B , S_W , and total recruitment (M , including H_1 and renesting), if combined with data more specific to a local area, would guide management aimed at affecting multiple life history stages whose relative importance will vary across the landscape. (JOURNAL OF WILDLIFE MANAGEMENT 72(7):1605–1613; 2008)

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Ring-necked pheasants (*Phasianus colchicus*) in North America have been a focus of wildlife management and research for nearly a century, especially in the midwestern United States where pheasants have been historically most abundant (Giudice and Ratti 2001). Decline in population levels since the 1950s has been used as an indication of the impacts of intensive agriculture on wildlife populations, and conversely, increases in pheasant numbers after the implementation of the Conservation Reserve Program have been used to validate impact of agricultural policy (Best et al. 1997, Haroldson et al. 2006, Nielson et al. 2008).

Intensive study aimed at understanding the local- and landscape-scale complexities that make up the mechanisms by which pheasant populations respond to changing ecological conditions is costly and necessarily restricted in geographic extent. Biologists from states in the northern part of the range frequently report that interactions between habitat and snowy, cold winters may be important to the survival of adults (Larsen et al. 1994, Bogenschütz et al. 1995, Perkins et al. 1997, Gabbert et al. 1999), whereas more southerly states have noted that changes in land management practices have particularly influenced the ecology of broods (Rodgers 1999). Often management of pheasants has focused on the abundance and quality of nesting habitat, along with patterns of spring temperature and rainfall, that influence nesting, chick survival, and ultimately recruitment of pheasants, as it does other

gallinaceous birds (Farris et al. 1977, Potts 1986, Aebischer 1990, Riley et al. 1998). Not only are local habitat conditions important but also landscape composition and configuration influence pheasant dynamics, affecting both survival and recruitment (Perkins et al. 1997, Clark et al. 1999, Schmitz and Clark 1999).

Despite volumes of data on life history of pheasants, researchers have not incorporated data on recruitment and survival into a population projection model. Matrix analyses have been widely used to understand demographics (Caswell 2001, Morris and Doak 2002), to judge the relative importance of life history parameters for conservation and management (Crouse et al. 1987, Doak et al. 1994, Heppell et al. 1994, Wisdom et al. 2000), and to assess how variation in vital rates contributes to variation in λ (Brault and Caswell 1993, Cooch et al. 2001). Ornithologists interested in both game birds and songbirds have used modeling as a tool to summarize demographic data and to address questions about the sensitivity of various life history parameters (Wisdom and Mills 1997, Flint et al. 1998, Powell et al. 1999, Hoekman et al. 2002, Fletcher et al. 2006). For many years, waterfowl management has been guided by a model of mallard (*Anas platyrhynchos*) populations that was used to estimate that a rate of nest success of 15–18% is necessary to sustain populations (Johnson et al. 1987). More recent analyses of mallard populations (Hoekman et al. 2002, 2006) and lesser scaup (*Aythya affinis*; Koons et al. 2006) based on matrix models examined the

¹ E-mail: wrclark@iastate.edu

sensitivity of a combination of life history parameters and revealed regional differences that are important to management of the species. In contrast, we are aware of only one published life history model of pheasants that considered the interactions between recruitment and survival and provided an estimate of nest success that would sustain populations (Hill and Robertson 1988).

In the form of projection matrix most often used in conservation, estimates of mean stage-specific survival (S_i) and stage-specific fertility (F_i) of the females in a population are used to estimate the average finite rate of increase (λ) under conditions of a stable stage distribution. Projection is frequently followed by analytical and numerical sensitivity and elasticity analyses to understand the relative influence of vital rates. Sensitivity is defined as the resulting change in λ ($\Delta\lambda$) when one element of the matrix (e.g., F_i) is changed, whereas all other elements are held constant. Elasticity is defined as the proportional $\Delta\lambda$ with respect to proportional changes in matrix elements and is often interpreted as the contribution of variation in each element to variation in λ because they sum to one (Caswell 2001). The effects of additive perturbations on λ that are revealed by sensitivity will be of value to managers interested in manipulating the absolute changes in λ (Hoekman et al. 2002), whereas elasticity is useful in understanding the comparative effects of perturbations (Wisdom and Mills 1997).

Sensitivity and elasticity are functions of both the elements of the reproductive value vector and the stable stage distribution vector and do not completely separate the effects of life history parameters related to reproduction and survival. It is often instructive to study sensitivity at the level of the component life history parameters (e.g., nest success rate), sometimes called lower-level parameters, rather than concentrate analyses at the level of the matrix elements (Morris and Doak 2002). For example, in a posthatching matrix, fertility is a product of survival and reproduction because females must survive until they produce offspring (Noon and Sauer 1992). Furthermore, variation in reproduction is a function of life history parameters that include the probability of initiating a nest, clutch size, and nest success rate.

