# MATHEMATICAL DEMOGRAPHY OF SPOTTED OWLS IN THE PACIFIC NORTHWEST

BARRY R. NOON U.S. Forest Service, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, CA 95521
CHARLES M. BILES Department of Mathematics, Humboldt State University, Arcata, CA 95521

*Abstract:* We examined the mathematical demography of northern spotted owls *(Strix occidentalis caurina)* using simple deterministic population models. Our goals were to gain insights into the life history strategy, to determine demographic attributes most affecting changes in population size, and to provide guidelines for effective management of spotted owl populations. The spotted owl apparently has evolved high adult survival rates associated with irregular and unpredictable reproduction. The finite rate of population change ($\lambda$) in this subspecies is most sensitive to variation in adult survival rate and relatively insensitive to variation in fecundity and age at first reproduction. However, rates of population change are strongly affected by reproductive senescence if it occurs before 15 years of age. Sound management practices should include efforts to control factors that adversely affect the survival rate of adult females.

***J. WILDL. MANAGE. 54( I): 18-27***

Considerable interest has developed over the harvesting of old-growth forests in the Pacific Northwest and impacts on the long-term survival of the spotted owl. Current information suggests that the northern subspecies (S. *o. caurina)* is restricted to coniferous forests in mature and old-growth age classes (Forsman et al. 1984, see Gutiérrez and Carey 1985) and that continued loss and fragmentation of the remaining old-growth forests may threaten the viability of the subspecies. The possible endangerment of the subspecies and the need to retain large areas of suitable habitat have generated heated debate because of perceived economic costs to the timber industry associated with setting aside large areas of older forests for the spotted owl (Dixon and Juelson 1987, Salwasser 1987, Simberloff 1987).

In a search for solutions to this dilemma, the Forest Service (U.S. For. Serv. [USFS] 1986) and the academic community (Dawson et al. 1986) identified various aspects of the owl's biology and life history for further investigation and proposed guidelines for spotted owl research. An aspect of the owl's biology that was addressed in detail by both groups was the species' demographic life history. The apparent decline of the northern subspecies may be exacerbated by low preadult survivorship, low adult fecundity, and delayed age at first reproduction. These were features identified as primary parameters that should be estimated more precisely. Neither report gave a high priority to the annual adult survival rate even though adult survival rate significantly affects the rate of population change of both the California condor (*Gymnogyps californianus)* (Mertz 1971, Verner 1978) and the snail kite (formerly the Everglade kite [*Rostrhamus sociabilis*]) (Nichols et al. 1980), species with demographic characteristics similar to those of the spotted owl. The conclusions by Dawson et al. (1986) and the USFS (1986) concerning the relative importance of various demographic parameters of the spotted owl have recently been criticized by Lande (1988).

Our goal was to characterize the life history structure of the spotted owl and to determine demographic parameters that most influence rates of population change. Detailed, analytical analyses of a species' life history structure are not only a necessary prerequisite to understanding its population dynamics, but also suggest direction for future research. We analyzed the available demographic data of the northern spotted owl using life history and demography in an approach similar to Mertz (1971) and Nichols et al. (1980). We also assessed the direction of current spotted owl research and suggest future priorities indicated by our demographic analyses.

The owl's basic demographic life history includes several parameters; however, accurate and precise estimates of all parameters are not available and these parameters might exhibit substantial geographic variation throughout the range of the northern spotted owl. It is thus of considerable interest to examine the effects of parameter variation on projected population growth of the species and to infer which parameters may be most influenced by management decisions.

We thank J. A. Baldwin, A. B. Franklin, D. G. Hankin, B. G. Marcot, J. D. Nichols, J. Verner, and an anonymous reviewer for critical comments on the manuscript. The final product has benefited greatly from their comments and suggestions.

## METHODS

Standard Lotka-Leslie methods were applied to make inferences about the effects of variation in certain life history parameters and different management practices on population growth rate (Keyfitz 1968, Mertz 1971, Nichols et al. 1980). We examined the effect of changes in 1 demographic character at a time with all others held constant. We assumed (1) reproduction was characteristic of a birth-pulse population (Caughley 1977:6), (2) no density dependence, and (3) a 1:1 sex ratio. Further, our analyses were formulated exclusively in terms of females. Parameter estimates and model structure were based on existing information from studies of the northern spotted owl. Despite the lack of precise and accurate estimates of most demographic parameters, the models employed were general enough to estimate the effects of parameter variation on various measures of population growth rate.

