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Source: *The Journal of Wildlife Management*, Vol. 61, No. 2 (Apr., 1997), pp. 302-312

Published by: Allen Press

Stable URL: <http://www.jstor.org/stable/3802585>

Accessed: 24/02/2009 14:39

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SENSITIVITY ANALYSIS TO GUIDE POPULATION RECOVERY: PRAIRIE-CHICKENS AS AN EXAMPLE

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Abstract: Calculation of elasticities in matrix population models is a formal type of sensitivity analysis that is used increasingly to guide recovery of declining populations. Results presumably allow recovery efforts to focus on the life stage most responsible for change in population growth, as indexed by the highest elasticity. Specifically, the highest elasticity denotes the vital rate whose proportionate change exerts the largest proportionate effect on the finite rate of increase (λ). We examined the utility of this analysis given uncertainty in parameter estimates and random variation in vital rates. We modeled these conditions to test the hypothesis that nest success and brood survival exert the greatest effect on population growth of greater prairie-chickens (*Tympanuchus cupido pinnatus*). We calculated elasticity associated with each age-specific vital rate contained in 1,000 randomly-generated replicates of a Leslie matrix model, and regressed λ on each randomly-varying rate. Age 0 survival (S_0) was associated with highest elasticity for 100% of the replicates and accounted for most of the variation in λ ($r^2 = 0.95$). Within S_0 , nest success and brood survival accounted for more variation in λ than other life stage combinations. These results demonstrate the utility of sensitivity analysis, but additional results point to its limitations. For example, the vital rate consistently associated with the second highest elasticity (S_1) accounted for minuscule variation in λ ($r^2 = 0.0009$), implying that rank of elasticities can fail to index the magnitude of a vital rate's effect on λ when vital rates vary simultaneously and disproportionately. To ensure that results are reliable, we recommend that sensitivity analysis be performed across the range of plausible vital rates, that simulations involve randomization of values within these ranges, and that elasticities be calculated in tandem with regression analysis to fully illuminate potential relations of vital rates with λ . A critical assumption is that variance of vital rates is estimated accurately.

J. WILDL. MANAGE. 61(2):302-312

Key words: brood survival, elasticity, greater prairie-chicken, life stage, matrix population model, nest success, population recovery, rate of increase, sensitivity analysis, *Tympanuchus cupido*.

Many wildlife populations are scattered and small relative to their former status. These populations require intensive management and monitoring to ensure their viability. Given limited time and money, prioritizing management efforts would benefit from knowledge about which life stages or vital rates exert greatest effect on population growth. Recently, researchers have begun to question the utility of either ecological or genetic information on rare or endangered species without prior quantitative assessment of the effects of life history stages on population growth (Schemske et al. 1994).

One method of evaluating life stage importance is to measure the sensitivity of population growth to variation in age- or stage-specific vital rates. By successively changing each vital rate, the relative effect of each change on the

population growth rate can be measured. Nelson and Peek (1982) and Noon and Biles (1990) used this technique to evaluate life stage importance for elk (*Cervus elaphus*) and northern spotted owls (*Strix occidentalis caurina*).

A related approach is to use analytical sensitivity analysis (Caswell 1989) to calculate elasticity of λ associated with each vital rate. Elasticity is defined as the proportional change in λ with proportional changes in life stage parameters (Caswell 1989). Put simply, elasticity is the sensitivity of λ standardized to a scale from 0 to 1; the higher the elasticity of a vital rate, the greater the proportionate effect on λ . Because elasticities of individual elements of a population matrix sum to 1, comparisons among vital rates can be interpreted clearly (de Kroon et al. 1986, Groenendael et al. 1988).

The utility of this metric for judging the relative importance of life stages for management was illustrated by Crouse et al. (1987), Crowder et al. (1994), Doak et al. (1994), Escos et al. (1994), Heppell et al. (1994), Marschall and

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Crowder (1996), and Silvertown et al. (1996), among others. However, these authors calculated elasticities from point estimates of mean vital rates. Scientific conclusions and management recommendations made from such calculations imply that the rank and magnitude of elasticities are robust indices of each vital rate's relative effect on λ , regardless of potential fluctuations in such rates.

How this relation is affected by multiple sources of variation is little known. Brault and Caswell (1993) demonstrated how sensitivities can be weighted by variance and covariance of vital rates; results of the weighting suggested that inferences about life stage importance could change markedly when variance in vital rates is considered in tandem with traditional elasticity analysis. Other researchers (Gotelli 1991, Benton and Grant 1996) have calculated elasticities or surrogates for elasticities (Johnson et al. 1992) under extreme and changing environments. However, the typical assumption has been that elasticities accurately measured the effect of each vital rate on λ under all environmental conditions.

Whether that assumption is true is largely unanswered. For example, how are elasticities affected by random variation in vital rates, by differences in the ranges of vital rates, by simultaneous, multiple changes across vital rates, and by inaccuracies in the estimation of the rates themselves? In this paper, we examine whether elasticities reliably index the relative effect of each vital rate on λ under these conditions. We also use a simulation-based regression approach for directly evaluating vital rate effects on population growth, given simultaneous, disproportionate changes among all rates. This knowledge is critical to understanding the limitations of analytical sensitivity analysis in helping guide the recovery of threatened and endangered populations.