Researchers have published a large literature during recent decades about the promises and pitfalls associated with the application of matrix models to conservation and management. Our approach would be characterized as prospective analyses that focus on the functional mathematical dependence of λ on parameters, exploring the question, "If a parameter is changed by some amount, how will λ be changed?" (Caswell 2001, Morris and Doak 2002). Increasingly, conservation biologists are also using retrospective analyses such as life-stage simulation analyses that explore questions like "given the functional dependence of λ on parameters, how is variation in the observed parameter sets reflected in variation in λ ?" (Wisdom et al. 2000, Cooch et al. 2001, Fieberg and Ellner 2001). An important consideration regarding any interpretation of models is that projections are subject to many sources of uncertainty

including the appropriate model structure (e.g., density-dependent or not, Grant and Benton 2000; deterministic or stochastic, Doak et al. 2005a), uncertainty in model parameter estimation (Morris and Doak 2002), and inherent stochasticity of the population (Fieberg and Jenkins 2005).

Our objective was to estimate rates of increase of pheasant populations in landscapes differing with regard to composition of habitat by developing a stage-based matrix model and to compare the relative importance of vital rates to change in λ .

METHODS

Model Structure

We constructed a female-only, 2-stage-class, posthatching matrix model with a yearly projection interval that began on 15 June, the median date of hatch of first nests in our study (Noon and Sauer 1992, Clark and Bogenschutz 1999). Hatch year birds (HY, age class 0) survive as chicks and through their first winter to breed for the first time about a year after they hatched. After hatch year (AHY, age class 1) birds are adults that may survive to breed a second time. A 3-stage-class model was unnecessary because we found no evidence of differences in reproduction or survival among age classes of pheasants in Iowa (Perkins et al. 1997, Clark and Bogenschutz 1999, Clark et al. 1999).

Vital Rates and Life History Parameters

We defined vital rates for the matrix $A = \begin{pmatrix} F_0 & F_1 \\ S_0 & S_1 \end{pmatrix}$, where S_0 is survival from hatch to age 1 year and S_1 is survival from age 1 year to age ≥ 2 years. In a posthatch matrix, stage-specific fertility is $F_i = S_i M$, where M is reproductive rate, and F_i is the number of female chicks hatched per female beginning stage class i that survived the year. Reproduction (M) is complicated by reneesting attempts and the probability of initiating the j th nest, $j = 1, 2, 3, \dots$. We grouped our data into first nesting attempts and all reneesting attempts so $M = \sum_{j=1}^2 M_j$ (Clark and Bogenschutz 1999). In deriving an expression for M_j , we followed the logic expressed by Johnson et al. (1992), $M_j = A_j C_j H_j E$, where A_j is probability of initiating the j th nest attempt, C_j is female clutch size of j th nest (assuming 0.5 proportion F chicks), H_j is nest success rate of the j th nest attempt, and E is survival rate of eggs in successful nests. We assumed $E = 1.0$ because hatchability of pheasant eggs is consistently near 1.0 and also because we observed very little partial clutch loss (Riley et al. 1998, Clark and Bogenschutz 1999). In general, A_j is the product of the probability of making a j th nesting attempt given that the $j - 1$ attempt failed, times the probability that attempt $j - 1$ was made and failed. We assumed all female pheasants attempted a first nest, that females did not produce >1 brood in a year (Clark and Bogenschutz 1999), and that nesting intensity did not vary with weather conditions. Like Johnson et al. (1992), we assumed that the conditional probability of reneesting decreased with j and that it also varied inversely with H . With these assumptions, $A_1 = 1$ for

Table 1. Definition, mean and empirical standard deviation, and source of parameters of a demographic model of female ring-necked pheasants from data collected on townships in Palo Alto and Kossuth counties, Iowa, USA, 1990–1994.

Parameter	Symbol	Palo Alto		Kossuth		Source
		\bar{x}	SD	\bar{x}	SD	
Probability of initiating first nest	A_1	1.0		1.0	none ^a	W. R. Clark and T. R. Bogenschutz (Iowa Department of Natural Resources, unpublished data)
Probability of initiating second nest	A_2	0.23	0.16	0.44	0.27	Clark and Bogenschutz (1999)
Clutch size first nest	C_1	12	0.63	13	1.16	Clark and Bogenschutz (1999)
Clutch size second nest	C_2	10	1.49	10	1.41	Clark and Bogenschutz (1999)
Nest success first nest	H_1	0.57	0.18	0.45	0.13	Clark and Bogenschutz (1999)
Nest success second nests	H_2	0.46	0.23	0.27	0.23	Clark and Bogenschutz (1999)
Survival of chicks, brood period (2 months)	S_B	0.46	0.11	0.37	0.15	Riley et al. (1998)
Survival in fall (3 months)	S_F	0.86		0.86	none ^a	Wooley and Rybarczyk (1981)
Survival in winter (5 months)	S_W	0.66	0.18	0.61	0.25	Perkins et al. (1997)
Survival in spring (2 months)	S_S	0.79	0.04	0.84	0.10	Schmitz and Clark (1999)

^a Assumed constant.

first nesting attempts and the expression of Johnson et al. (1992) reduces to $A_2 - (1 - H_1)^2$ for combined re-nesting attempts.

We derived survival from hatching to 1 year (S_0) from the radiotelemetry observations of pheasants marked during the Iowa field studies. We defined $S_0 = S_B S_F S_W S_S$, where S_B is survival of chicks during the brood period (2 months, from 15 Jun to 15 Aug), S_F is survival during late summer and fall (3 months, from 16 Aug to 15 Nov), S_W is survival during winter (5 months, from 16 Nov to 15 Apr), and S_S is survival during spring of calendar year $t+1$ (2 months, from 16 Apr to 14 Jun). In calculating survival of the AHY stage (S_1), we replaced chick survival, S_B , with S_S , survival during spring of year t . Parameter definitions, average observed values, and data sources are given in Table 1.