## DEMOGRAPHIC LIFE HISTORY

The basic demographic life history of the spotted owl is presented in standard form (Table 1). The parameter b, denotes the expected number of female fledglings produced by a female of age $x$. There is some discrepancy in the estimate of this parameter (Barrowclough and Coats 1985, Franklin et al. 1986). However, following Lande (1988), we have used the recent estimate of Marcot and Holthausen (1987) in which $b_x = b = 0.24$ $(x \geq 2)$. Annual survival probabilities were assumed distinct for 3 age classes: juvenile $(s_0)$, subadult $(s_1)$, and adult (s). The parameter $l_x$ represents the probability of survival to age $x$ (by definition $l_0 = 1.0$). For $x \geq 2$, probability of survival to age $x$ is given by $l_x = s_0 s_1 s^{x-2}$ (Table 1). We used $s_0 = 0.11$ (Marcot and Holthausen 1987), $s_1 = 0.71$, and $s = 0.94$ (Franklin et al. 1986), except where otherwise noted.

Table 1. Spotted owl life history. Age at first reproduction is 2 years.

| $x$[a] | $l_x$[b] | $b_x$[c] | $l_x b_x$[d] |
|---|---|---|---|
| 0 | 1.0 | 0 | 0 |
| 1 | $s_0$ | 0 | 0 |
| 2 | $s_0 s_1$ | $b$ | $s_0 s_1 b$ |
| 3 | $s_0 s_1 s$ | $b$ | $s_0 s_1 s b$ |
| 4 | $s_0 s_1 s^2$ | $b$ | $s_0 s_1 s^2 b$ |
| . | . | . | . |
| . | . | . | . |
| . | . | . | . |
| $x$ | $s_0 s_1 s^{x-2}$ | $b$ | $s_0 s_1 s^{x-2} b$ |

[a] $x$ denotes age expressed in years.

[b] $l_x$ denotes the probability that an individual aged 0 (a newly hatched bird) will survive to enter age class $x$.

[c] $b_x$ denotes the expected number of female fledglings produced by a surviving female aged $x$.

[d] $l_x b_x$ denotes the net maternity function.

Adult refers to ages after the second year of life. Within the adult age class, survival rate was assumed to be constant. Preadult survival rate $(l_2)$ represents the probability of survival from fledging to age 2 and is given by the product of $s_0$ and $s_1$.

### Variations in the Demographic Life History

One area of uncertainty in the basic life history of the spotted owl is the frequency and magnitude of reproduction at age 2. Barrowclough and Coats (1985) and Lande (1988) assumed that individuals do not regularly breed until age 3. However, Barrows (1985) and Miller et al. (1985) documented breeding at age 2 years, and we have recently discovered breeding attempts by 2 2-year-old females (P. W. C. Paton, US. For. Serv., unpubl. data). We examined the effects of variation in age at first reproduction, beginning at age 2, on population growth rate. A number of previously published life tables reflect the uncertainty of many aspects of the species' biology as well as the accumulation of new information (Table 2). Our analyses encompass the range of variation in life history parameters and examine the effects of parameter variation on estimates of growth rate.

## MODELS AND RESULTS

### Net Reproductive Rate

The sum of the $l_x b_x$ column (Table 1), often called the net maternity function $(R_0)$, measures the net reproductive rate of the population, i.e.,

Table 2. Comparison of parameters used in the demographic analyses of the northern spotted owl.

| Parameter[a] | Barrowclough and Coats (1985) | Draft EIS (USFS 1986) | | Final EIS (USFS 1988) | | Marcot and Holthausen (1987) | Lande (1988) | This study |
|---|---|---|---|---|---|---|---|---|
| $s_0$ | 0.19 | 0.20 | 0.60 | 0.11 | 0.34 | 0.11 | 0.11 | 0.11 |
| $s_1$ | 0.85 | 0.85 | 0.85 | 0.96 | 0.97 | 0.96 | 0.71 | 0.71 |
| $s$ | | 0.85 | 0.85 | 0.96 | 0.97 | 0.96 | 0.942 | 0.942 |
| $b$ | 0.34 | 0.275 | 0.40 | 0.24 | 0.24 | 0.24 | 0.24 | 0.24 |
| $T$ | 3 | 2 | 2 | 2 | 2 | 2 | 3 | 2 (3) |
| $w$ | 10 | 10 | 10 | 15 | 15 | 15 | $\infty$ | $\infty$ (16, 21, 26) |
| Estimates | | | | | | | | |
| $r$ | -0.237 | -0.249 | 0.008 | -0.164 | -0.011 | -0.170 | -0.040 | -0.040 |
| $\lambda$ | 0.789 | 0.779 | 1.008 | 0.850 | 0.989 | 0.840 | 0.961 | 0.961 |