As a case example, we test a long-standing hypothesis about vital rate effects on population growth of greater prairie-chickens, a species whose populations are declining, scattered, and vulnerable to extirpation (Johnsgard 1973:277–284). Our hypothesis is that nest success and brood survival act together as the single-most limiting factor to population growth (Hamstrom et al. 1957:80–111, Kirsch 1974:124, Bergerud 1988).

Funding was provided by the Pacific Northwest Region and the Washington Office of

U. S. Department of Agriculture Forest Service. We thank H. Caswell, D. F. Doak, F. B. Edelman, E. O. Garton, M. W. Gratson, S. G. Hayes, and R. S. Holthausen for reviews and guidance. We also thank 2 anonymous reviewers for comments, and D. F. Doak for software development. L. S. Mills worked on the initial analysis as a visiting professor at the University of Idaho, Moscow. The paper is contribution 97-1 of the Montana Forest and Conservation Experiment Station, Missoula.

METHODS

Modeling Process

Our purpose for modeling was to place the prairie-chicken management hypothesis in a context that is typical for a sensitive species targeted for recovery, and to test the reliability of inferences for recovery that are commonly made from traditional elasticity analysis (e.g., Crouse et al. 1987). Specifically, we wanted to examine how well elasticities indexed each vital rate's effect on λ under stochastic conditions; that is, when demographic data contain a moderate-to-high level of uncertainty in the point estimates due to sampling (measurement) and process (environmental) errors across space and time. These specifications are important because they describe a typical level of uncertainty and quality of data in which most recovery efforts are undertaken.

To meet these specifications, we: (1) gathered demographic data that could be used to estimate the lower and upper bounds on vital rates for greater prairie-chickens, including all possible variation in estimates in space and time (Table 1); (2) randomly selected values of each vital rate within their respective ranges and parameterized them in a Leslie matrix population model (Leslie 1945, 1948); (3) generated 1,000 replicates of the model, with each replicate representing a random combination of vital rates chosen from the specified bounds (Table 2); and (4) calculated λ for each replicate (time-invariant model, Gotelli 1991). Any distribution of random numbers for a given vital rate is possible, but as a first cut we chose each vital rate independently from a uniform probability distribution; this was in keeping with our goal of testing the reliability of elasticities under all potential combinations of vital rates.

We then tested our hypothesis using 2 approaches. First, we calculated elasticity of λ as-

Table 1. Annual demographic components, their range of values, the associated vital rates in which components fit, and the associated elements of the Leslie matrix in which values are imbedded to calculate elasticities of λ for greater prairie-chickens. Low and high values found in the literature, shown below, were used to establish the lower and upper bounds on vital rates of survival (S_x) and reproduction (R_x), and to parameterize the associated elements of age-specific fertility (F_i) and survival (P_i) in a Leslie matrix population model (Table 2).

Demographic components	Range of values (source)	Vital rate	Element of matrix
No. eggs/1st clutch/female/year, unadjusted (E1)	^a 12.0 (Johnsgard 1973:297) to 14.0 (Johnsgard 1973:297)	R_1 through R_8	F_1 through F_8
No. eggs/2nd clutch/female/year, unadjusted (E2)	^a 7.0 (Johnsgard 1973:297) to 10.0 (Johnsgard 1973:297)	R_1 through R_8	F_1 through F_8
Proportion female eggs in population (PFE)	0.50 (assumed) to 0.50 (assumed)	R_1 through R_8	F_1 through F_8
Proportion eggs that are fertile (EF)	0.91 (Johnsgard 1973:69) to 1.00 (Schwartz 1945:66)	R_1 through R_8	F_1 through F_8
Proportion females producing a 1st clutch (PN1)	^b 0.90 (Bergerud 1988:583) to 1.00 (Svedarsky 1988:202)	R_1 through R_8	F_1 through F_8
Proportion females producing a 2nd clutch (PN2)	^c 0.00 (Robel 1970:309) to ^d 0.17 (Svedarsky 1988:203)	R_1 through R_8	F_1 through F_8
Egg survival of fertile eggs (ES) (=nest success when all eggs are fertile)	0.20 (Bowen et al. 1976:145) to 0.80 (Svedarsky 1988:203)	S_0	P_0, F_1
Brood survival (BS)	^e 0.15 (Svedarsky 1988:209) to ^f 0.55 (Baker 1953:29)	S_0	P_0, F_1
Post-brood (fall-winter) survival (PBS)	^g 0.39 (assumed) to 0.69 (assumed)	S_0	P_0, F_1
Adult survival (AS)	Lowest and highest values from Tables 18, 19, or 20, Hamerstrom and Hamerstrom (1973:37–38)	S_1 through S_7	P_1 through P_7 F_2 through F_8

^a Clutch sizes for yrl reduced by 1 egg (Bergerud 1988:590).

^b 0.56 to 0.91 for yrl, based on ranges for other North American grouse (Bergerud 1988:582–583).

^c 0 renews during 2 of 5 nesting seasons (Robel 1970:309).

^d High proportion of F producing second clutch = $1.0 - 0.80$ or 0.20 of nesting F available to renest under highest rate of nest success for first nests (lowest proportion of nesting F with first nest failures, Svedarsky 1988:203) \times 0.83 of these F actually renesting (Svedarsky 1988:203) \times 1.0 of F nesting = 0.17 of all ad F producing 2nd clutch. High proportion of all yrl F assumed to produce a 2nd clutch = 0.01, based on general relations described by Bergerud (1988:595–599).

^e Low estimate of brood survival = 0.532 (Svedarsky 1988:209) estimated for 4 weeks, or 0.854 survival/week, taken to the 12th power to obtain a survival rate of 0.15 for the BS period of 12 weeks.