Projections

We calculated the asymptotic finite rate of increase (dominant eigenvalue, λ_1), stable stage distribution (w , expressed as the proportion of individuals in each stage), projected age ratio (ratio of HY to AHY birds in w), vector of reproductive values (v , scaled to 1 for the HY birds), net reproductive rate (R_0), and generation time (T , yr) of populations described by matrix \mathbf{A} from the average values observed at Palo Alto and Kossuth, using MATLAB (Mathworks Inc., Lowell, MA; Morris and Doak 2002). These quantities are measures of what would happen to these populations in a deterministic, asymptotic manner, with no environmental variability. However, because of demographic and environmental variability, deterministic growth rate, λ_1 , is often an overestimate of long-term growth, which can be predicted by the most-likely log population growth rate ($\log \lambda_s$) over a series of years (Caswell 2001, Morris and Doak 2002). However, depending on life history and the correlations among vital rates, it may difficult to predict whether the effect of stochasticity in vital rates will increase or decrease long-term population growth rate (Pfister 1998, Doak et al. 2005b).

There are several alternatives used to incorporate variability into stochastic matrices because there are many levels

of variability that potentially can be accounted. One frequently used approach is to select each element of the matrix at random from some statistical distribution most often assuming that the parameters are independent (Lande 1988, Caswell 2001, Fieberg and Ellner 2001, Doak et al. 2005a). With enough data it may be possible to partition variation into the natural variation in vital statistics from uncertainty in parameter estimation (Hoekman et al. 2002, Koons et al. 2006). This approach may account for environmental variability and uncertainty in parameter estimation but independent variation of matrix entries can sometimes lead to unreasonable results unless variation of individual vital rates is small and covariation among rates is incorporated (Hoekman et al. 2002, Doak et al. 2005a). Another approach is to randomly select whole observed matrices at each time step of the projection (Fieberg and Ellner 2001, Morris and Doak 2002, Kaye and Pyke 2003). Parameters of such matrices would include both environmental variation and sampling variation but incorporate the covariance among survival and reproductive rates in a natural way because the parameters were measured at the same time and place (Kaye and Pyke 2003).

We chose this latter alternative because we wanted to explore the relative importance of various vital rates under naturally varying conditions and because it maintains the pattern of covariation observed among the vital rates in a given year in a straightforward way. We calculated an estimate of the log population growth rate (λ_{iid}) and 95% bootstrap probability limits of the estimate by resampling from the 5 observed matrices estimated from each landscape with 5,000 bootstrap replicates. We assumed that the environments among years were independent and identically distributed (*iid*; Morris and Doak 2002), which is reasonable given the unpredictable weather patterns of the Great Plains and their influences on vital rates of pheasants. We chose 15-year projections because landscape level habitat changes can be expected to be reasonably consistent in such a time frame and because managers view this as a practical planning time frame.

When estimating λ_{iid} we incorporated the potential effects

Table 2. Demographic parameters of ring-necked pheasant populations in Palo Alto and Kossuth counties, Iowa, USA, 1990–1994.

Parameters	Palo Alto	Kossuth
Mean projection matrix	$\begin{pmatrix} 0.805 & 1.443 \\ 0.205 & 0.353 \end{pmatrix}$	$\begin{pmatrix} 0.644 & 1.256 \\ 0.182 & 0.372 \end{pmatrix}$
Stable stage distribution (w)	$\begin{pmatrix} 0.80 \\ 0.20 \end{pmatrix}$	$\begin{pmatrix} 0.78 \\ 0.22 \end{pmatrix}$
Reproductive values (v)	$\begin{pmatrix} 1.00 \\ 1.77 \end{pmatrix}$	$\begin{pmatrix} 1.00 \\ 1.99 \end{pmatrix}$
Dominant eigenvalue (λ_1)	1.169	1.005
Mean growth rate in variable environment (λ_{iid})	1.105	0.739
95% bootstrap interval for λ_{iid} ^a	(1.102–1.109)	(0.733–0.745)
Generation time (T , yr)	1.500	1.573
Net reproductive rate (R_0)	1.262	1.008

^a Based on percentiles of 5,000 bootstrap resamples.

of environmental fluctuation by varying the probability of favorable or unfavorable environmental conditions based on weather patterns for our study area. We considered winters with more than average snow cover and below average temperatures as detrimental to population growth and springs with above average precipitation and below average temperatures as detrimental (Perkins et al. 1997, Riley et al. 1998; T. Bogenschutz, Iowa Department of Natural Resources, unpublished data). We input the selection probability for the matrices according to the likelihood of such weather combinations based on weather records from 1961 to 1990. For example, the combination of a cold, snowy winter followed by a cool, wet spring occurred in 13% of the above-mentioned 30-year period. We observed such conditions during 1993, so the matrix corresponding to conditions in 1993 was given a probability of selection of 0.13 to simulate that environmental variability.