[a] $s_0$ = probability of survival to age 1 (first year survival rate); $s_1$ = probability of survival to age 2 (second year survival rate); $s$ = annual survival rate from age 2 onward (ad survival rate); $b$ = number of female fledglings produced by an adult female; $T$ = age (yr) at first reproduction; $w$ = age (yr) at reproductive senescence; $r$ = intrinsic rate of natural increase (= ln $\lambda$).

the overall expected lifetime production of females by a female fledgling. The individual $l_x b_x$ terms of $R_0$ specify the number of fledglings that a new fledgling is expected to produce upon attaining age $x$. At a stable age distribution, $R_0 > 1.0$ indicates that the population is increasing, $R_0 < 1.0$ decreasing, and $R_0 = 1.0$ stable. The net maternity function for the basic spotted owl life history is computed by

$$\begin{aligned} R_0 &= \sum_{x=0}^{w} l_x b_x \\ &= b s_0 s_1/(1 - s),\ 0 < s < 1. \end{aligned} \quad (1)$$

We plotted adult survival rate (s) versus preadult survival rate ($s_0 s_1$) (Fig. 1). Curves (isopleths) represent combinations of adult and preadult survival that yield constant values of $R_0$. Current estimates of age-specific survival rates of the spotted owl suggest that cases with high s and low $s_0 s_1$ (upper left portion of Fig. 1) are of primary interest. In this region slight changes in estimates of survival rates can produce dramatic changes in estimates of $R_0$. The area below the heavy diagonal line represents the condition of preadult survival exceeding adult survival, an unlikely scenario for spotted owls. As $R_0$ approaches 1.0, the isopleths become more horizontal, reflecting the increasing importance of annual adult survival rate to net reproductive rate.

The $R_0 = 0.32$ isopleth is the estimate from equation (1) based on the parameter estimates used in our analysis (Table 2). This value suggests that the population is declining. However, the estimate of $R_0$ is extremely sensitive to the value of adult survivorship used in equation (1) and provides no information on the rate of population change. Thus, we focus on the finite rate of increase of the population to evaluate both the direction and magnitude of population change.

## Finite Rate of Increase

The finite rate of increase ($\lambda$) of a population represents the factor by which total population size, as well as the size of each age class, changes each year given constant $l_x$ and $b_x$ values and a stable age distribution (Nichols et al. 1980:218). Assuming a closed population, $\lambda$ can be computed empirically as the ratio of population sizes estimated from the same location at 2 different time periods ($\lambda = N_t/N_{t-1}$, where $N_t$ is population size in year $t$). For the spotted owl, $\lambda$ can be defined as the single, positive, real root of the equation

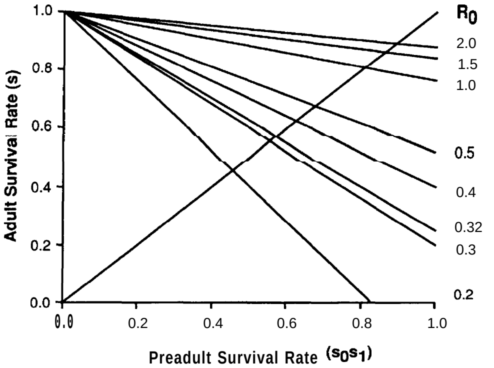

Fig. 1. Net reproductive rate (R,) with age at first reproduction at 2 years for various values of adult (s) and preadult ($s_0 s_1$) survival rates.

$$1 = \sum_{x=0}^{\infty} \lambda^{-x} l_x b_x$$
$$= bs_0s_1/(\lambda^2 - \lambda s),\ 0 < s < 1,\ \lambda > s. \quad (2)$$

Equation (2) can be rewritten as (Appendix)

$$\lambda^2 - s\lambda - bs_0s_1 = 0 \quad (3)$$

and solved for λ as

$$\lambda = [s + (s^2 + 4s_0s_1b)^{1/2}]/2. \quad (4)$$

The isopleths (Fig. 2) illustrate values of preadult and adult survivorship that give constant values of λ assuming a stable age distribution. Thus, inferences drawn from these and similar analyses apply only to long-term trends.

The solution to equation (4) based on the parameter estimates we used (Table 2) yields the estimate λ = 0.96. This is equivalent to a 4.0% annual decline in population size with a population half-life (time for the population to decrease to ½ its current size) of 17 years. However, given the precision of the parameters used to estimate λ, this value may not be significantly different from λ = 1.0 (Lande 1988).