^f High estimate of brood survival = 0.55 for 12 weeks (Baker 1953:29) based on change in no. chicks/brood from 12.0 [no. eggs/clutch, Baker (1953:30)] at the end of May to 6.6 (Baker 1953:29) at the end of August.

^g No estimate available. We therefore assumed that post-brood survival could be as low and as high as the lowest and highest estimates of S_x reported by Hamerstrom and Hamerstrom (1973) for any subsequent age class, excluding zero values of S_x . Thus, low PBS = 0.24 (Table 20, Hamerstrom and Hamerstrom 1973:38) taken to the 12th root to obtain a monthly survival rate of 0.888, taken to the 8th power to obtain a survival rate for 8 months (duration of PBS) of 0.39. Similarly, high PBS = 0.57 (Table 18, Hamerstrom and Hamerstrom 1973:37) taken to the 12th root to obtain a monthly survival rate of 0.954, taken to the 8th power to obtain a survival rate for 8 months of 0.69.

sociated with each vital rate of each replicate. We then ranked the vital rates by order of their elasticities, by replicate, and calculated mean elasticity associated with each vital rate among the replicates. Second, we regressed λ on each vital rate, across all replicates, and calculated coefficient of determination (r^2) for each vital rate, and for all combinations of nest success, brood survival, and post-brood survival contained within age 0 survival (S_0) of the replicates. Values for S_0 were derived by randomly selecting separate values for nesting, brood-rearing, and post-brood life stages, respectively, within the upper and lower bounds on each (Table 1), and then calculating the product.

Three composite variables of the S_0 life stages were examined in relation to λ : (1) nesting and brood-rearing; (2) nesting and post-brood; and (3) brood-rearing and post-brood.

Vital Rates

Low and high values of vital rates were defined as the lowest and highest sample means that we found for any given year among the available studies (Table 1). Some studies reported published sample means that encompassed multiple years only. We considered these data as well, and simply used whatever sample means were highest and lowest among all research that was available (Table 1). These esti-

Table 2. Estimates of the lower (a) and upper (b) bounds on age-specific fertility (F_i) and survival (P_i) for greater prairie-chickens. Low range values from Table 1 were used to establish the lower bounds (a). High range values (Table 1) were used to establish the upper bounds (b). Estimates are arranged in a post-birth pulse Leslie matrix, with F_i along the top row and P_i down the sub-diagonal. Lower bound matrix (a) contains values of 0 in rows and columns 8 and 9.

a							b								
0.03 ^a	1.87 ^b	2.21	1.87	1.18	1.18	0	1.81 ^c	4.00 ^d	4.48	3.61	3.45	3.53	2.67	2.28	0
0.01 ^e	0	0	0	0	0	0	0.30 ^f	0	0	0	0	0	0	0	0
0	0.38 ^g	0	0	0	0	0	0	0.51 ^h	0	0	0	0	0	0	0
0	0	0.45	0	0	0	0	0	0	0.57	0	0	0	0	0	0
0	0	0	0.38	0	0	0	0	0	0	0.46	0	0	0	0	0
0	0	0	0	0.24	0	0	0	0	0	0	0.44	0	0	0	0
0	0	0	0	0	0.24	0	0	0	0	0	0	0.45	0	0	0
							0	0	0	0	0	0	0.34	0	0
							0	0	0	0	0	0	0	0.29	0

^a Low $F_1 = [11.0 \text{ eggs/1st clutch/female/YR (E1 at } R_1) \times 0.50 \text{ proportion of female eggs (PFE)} \times 0.91 \text{ egg fertility (EF)} \times 0.56 \text{ females producing a 1st clutch (PN1 at } R_1)] + [0.00 \text{ females producing 2nd clutch (PN2)}] = 2.8028 \text{ female eggs/female/YR} \times \text{probability of females surviving during the previous time step (S}_{x-1}) \text{ for the opportunity to nest. This and all other algorithms follow a post-birth pulse model (Noon and Sauer 1992:443-450) where F have first birthday simultaneous with being censused and laying eggs. Thus, age 0 females are censused at birth, in the form of eggs in the nest, and have their first offspring at first birthday.}$

^b Low F_2 through $F_8 = [12.0 \text{ eggs/1st clutch/female/YR (E1)} \times 0.50 \text{ proportion of female eggs in population (PFE)} \times 0.91 \text{ egg fertility (EF)} \times 0.90 \text{ females producing 1st clutch (PN1)}] + [0.00 \text{ females producing 2nd clutch (PN2)}] = 4.914 \text{ female eggs/female/YR} \times \text{probability of females surviving during previous time step (S}_{x-1}) \text{ for the opportunity to nest.}$

^c High $F_1 = [13.0 \text{ eggs/1st clutch/female/YR (E1 at } R_1) \times 0.50 \text{ proportion of female eggs (PFE)} \times 1.0 \text{ egg fertility (EF)} \times 0.91 \text{ of all females producing 1st clutch (PN1 at } R_1)] + [9.0 \text{ eggs/2nd clutch/female/YR (E2 at } R_1) \times 0.50 \text{ proportion of female eggs in population (PFE)} \times 1.0 \text{ egg fertility (EF)} \times 0.01 \text{ YRL females producing 2nd clutch (PN2 at } R_1)] = 5.96 \text{ female eggs/female/YR} \times \text{probability of YRL females surviving during the previous time step (S}_{x-1}) \text{ for the opportunity to nest.}$