Sensitivity and Elasticity Analyses

We calculated sensitivity and elasticity of matrix elements using standard definitions based on the characteristic equation of the matrix (Caswell 2001). Sensitivity is the $\Delta\lambda$ resulting from a small change in any matrix element, a_{ij} , whereas elasticity is the proportional $\Delta\lambda$ in relation to a small proportional change in a_{ij} . For any matrix element, the elasticity is $e_{ij} = \frac{a_{ij}}{\lambda} \left(\frac{\partial\lambda}{\partial a_{ij}} \right)$. For example, for F_0

$$e_{1,1} = e_{F_0} = \left(\frac{F_0}{\lambda} \right) \left(\frac{\lambda - S_1}{(2\lambda - F_0 - S_1)} \right)$$

We extended these analyses to the lower-level parameters by deriving analytical expressions that link $\Delta\lambda$ as a function of the derivative of the matrix characteristic equation with respect to each lower-level parameter. We derived both sensitivities and elasticities in this fashion. Elasticity for any lower-level parameter (x) is expressed as

$$e_x = \left(\frac{x}{\lambda} \right) \left(\frac{\partial\lambda}{\partial x} \right) = \left(\frac{x}{\lambda} \right) \left(\sum_{i,j} \frac{\partial\lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x} \right).$$

For example, for reproduction (M),

$$e_M = \left(\frac{M}{\lambda} \right) \left(\frac{\lambda S_0}{(2\lambda - F_0 - S_1)} \right)$$

Likewise, the analytical expression of elasticity to the lower-level parameter of success of first nests (H_1) is

$$e_{H_1} = \left(\frac{H_1}{\lambda} \right) \left(\frac{(S_B S_F S_S A_1 C_1)(\lambda - S_1) + (S_F S_S^4 A_1 C_1 S_0)}{(2\lambda - F_0 - S_1)} \right) S_W$$

Lower-level elasticities do not generally sum to one, so the contribution to λ must be interpreted carefully (Caswell 2001).

We followed the analytical estimation of sensitivity and elasticity with less formal examination of the tradeoff between reproductive rate (M) and survival in winter (S_W) and survival of chicks during brood rearing (S_B). We estimated the minimum nest success of initial attempts (H_1) that would result in $\lambda = 1.0$ by holding all other parameters constant at the observed averages from study areas combined and then for each study area separately.

We estimated the value of M that would be necessary to maintain $\lambda = 1.0$ in response to observed variation in either S_W or S_B , holding all other parameters constant at the observed averages from each study area. We visualized the relationship between these estimates of M and S_W or S_B with plots followed by linear regression.

RESULTS

Vital Rates and Projections

To broadly visualize the demographics of pheasants in Iowa we first calculated an average matrix with parameter values for all 5 years and both study landscapes combined, $\bar{A} = \begin{pmatrix} 0.725 & 1.350 \\ 0.193 & 0.362 \end{pmatrix}$, with $\lambda_1 = 1.08$. The stable stage distribution was $w = \begin{pmatrix} 0.79 \\ 0.21 \end{pmatrix}$ and the reproductive value vector was $v = \begin{pmatrix} 1.00 \\ 1.87 \end{pmatrix}$. Simulated mean $\lambda_{iid} = 0.90$ with 95% bootstrap interval = (0.89–0.91).

Naturally the demographic parameters from the Palo Alto and Kossuth landscapes differed from each other (Table 2) and from the above-mentioned statistically averaged population. When we estimated matrices from life history parameters observed in individual years at Palo Alto, λ_1 ranged from 0.661 to 1.865, with 3 of 5 years $\lambda_1 > 1.0$. For matrices calculated from the parameters observed in individual years at Kossuth, λ_1 ranged from 0.179 to 1.832, with 3 of 5 years $\lambda_1 > 1.0$ (Table 3).

The mean age ratio projected from Kossuth data (3.16, SD = 0.94) was not lower than that projected from Palo Alto data (4.04, SD = 0.98; $t = -1.44$, $df = 8$, $P = 0.09$). Age ratios estimated from the roadside surveys during 1990–1994 of 4.39 (SD = 1.30) from Palo Alto and 3.08 (SD = 1.76) are superficially similar to the model projected ratios. The projected ratio of HY to AHY birds in the populations that we estimated from the stable stage distribution is almost identical to that observed in Iowa roadside surveys (Bogenschutz and Monen 2006).

The distribution of λ_{iid} simulated over 15 years was also different between the 2 populations (Fig. 1), with somewhat

Table 3. Dominant eigenvalue (λ_1) and projected age ratio (hatch yr:after hatch yr) derived from projection matrices of ring-necked pheasant populations in Palo Alto and Kossuth counties, Iowa, USA, 1990–1994.

Yr	Palo Alto		Kossuth	
	λ_1	Projected age ratio	λ_1	Projected age ratio
1990	1.885	4.00	1.832	3.67
1991	0.961	5.45	0.450	1.72
1992	1.197	4.49	1.004	3.78
1993	1.109	3.07	0.179	2.70
1994	0.661	3.18	1.598	3.93

greater skewness among values calculated from Kossuth data. Based on the non-overlapping confidence intervals, estimated λ_{iid} was significantly lower with data from the Kossuth landscape than with data from Palo Alto (Table 2). Estimated λ_{iid} was ≥ 1 in only 9% of the simulations for Kossuth, whereas estimated λ_{iid} was ≥ 1 in 88% of the simulations for Palo Alto. A small sample of realizations of projected populations at Palo Alto exhibits realistic trends but also reveals that there could be considerable variation among potential trends (Fig. 2).