^d High F_2 through $F_8 = [14.0 \text{ eggs/1st clutch/female/YR (E1)} \times 0.50 \text{ proportion of female eggs in population (PFE)} \times 1.0 \text{ egg fertility (EF)} \times 1.0 \text{ females producing 1st clutch (PN1)}] + [10.0 \text{ eggs/2nd clutch/female/YR (E2)} \times 0.50 \text{ proportion of females in population (PF)} \times 1.0 \text{ egg fertility (EF)} \times 0.17 \text{ females producing 2nd clutch (PN2)}] = 7.85 \text{ female eggs/female/YR} \times \text{probability of females surviving during previous time step (S}_{x-1}) \text{ for the opportunity to nest.}$

^e Low $P_0 = 0.20 \text{ egg survival (ES) (1 month)} \times 0.15 \text{ brood survival (BS) (3 months)} \times 0.39 \text{ post-brood survival (PBS) 8 months} = 0.012.$

^f High $P_0 = 0.80 \text{ egg survival (ES)} \times 0.55 \text{ brood survival (BS)} \times 0.69 \text{ post-brood survival (PBS)} = 0.304.$

^g Low P_1 through $P_7 =$ lowest estimates of age-specific survival (S_x) found in Tables 18, 19, or 20, Hamerstrom and Hamerstrom (1973:37-38).

^h High P_1 through $P_7 =$ highest estimates of age-specific survival (S_x) found in Tables 18, 19, or 20, Hamerstrom and Hamerstrom (1973:37-38).

mates were collected under a variety of conditions and sampling methods, and thus include both sampling error and variation due to environmental effects in space and time. Data from studies of Attwater's greater prairie-chicken (*T. c. attwateri*) were not considered due to the unique nature of these estimates as they apply specifically to 3 isolated, remnant populations of this subspecies in Texas (Peterson and Silvy 1996).

Age-specific reproduction (R_x) was defined as the number of fertile eggs produced/female/age class, not accounting for the probability of females surviving the previous year (S_{x-1}) for the opportunity to nest (Table 1). To calculate R_x , we had to adjust fecundity, defined as the number of eggs/first clutch/breeding female/age class and number of eggs/second clutch/breeding female/age class ($E1$ and $E2$), by the proportion of female eggs in the population (PFE), the proportion of female eggs that are fertile (EF), the proportion of available females that produce a first clutch (PNI), and the proportion

of available females, both nesting and non-nesting, that produce a second clutch ($PN2$):

$$R_x = \frac{[(E1)(PFE)(EF)(PNI)] + [(E2)(PFE)(EF)(PN2)]}{S_{x-1}}$$

To establish the range for clutch size ($E1$ and $E2$), we used generalized estimates of the lowest and highest sample means (Johnsgard 1973:297). We did so because most nesting studies did not or could not group nest samples reliably into categories of first nests versus re-nests when computing sample means, thus making it difficult to determine systematically the absolute range across all studies. To estimate the proportion of yearling females that produce a first clutch (PNI at R_1), we used sample means from other North American grouse (Table 1) because no estimates were available for prairie-chickens, and because PNI generally is lower for yearling than adult grouse (Bergerud 1988:582-583). We also reduced the low and high values of $E1$ and $E2$ for yearling females by 1 egg, in accordance with slightly

smaller clutch sizes observed for yearlings (Bergerud 1988:590). Yearlings also were assumed to have a lower rate of reneating than adults (Bergerud 1988:595–599).

The period that R_x encompassed began with ovulation and ended with egg-laying. Age 0 survival (S_0) began with fertile female eggs in the nest where $S_0 = (ES)(BS)(PBS)$; ES = egg survival, starting at the date that fertile eggs are laid and ending when the eggs hatch, encompassing 1 month; BS = brood survival, starting with hatching of eggs and ending with the loss of neoteny and the beginning of brood dispersal, encompassing 3 months; and PBS = post-brood survival, starting with the beginning of brood dispersal and ending with the first birthday of the age 0 cohort, encompassing 8 months.

Following convention, we used estimates of nest success, defined as the percentage of nests hatching ≥ 1 egg, to estimate egg survival (Table 1). Using nest success to estimate egg survival was acceptable for 2 reasons: (1) all infertile eggs were accounted for previously in the calculation of R_x ; (2) egg mortality due to predation, abandonment, and weather invariably affect or are assumed to affect all eggs in a nest (see Johnsgard 1973:73–75 and Bergerud 1988:592–609 for typical examples of nest success used for grouse as a surrogate for egg survival and Rearden [1951] for general effects of predators on ground-nesting birds). Consequently, we use the term nest success as a surrogate for egg survival.

Estimates of nest success were summarized by Evans (1968), Schroeder and Braun (1992), and Peterson and Silvy (1996). We augmented these summaries with estimates for individual years from multi-year studies, when available, to establish the range of values (Table 1). In 1 case (Bowen 1976), estimates of nest success did not agree among the summaries. Consequently, we used the generalized estimate of 0.2 that was given in the original study (Bowen 1971:145).

To estimate brood survival, we used data from studies that reported changes in brood size over time (Yeatter 1943, Baker 1953, Edminister 1954 as cited by Evans 1968, Sisson 1976, Bowman and Robel 1977, Newell et al. 1988, Svedarsky 1988). One additional study (Amman 1957:96–99) was excluded because brood size was reported for 4 non-metric categories of chick growth, but quantitative changes in brood

size over time were not provided. Because only 1 study (Baker 1953) reported changes in brood size for the full 3 months that we defined for brood-rearing, we calibrated the estimates from the other studies to fit a 3-month period. The 2 studies that yielded the low and high values were used to establish the range (Table 1).

Data related to post-brood survival of 24 radiotagged juveniles were available from 1 study (Bowman and Robel 1977), but no specific estimates of survival were provided. Moreover, the small sample size/year ($n \leq 6$), large percentage of transmitter failures and removals (67%), and short time interval over which birds were monitored ($\bar{x} = 35.5$ days) did not meet assumptions for survival estimation (Pollack et al. 1989). We therefore assumed that annual post-brood survival could be as low as the lowest estimate of adult survival that was available (0.24, Table 20; Hamerstrom and Hamerstrom 1973:38); this equals a higher monthly survival (0.888) than that for broods (0.532) and a lower monthly survival than that for adults <7 years old (0.923–0.954).

Juvenile survival intermediate to chick and adult survival is plausible for 3 reasons: (1) mean survival of juveniles for other North American grouse (Bergerud 1988:618), when calculated on a monthly basis, is higher than that for chicks but lower than that for adults; (2) the lowest estimates of adult survival (Hamerstrom and Hamerstrom 1973:37–38) included estimates for adults of old age (≥ 7 yr old) whose annual survival was low (0.24–0.34) in contrast to younger adults (0.38–0.57); and (3) immature birds during post-brood dispersal and wintering periods probably have low survival rates (Bowman and Robel 1977). Consequently, our lower bound on post-brood survival is lower than that for most adult age classes (Table 1). Similarly, we chose the highest estimate of adult survival that was available (0.57, Table 18; Hamerstrom and Hamerstrom 1973:37) to represent the upper bound on post-brood survival (Table 1); we did so to encompass all potential sources of variation that might contribute to high survival of juveniles.

To establish the lower and upper bounds on age-specific survival of adults ($S_{x \geq 1}$, Tables 1 and 2), we used low and high estimates for a remnant population of greater prairie-chickens in central Wisconsin (Hamerstrom and Hamerstrom 1973:37–38). No other estimates were available. However, these data encompass a

wide and plausible range of survival values because: (1) data were collected on 16 cohorts of males and 16 of females, thus accounting for sex-specific differences in survival; (2) data were collected over a 22-year period that encompassed a broad range of variation due to changing environmental conditions and sampling (observer) error; (3) Hamerstrom and Hamerstrom (1973:37–38) summarized their data in a variety of ways under a variety of assumptions; these different summaries represented different ways of partitioning the variation in estimates due to sampling error, process error, and methods of analysis; and (4) Hamerstrom and Hamerstrom's range of survival values agrees closely with that for other North American grouse whose fecundity is similar to prairie-chickens (Bergerud 1988:584–592).

Matrix Construction

Each Leslie matrix was composed of randomly selected values of R_x and S_x . We parameterized these values using a post-birth pulse approach for females (Caswell 1989:12–15, Noon and Sauer 1992:443–450). Top row elements of such a matrix equal age-specific fertility (F_i), which we defined as the number of fertile female eggs/female/age class. Under a post-birth pulse model, F_i equals the product of (R_x)(S_{x-1}); elements on the sub-diagonal equal the probability of females surviving during the previous time step for the opportunity to nest (P_{i-1}), which equals S_{x-1} under our modeling assumptions. Parameterization of vital rates into F_i and P_i matrix elements, as described above, yielded the lower and upper bounded matrices (Table 2).

Elasticity and Regression Analysis

Although most authors have calculated elasticities of matrix elements, we calculated instead the elasticities of vital rates comprising these elements (Brault and Caswell 1993, Doak et al. 1994). Elasticity of a vital rate comprising a matrix element is a more direct measure of each vital rate's effect on λ because it accounts for the fact that survival rates are imbedded in both the sub-diagonal and the top row elements of the Leslie matrix (Noon and Sauer 1992:448). That is, elasticities of vital rates directly measure the contribution of survival among all matrix elements in which each survival rate is imbedded. By contrast, elasticities of matrix elements do not explicitly separate the contribu-

tion of survival from other components in the top row of fertility elements.

To calculate elasticities, we developed a computer program that used the power method (Burgman et al. 1993:127–139) to determine, for any projection matrix, the dominant eigenvalue (λ) and vectors representing the stable age distribution (w) and reproductive values (v). The elasticity (e_{ij}) of λ to changes in matrix element a_{ij} equals

$$\left(\frac{a_{ij}}{\lambda}\right) \left(\frac{v_i w_j}{\langle vw \rangle}\right)$$

where $\langle vw \rangle$ is the scalar product of the 2 vectors and where $(v_i w_j / \langle vw \rangle)$ represents s_{ij} , the sensitivity of λ to absolute unit changes in a_{ij} . For a vital rate x that is 1 component of 1 or more matrix elements, chain rule differentiation is required for each a_{ij} that contains x (Caswell 1989:126–136). In words, the sensitivity of λ to x reduces to summation, over all elements containing x , of: $[(s_{ij})(\text{product of all components other than } x)]$. The elasticity is the sensitivity associated with x times (x/λ) . Note that unlike elasticities of matrix elements, the elasticities of vital rates making up elements do not sum to 1 (Caswell 1989). However, elasticities of all vital rates are calculated on the same scale and thus can be compared directly, as can elasticities of elements.