The reproductive value vector from the averaged matrix with data from the combined study areas shows that AHY have 1.87 times the influence on projected λ_1 compared with HY birds. Although this statement is true for populations deterministically projected over the long term, from a simple accounting of the model outputs we also know that in any given year an average of 67% of the new chicks are hatched by HY birds nesting at the end of their first year of life.

We estimated minimum nest success under these conditions to be 42%. Using the average parameters from the Palo Alto area the minimum nest success estimate was 41%, whereas we estimated minimum nest success to be 45% at Kossuth.

Sensitivity and Elasticity

Sensitivity to variation in matrix elements of the combined averaged matrix is given by $S = \begin{pmatrix} 0.667 & 0.178 \\ 1.245 & 0.333 \end{pmatrix}$. The $\Delta\lambda$ was most sensitive to S_0 , which had about twice as large an effect on $\Delta\lambda$ as the next most important element, F_0 . In terms of elasticity of the elements, $E = \begin{pmatrix} 0.445 & 0.222 \\ 0.222 & 0.111 \end{pmatrix}$, F_0 had proportionally the largest influence on proportional $\Delta\lambda$.

Sensitivity and elasticity analyses of the lower-level parameters help to explain the details of the above-mentioned results regarding the matrix elements. The $\Delta\lambda$ was most sensitive to survival during brood rearing (S_B) and the subsequent winter (S_W ; Table 4), followed by success of the initial nesting attempt (H_1). However, the relative importance of S_W and S_B was reversed in terms of the proportional $\Delta\lambda$, as indicated by elasticity (Table 4). The $\Delta\lambda$ was not strongly sensitive to survival during spring (S_S ; Table 4).

The $\Delta\lambda$ was much less sensitive to changes in success of subsequent nesting attempts (H_2 ; Table 4) and the probability of reneating (A_2 ; sensitivity to $A_2 = 0.4039$).

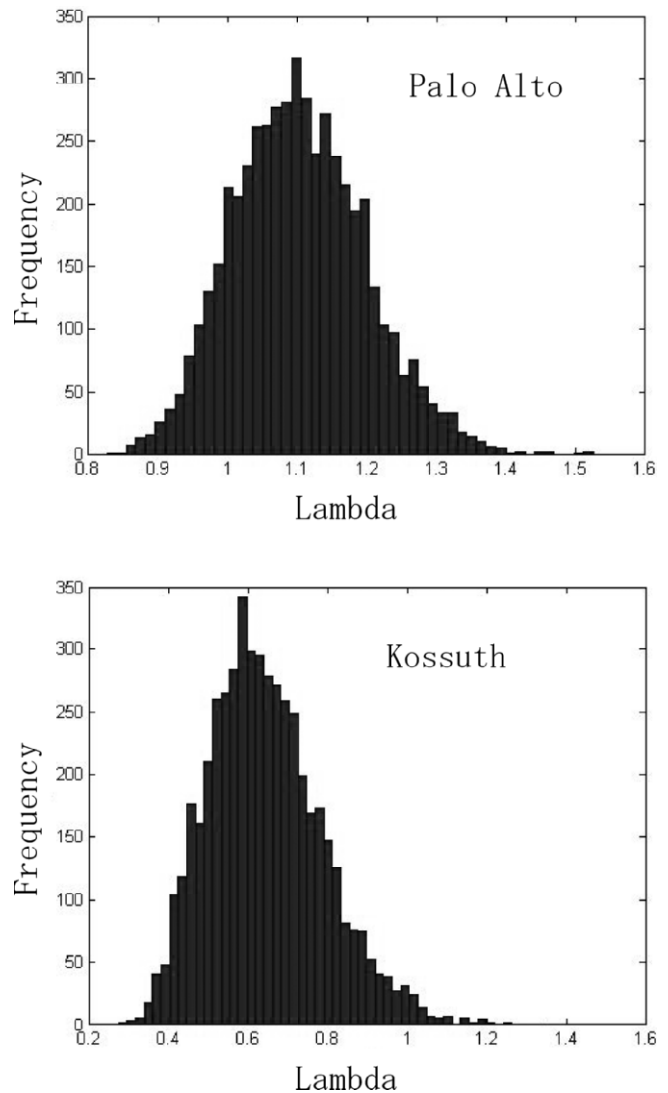


Figure 1. Frequency distribution of finite rate of increase of ring-necked pheasants over 15 years in a variable environment (λ_{iid}) generated from 5,000 bootstrap replicates of projections based on demographic data collected from 1990 to 1994 in Palo Alto and Kossuth counties, Iowa, USA. Mean $\lambda_{iid} = 1.105$ at Palo Alto and mean $\lambda_{iid} = 0.739$ at Kossuth.

The $\Delta\lambda$ was insensitive to clutch size of both initial clutches (C_1) and renests (C_2 ; sensitivity to $C_1 = 0.0535$ and sensitivity to $C_2 = 0.0115$).