We used regression to search for linear as well as non-linear responses of λ to changes in each vital rate or life stage. We did this by calculating r^2 values for all bivariate relations under both simple linear regression (SAS, PROC REG; SAS Inst. Inc. 1990) and non-linear regression (TableCurve 2D, Jandel Scientific Inc. 1994). We did not use multiple regression because of the difficulty in detecting non-linear relations when using multiple independent variables.

Elasticity and r^2 are related in the following way: $r^2 = [(\beta^2)(\text{variance of vital rate } x)/\text{variance of } \lambda]$, where β is the slope of vital rate x . When λ is a linear function of the vital rates, $\beta^2 = \text{sensitivity}^2$; thus, r^2 is approximated by the product of sensitivity^2 and the variance, adjusted for covariance among vital rates (Brault and Caswell 1993:1451, Boyce 1994:6–7). In turn, elasticity is the slope of $\log \lambda$ regressed on the \log of vital rate x . Consequently, if regression is done on \log transformed data, r^2 is approximated by the product of elasticity^2 and the variance (H. Caswell, Biol. Dep., Woods Hole Oceanographic Inst., pers. comm.).

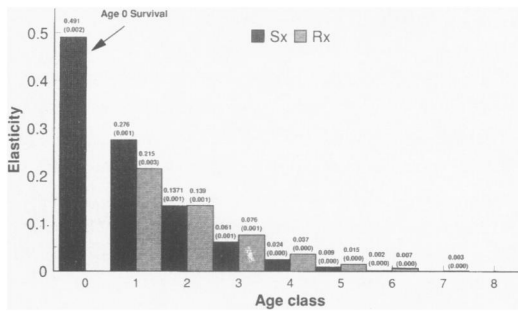


Fig. 1. Mean elasticities ($\pm 99\%$ CIs) of survival (S_x) and reproduction (R_x) for greater prairie-chickens, calculated from 1,000 replicates of a Leslie matrix population model. Values of S_x and R_x for each replicate were selected randomly from a uniform probability distribution within preestablished lower and upper bounds (Tables 1 and 2).

Elasticity and r^2 therefore measure the effect of each vital rate on λ in different but complementary ways. Elasticity measures the effect of small, proportional changes in each vital rate while ignoring variation in other rates. Coefficient of determination measures the same effect but weights the effect by the observed or projected variance. Presumably, under our modeling conditions, that expand on traditional sensitivity analysis, the vital rate consistently having greatest effect on λ should have (1) the highest ranked elasticity; (2) the highest mean elasticity; and (3) the highest r^2 .

RESULTS

Highest elasticity was associated with age 0 survival across the range of independently fluctuating vital rates (Fig. 1). All 1,000 replicates had the highest elasticity associated with S_0 . Mean elasticity associated with S_0 was higher ($P < 0.01$) than that associated with other age-specific estimates (Fig. 1). Moreover, S_0 accounted for most of the variation in λ ($r^2 = 0.95$, Fig. 2a). Within S_0 , the combination of nest success and brood survival accounted for more variation in λ than the composite of brood and post-brood survival or of nest success and post-brood survival (Figs. 2b–d). Thus, λ consistently was affected most by changes in S_0 , and by nest success and brood survival within S_0 , given the range and particular combinations of vital rates tested. The range and distribution of λ s associated with the replicates showed that these findings were robust to wide variation in population growth (Fig. 3).

These results indicated strong agreement between the elasticity calculations and the regres-

sion analysis in identifying the vital rate having greatest effect on λ . However, all other vital rates accounted for almost no variation in λ , even though their associated elasticities ranged widely in value (Fig. 4). For example, S_1 and R_1 had the second and third highest mean elasticities (Fig. 1), yet each accounted for minor amounts of variation in λ (S_1 , $r^2 = 0.0009$; R_1 , $r^2 = 0.04$). These minuscule r^2 values were similar to those for vital rates having much lower mean elasticities (Fig. 4).

DISCUSSION

Life Stage Importance

Our results support the hypothesis (Hamerstrom et al. 1957, Kirsch 1974) that the combination of nest success and brood survival exerts the greatest effect on population growth of greater prairie-chickens across a broad range of vital rates. Elasticities associated with S_0 consistently were higher than those for other age classes, and S_0 accounted for most of the variation in λ . Within S_0 , the composite of nest success and brood survival accounted for more variation in λ than other life stage combinations. These results agree with other analyses of life stage importance for short-lived birds, all of which demonstrated the strong effect of early life stages on population growth, as summarized by Meyer and Boyce (1994).

Site- and time-specific effects of life stages or vital rates on λ will vary, however, according to the underlying probability distribution of values, as well as the covariance of these values among stages or rates (Caswell 1989, van Tien-deren 1995). Underlying distributions of vital rates, in combination with covariance among vital rates, reflect a variety of factors, including effects of density dependence. Our simulations assumed independence among vital rates or life stages. Because the underlying distributions and covariances of vital rates for prairie-chickens are unknown, a conservative assumption is that any combination of life stages during the first year can limit population growth, depending on the specific values that might occur. Further simulations that assume a variety of probability distributions, especially those that also mimic plausible types of density dependence, would provide further insight about potential effects of life stages and vital rates on λ . Such simulations could easily be done under our modeling process. Brault and Caswell (1993) and van Tien-