Examination of a plot of the relationship between variation in observed winter survival (S_W) and the estimated recruitment (M) that would be necessary to maintain $\lambda = 1$ illustrates that M often would have to approach or exceed 0.8 when S_W was less than approximately 0.6 (Fig. 3). However, the regression of M versus S_W was not significant ($b = -0.448$, $r^2 = 0.179$, $P = 0.227$). Given that the maximum M that we measured at Kossuth was 0.67 and at Palo Alto was 0.91, the plot suggests that to compensate for winters with especially low survival, recruitment often would have to exceed the observed maximum at Kossuth and even the recruitment observed at Palo Alto.

A regression of estimated M versus S_B was significant ($M = 1.295 - 1.471 [S_B]$; $r^2 = 0.802$, $P < 0.001$; Fig. 4). From

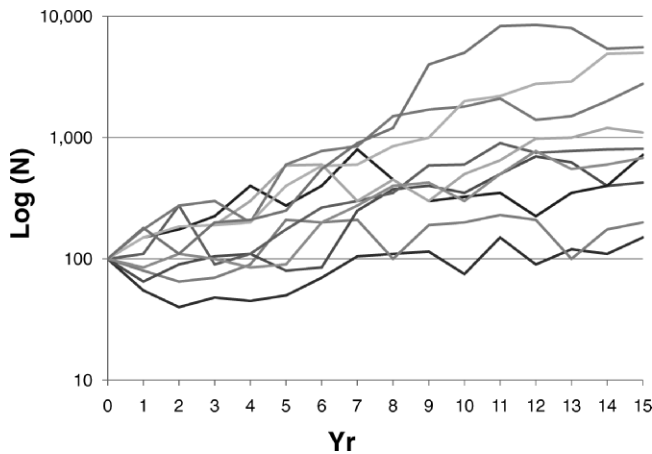


Figure 2. A sample of 10 realizations of projections of ring-necked pheasant populations over 15 years in a variable environment based on demographic data collected from 1990 to 1994 in Palo Alto County, Iowa, USA. Mean $\lambda_{iid} = 1.105$, for this population, estimated from 5,000 bootstrap replications.

the regression equation, we calculated that if S_B was < 0.425 , M would have had to exceed the observed maximum of 0.67 at Kossuth. If S_B was < 0.262 , M would have had to exceed recruitment of 0.91 at Palo Alto. When survival of chicks is as low as these values recruitment the following spring must be unrealistically great to prevent the population from decreasing in the short term.

DISCUSSION

Our simplest analysis, the deterministic projection model derived from combining all years, showed that pheasant populations could potentially increase at 8% per year under constant environmental conditions. Our projection matrix estimate is consistent with the annual rate of increase of 4% to 7% per year that we observed on roadside counts during 1990 to 1994 in the Kossuth and Palo Alto areas (T. Bogenschutz, unpublished data). The projection estimate is also similar to the 4% rate of increase from 1988 to 1995 that Nusser et al. (2004) estimated from time series analyses of roadside counts throughout the Northern Row Cropland region of Iowa. Deterministic projections are known to be positively biased but have proven to be useful, even preferable to fully stochastic models, for understanding population behavior when sampling duration is limited or vital rates are highly variable (Doak et al. 2005a).

In comparison, the estimated growth rates (λ_{iid}) from the

Table 4. Sensitivity and elasticity of lower-level parameters of a deterministic matrix model of female ring-necked pheasants constructed from averaged data collected on townships in Palo Alto and Kossuth counties Iowa, USA, 1990–1994.

Parameter	Symbol	Sensitivity	Elasticity
Nest success, first nest	H_1	1.2104	0.6105
Nest success, renests	H_2	0.2872	0.1093
Survival of chicks, brood period	S_B	1.9452	0.8091
Survival in winter	S_W	1.7932	1.0958
Survival in spring	S_S	0.2143	0.1131

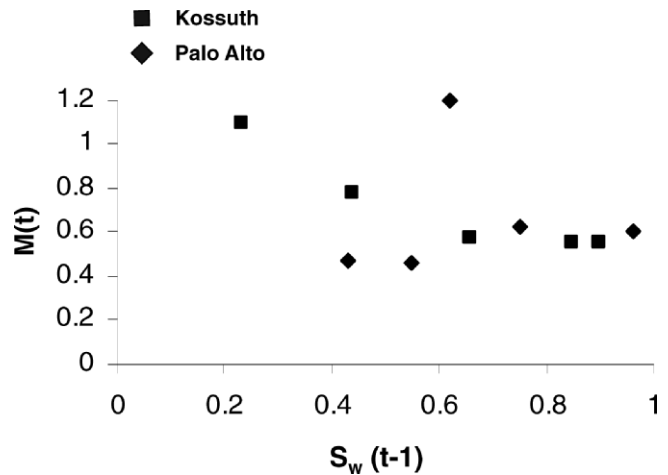


Figure 3. Estimated recruitment (M) necessary to maintain $\lambda = 1$, plotted as a function of observed winter survival of ring-necked pheasants females (S_W) based on demographic data collected from 1990 to 1994 in Palo Alto and Kossuth counties, Iowa, USA ($r^2 = 0.179$, $P = 0.227$).