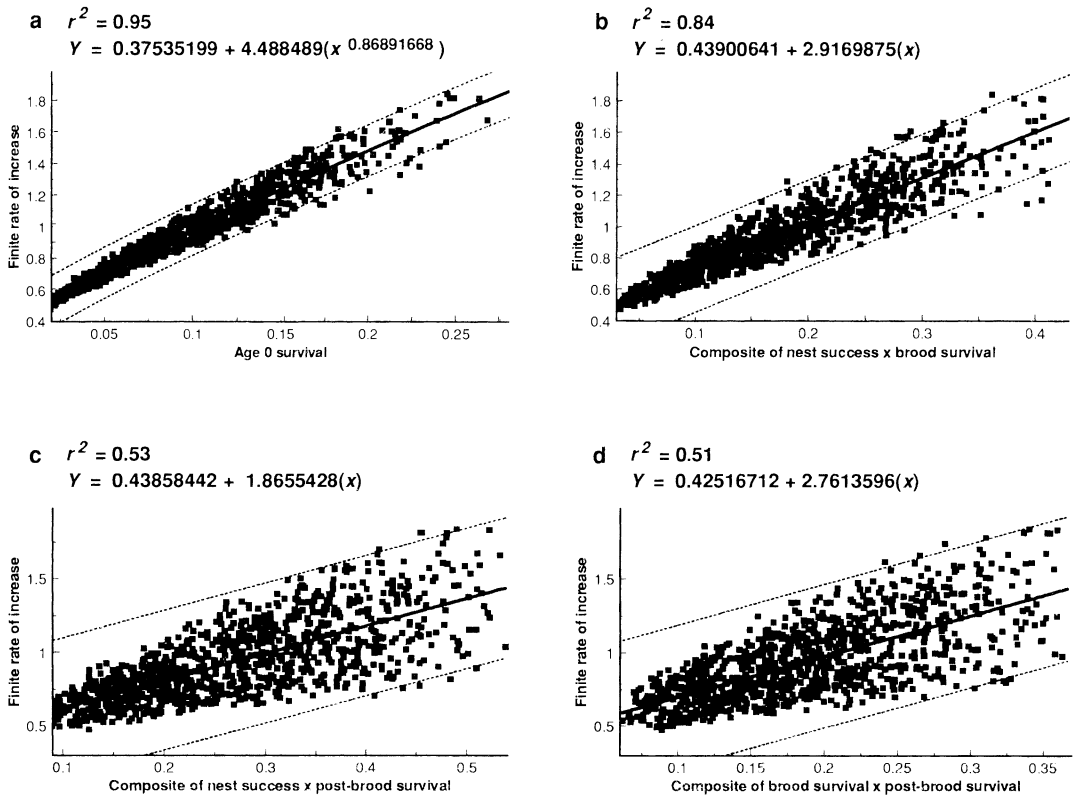


Fig. 2. Finite rate of increase (λ) for greater prairie-chickens regressed on age 0 survival (a), nest success and brood survival (b), nest success and post-brood survival (c), and brood and post-brood survival (d), encompassed by 99% prediction intervals. Relations are based on 1,000 replicates of a Leslie matrix population model. Life stage values for each replicate were selected randomly from a uniform probability distribution within preestablished lower and upper bounds (Tables 1 and 2).

deren (1995) also provide methods that account for covariance when conducting elasticity analysis.

Simulations that assume different levels of measurement error, and different levels of total

variance than that observed for each vital rate, would also provide further insight about how robust the effect of each vital rate is on population growth. This would be especially important for vital rates that account for a large portion of the variation in λ , such as S_0 in our analysis. Reduced variation will reduce r^2 for any given vital rate, but the change may not be significant in terms of biological or management insights.

As an example, we reduced the range in S_0 by 50% under the assumption that this amount represented measurement error, and conducted the same simulations as before. As expected, r^2 for S_0 declined, but the decline was only from 0.95 to 0.82. Moreover, rankings of the elasticity and r^2 values did not change. Finally, some of the values for adult survival, such as S_7 and S_8 , had ranges larger than S_0 , yet their r^2 values were 0.00 and 0.00. In fact, when we expanded the ranges of S_7 and S_8 to fluctuate between 0.10 and 0.90 (more than twice the range

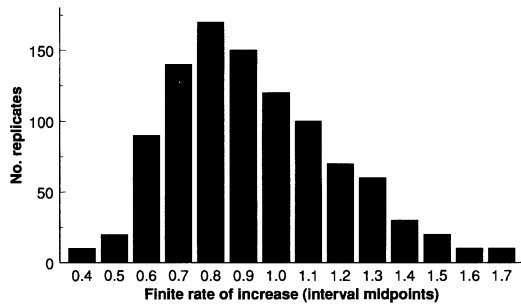


Fig. 3. Distribution and range of the finite rate of increase (λ) for greater prairie-chickens, based on 1,000 replicates of a Leslie matrix population model. Vital rates for each replicate were selected randomly from a uniform probability distribution within preestablished lower and upper bounds (Tables 1 and 2).

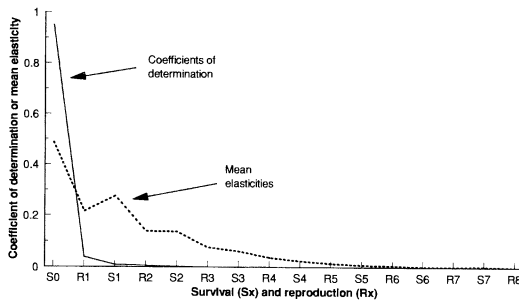


Fig. 4. Coefficient of determination (r^2) and mean elasticity associated with each vital rate of survival (S_x) and reproduction (R_x) contained in 1,000 replicates of a Leslie matrix population model for greater prairie-chickens. Coefficient of determination is the proportion of variation in λ explained by each vital rate under simple linear or non-linear regression. Mean elasticities are from Fig. 1.

of S_0 , S_7 and S_8 still accounted for <1% of the variation in λ . Further simulations such as these are needed to fully evaluate the effect of changes in variance on λ .

Utility of Modeling Process

Our analysis demonstrates the utility of our regression-based approach, which is complementary to traditional elasticity analysis. With randomization, the regression approach explicitly accounts for effects of both the sensitivity and the variance of vital rates in relation to changes in λ . Elasticities also are evaluated across the range of vital rates using the same method of randomization. Our findings suggest that by using such randomization procedures, r^2 and elasticity calculations provide complementary metrics for gaining insight about vital rate effects on λ . These findings are especially important considering that calculation of both r^2 values and elasticities under random conditions has rarely been adopted (but see Brault and Caswell [1993] for a similar approach).

Results of our modeling process also illustrate the potential weaknesses of elasticity calculations as a sole measure of the effect of each vital rate on λ . Although the vital rate consistently associated with the highest elasticity (S_0) also accounted for the majority of variation in λ , none of the other vital rates accounted for >4%, and only R_1 accounted for >1%, even though elasticities for these rates ranged widely in value (Figs. 1 and 4). Thus, if management relied exclusively on elasticity calculations to prioritize recovery efforts, one might assume that increasing the vital rates having second or third highest elasticity consistently would yield

positive, non-linear changes in λ (Caswell 1989). This was not true when variance in vital rates was considered, as was done through the regression analysis.

Limitations of sensitivity analysis stem from the fact that such calculations only measure the effect on λ from small, one-at-time, proportional (or absolute) changes in single vital rates while holding all other vital rates constant (de Kroon et al. 1986). In the real world, vital rates change simultaneously, in different proportions, and across wide ranges. This is true in nature and under management. Effects of these latter characteristics on λ can be evaluated with randomization and regression procedures that account for changes among vital rates that are simultaneous, stochastic, and that vary in proportion and range.

Effects of simultaneous, disproportionate changes among all vital rates on population growth also can be evaluated with other variance decomposition methods that are analogous to our regression approach. For example, Brault and Caswell (1993) demonstrated a technique similar to our regression approach, where sensitivities are weighted by variance and covariance of vital rates. Another analogue to our regression approach involves "Life Table Response Experiments" (LTRE, Caswell 1989: 139–151). While conceptually similar, LTRE uses contrasts between pre-determined matrices with rigid correlation structures, thereby making it somewhat less flexible than our approach. Through its use of sensitivity calculations, LTRE also assumes a linear response of population growth to changes in vital rates, a restrictive assumption that we avoid with our inclusion of non-linear regression.

Elasticity analyses that incorporate variation in vital rates and our regression approach depend on accurate estimates of the ranges or variances of vital rates, currently and under future management. The regression approach, in particular, may suffer from some of the variance problems identified for key factor analysis (Royama 1996). Nonetheless, a vital rate having a wide range does not necessarily lead to a spurious r^2 , unless that range is due to a disproportionately high measurement error compared to other rates. If a high amount of measurement error is suspected, then a smaller range or variance should be examined to ensure that results of the regression analysis do not change substantially. As with vital rates having high measurement error, a vital rate that has

wide natural variation but that is immune or expensive to change also would not be a logical target for management.

Those cautions in mind, a modeling process like that used here could help prioritize management or monitoring efforts. This could be done by identifying those vital rates or life stages that presumably have greatest effect on λ , so that improved estimates for those parameters could be obtained in the field. Management costs could be reduced by lessening or eliminating efforts to monitor vital rates or life stages that appear to have little effect on λ , and by focusing efforts on monitoring or modifying those rates having greatest effect.

Researchers could also use our modeling process to gain insight about the life stages most important to study, and to formulate more structured hypotheses and study designs, in much the same way that researchers have suggested that elasticities be used by themselves (Crouse et al. 1987, Doak et al. 1994). Our process would strengthen that approach by measuring the response of λ in terms of both elasticities and regression. Analyzing the effect of vital rates on λ under such a process might be thought of as a presampling technique, results that might direct the sampling effort to the age or stage consistently associated with the highest growth rate.

MANAGEMENT IMPLICATIONS

Our results support population and habitat management for greater prairie-chickens that emphasizes high rates of nest success, brood survival, and post-brood survival. These stages encompass the first year of life that is associated with the highest elasticity of population growth and that accounts for most of the variation in population growth. Habitat needs for the 3 life stages should be defined for each local population through site-specific research. Site-specific research may be especially important if prairie-chickens require a different type of habitat for each life stage.

Our analysis indicates that elasticities by themselves may not provide a robust index of each vital rate's effect on λ . To ensure that results are reliable, we recommend that analytical sensitivity analysis be performed across the range of plausible vital rates, that simulations involve randomization of values within these ranges, and that elasticities be calculated in tandem with regression analysis to fully illuminate potential relations of vital rates with λ . The

modeling process used here illustrates this kind of evaluation, and provides a stronger basis for analyzing life stage importance as part of recovery efforts. This process could be strengthened further by simulating plausible types of density dependence and vital rate covariance that might exist for the species of interest.

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Received 15 May 1995.

Accepted 9 August 1996.

Associate Editor: Noon.