stochastic projection model indicated that populations at Kossuth would decline over time, whereas those at Palo Alto would increase. Based on the estimated rate, the Kossuth population and the landscape in the township within which it resides could be characterized as a sink (Pulliam and Danielson 1991, Perkins et al. 1997, Clark et al. 1999, Runge et al. 2006). The projection analyses use the vital rates that are averaged over all individuals in the population and therefore do not account for spatially variable environmental conditions. Individually based analyses and modeling showed that even in a landscape like Kossuth with limited perennial habitat, some individuals select areas where they successfully survive and reproduce, thus contributing to population persistence (Schmitz 1997, Clark et al. 1999). Our approach to accounting for temporal variation in vital rates by randomly selecting whole observed matrices at each time step of the projection captured the effects of temporal

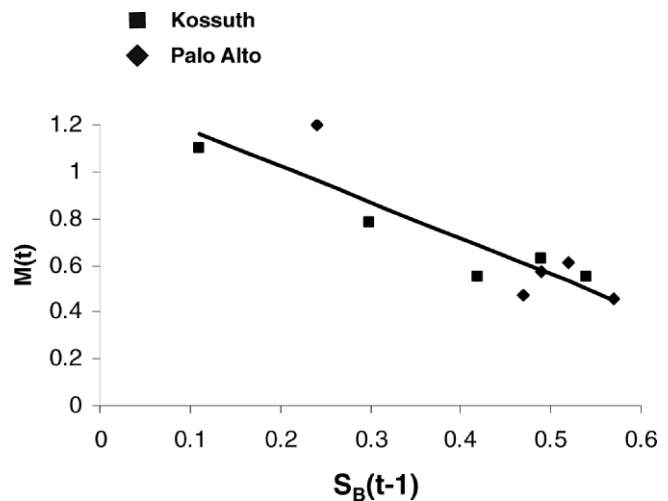


Figure 4. Estimated recruitment (M) necessary to maintain $\lambda = 1$, plotted as a function of observed survival of ring-necked pheasants chicks during brood rearing (S_B) based on demographic data collected from 1990 to 1994 in Palo Alto and Kossuth Counties, Iowa, USA ($r^2 = 0.802$, $P < 0.001$).

variation realistically showing that in some years, the population on Kossuth exhibited projected rates of increase well above 1.5 (Fieberg and Ellner 2001, Kaye and Pyke 2003, Doak et al. 2005a). So, although the estimated average λ_{iid} suggests decline, frequency distributions (Fig. 1) emphasize that it is possible for this population to persist because of a combination of factors, including years with high rates of increase that occur frequently enough to prevent extinction, but also through immigration and through survival and recruitment, which could be density dependent (Hanski et al. 1996). There are local areas on Kossuth where the habitat is as conducive to survival and recruitment of individuals as it is on most of the Palo Alto township; however, such areas are much fewer in the highly altered landscape of Kossuth (Clark et al. 1999). Given that the landscape composition and configuration did not change substantially during 1990–1994, the estimated rates reflect the composite habitat value of the contrasting landscapes. In a short-lived species such as pheasants, temporal variation in weather conditions and local habitat influences on the success of individuals are especially important to overall population dynamics.

Survival from hatch to age 1 year (S_0), and its component lower-level parameters, survival of chicks during brood rearing (S_B) and survival through the first winter (S_W), accounted for largest fraction of variation in λ , with a much larger effect than nesting success. Analyses of mallards (Hoekman et al. 2002) and lesser scaup (Koons et al. 2006) have indicated that $\Delta\lambda$ is highly sensitive to nest survival. Extremely low nest survival has been referred to as a demographic bottleneck (Hoekman et al. 2002).

The importance of early survival of pheasants is consistent with similar analyses of other short-lived gallinaceous birds (Wisdom and Mills 1997) but contrasts with waterfowl and passerines with higher adult survival (Flint et al. 1998, Sæther and Bakke 2000, Koons et al. 2006). In a life history sense, S_W reflects survival of maturing juvenile pheasants until the following spring when they reproduce for the first (and often only) time in their short lifetimes. In our modeling, survival in spring (S_S) was relatively less influential on $\Delta\lambda$ than breeding season survival has been reported to be among waterfowl (Hoekman et al. 2002, Koons et al. 2006). In part, the lesser importance of breeding season survival of pheasants compared with waterfowl may be related to the greater nest success of pheasants, many of which will hatch a brood after one nesting attempt thus freeing them from exposure to nest predators. Although losses to disturbances such as harvesting of small grains or mowing of hay were important sources of mortality to hen pheasants in the past (Farris et al. 1977), in our area such mortality is now less important than mortality to other life history stages because of the disappearance of these agricultural land uses. Pheasants obviously have evolved a life history adapted to rapid reproduction in response to a short life span (Saether and Bakke 2000, Koons et al. 2006), which contrasts with waterfowl with longer life spans and opportunity to attempt

breeding in >1 season. Interestingly, Hoekman et al. (2002) noted that increasing nest success from 0.13 to 0.21 caused duckling and adult survival to become more influential on $\Delta\lambda$ than did nest success in mallards, a waterfowl species that might be considered intermediate in life history adaptation (Koons et al. 2006). It would be valuable to study the behavioral differences between waterfowl, with such low nest success, and pheasants, with an average nest success of >0.50 , in situations where the 2 species are nesting at the same time in the same landscapes.

We were originally motivated to estimate minimum nest success that would ensure a stationary population partly because management of other game birds, notably waterfowl, has successfully focused around this parameter (Johnson et al. 1987, Hoekman et al. 2002). We note that our estimate of 42% success for pheasants is close to the 46% used by Hill and Robertson (1988) in their model, although they did not provide an analysis that could be interpreted as minimum success. We focused on success of first nests in the sensitivity analyses, but our plots of recruitment (M , which accounts for renesting) versus chick survival (Fig. 3) and winter survival (Fig. 4) both emphasize that there are limits to how much successful reproduction can compensate for poor survival of early life history stages. Regardless, it is essential to have defensible estimates of survival of each life history stage estimated from the same study areas in the same years to reasonably interpret the relative importance of nest survival to population dynamics.

The rapid turnover in the population is reflected in the stable stage vector that shows that 79% of the population will be <1 year old. The reproductive vector reveals that AHY females theoretically contribute proportionally more to future population growth because these females reproduce more than once in their short lives and therefore contribute disproportionately to the future gene pool. However from a practical viewpoint, the numerical recruitment is dominated by the HY contribution to reproduction at the end of the first year of life, making their output important to short-term demographics, which is reinforced by the large elasticity of F_0 .

We did not directly measure S_F during the northern Iowa studies, but we used results from other Iowa studies to estimate a value for modeling. Perkins et al. (1997) marked some females as early as September on our study areas and noted that this was a period of low mortality. Perkins et al. (1997) did not observe any losses to accidental shooting during the early part of the rooster pheasant season. Wooley and Rybarczyk (1981) estimated 0.82 survival from early October to December in southern Iowa, although this does not correspond closely to the mid-August to mid-November period we used in the model. Using the evidence we had, we calculated survival of 0.86 for the period (0.95/month) and assumed it to be constant. The latter assumption effectively eliminated S_F from meaningful sensitivity analysis.

The sensitivity and elasticity analyses were useful in understanding the relative importance of vital rates, although we recognize that there have been debates about the utility of

such analyses for conservation (Mills et al. 1999, 2001; Ehrlén et al. 2001). Part of the complicating issue is that interpretation depends on the analytical scale of perturbation (Caswell 2001, Link and Doherty 2002), although Koons et al. (2006) has recently shown that sensitivity and elasticity measures were robust to a wide range of vital rates in their study of waterfowl. In both a theoretical and practical sense, increased natural (process) variation in a vital rate will result in decreased sensitivity of λ to changes in that vital rate (Pfister 1998, Doak et al. 2005b).

For several reasons, we did not attempt to partition variation into natural variation in vital rates and sampling variation associated with estimating those vital rates. By the measures of Doak et al. (2005a) our analyses could be characterized as based on modest amounts of data to adequately model all sources of variation. Although we collected data on hundreds of females sampled during 5 years, with a highly integrated effort to estimate all vital rates, it could be argued that we did not cover the regional variation in pheasant vital rates the way they have been characterized in models of waterfowl (Hoekman et al. 2002, 2006; Koons et al. 2006). However, we argue that an even more compelling reason is that by selecting whole matrices we are likely to have captured more of the natural variation without treating uncertainty in the estimates as negligible (Fieberg and Ellner 2001, Kaye and Pyke 2003, Doak et al. 2005a). Local habitat and environmental conditions will undoubtedly affect vital rates simultaneously, although not necessarily all in the same way nor to the same degree (Wisdom et al. 2000, Doak et al. 2005a). In fact, for species with highly variable vital rates and a fast life history response to environmental variation, even hundreds of individuals and years of data would not be enough to completely predict λ (Doak et al. 2005a). Because of the fast life history of pheasants, we would expect that covariation among vital rates in response to varying habitat conditions in both a spatial and temporal sense might be rather mixed (sensu Doak et al. 2005a). Although researchers have improved efforts at estimating variance of vital rates, we rarely see research that concentrates on the covariance in vital rates that would be extremely useful when incorporated into population models.

MANAGEMENT IMPLICATIONS

Our analyses provide managers with guidance about the relative importance of demographic parameters that are most likely to influence pheasant dynamics when they are indirectly manipulated through habitat management. Our results emphasize the sequential nature of life history—chicks must survive through brood rearing and young of the year must survive through winter before successfully reproducing the following spring. Broadly, this demographic modeling supports management that will 1) enhance nesting and brood survival in spring and 2) survival of females in winter.

Our results certainly apply at the scale of landscapes and townships from which we derived our data, and we urge biologists to consider how the interactions among vital rates

might vary spatially and temporally with regard to local habitat and environmental conditions. The projection modeling has focused our efforts on applying habitat and landscape management such as secure nesting cover in clusters of large blocks (Clark et al. 1999), providing diverse vegetation for broods (Whitmore et al. 1986, Enck 1987), and integrating nearby winter cover (Gates and Hale 1974), thus connecting habitat management with the most responsive vital rates of pheasants that we have identified.

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