The relatively horizontal slope of the isopleths indicates the much greater importance of adult survivorship to λ than preadult survivorship (Fig. 2). To illustrate, with no preadult mortality ($s_0s_1 = 1.0$), adult survivorship ($s$) must = 0.76 to have λ = 1.0. The current estimates for $s$ (Table 2), ranging from 0.85 (USFS 1986) to 0.97 (USFS 1988), indicate that adult survivorship has little opportunity for improvement relative to preadult survivorship. In addition, the species has only a moderate potential for population growth. Even if the birds were immortal ($s_0 = s_1 = s = 1.0$), λ equals only 1.2, yielding an annual rate of population increase of 20% and a population doubling time of 3.8 years.

*Variation in Fecundity*.-The estimate of $b = 0.24$ (Marcot and Holthausen 1987) combines 2 important components: the number of females fledged per nest and the proportion of females ≥2 years of age that breed. Separate estimates of these parameters are not currently available. The low fecundity observed for spotted owls is likely a function of both a low proportion of ≥2-year-old females breeding and a large number of failed nesting attempts.

Both $R_0$ and λ increase as functions of $b$, but R, increases much more rapidly (Fig. 3). The λ isopleths are almost horizontal to the isopleth for $s = 0.94$, lying very close to the line λ = 1.0 for all values of $b$ examined. In contrast, the λ isopleth for $s = 0.85$ is always below the λ = 1.0 line. Given $s = 0.94$, the lower limit for λ (when $b = 0.0$) is 0.94, which gives a population half-life > 11 years. When $s = 0.85$, the lower limit for λ is 0.85, and the population half-life is >4 years. Thus, assuming $s > 0.90$, spotted owl populations can probably persist through long periods of low fecundity.

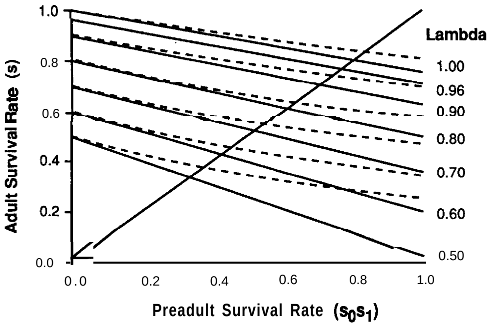

Fig. 2. Annual finite rate of increase (h) with age at first reproduction at 2 years (solid isopleths) and at 3 years (dashed isopleths) for various values of adult (s) and preadult ($s_0s_1$) survival rates.

## Distinct Adult Fecundity at Age 2 Years

Two- year-old adult females may have a fecundity value, $a$, distinct from that of females ≥3 years of age (we assume $a < b$, Barrowclough and Coats 1985). Incorporating a separate age 2 fecundity parameter changes the characteristic equation (3) to

$$\lambda^3 - s\lambda^2 \quad \lambda s_0s_1a - s_0s_1s(b \quad a) = 0. \quad (5)$$

Setting $a = 0.12$ in equation (5) yields the estimate λ = 0.96, which is equivalent to the estimate of λ from equation (3) when expressed to 2 significant digits. Thus, λ is virtually unaffected by a substantial decrease in the fecundity of subadults.

## Age at First Reproduction

Changes in the age at first reproduction affect the form of the characteristic equation. Defining $T$ as the age of sexual maturity with $T \geq 1$, equation (3) takes the general form

$$\lambda^T - s\lambda^{T-1} \quad bs_0s_1s^{T-2} = 0, T \geq 1 \text{ and } 0 < s < 1. \quad (6)$$

Defining the age at first reproduction as in equa-

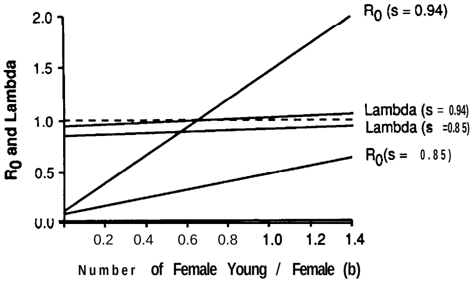

Fig. 3. Net reproductive rate ($R_0$) and finite rate of increase ($\lambda$) as functions of the annual number of female young per female for 2 values of adult survival rate (s). The dashed line indicates a constant $\lambda = 1.0$.

tion (6) follows Nichols et al. (1980) by treating changes in the age at sexual maturity independently from changes in prereproductive mortality; i.e., the probability of surviving to any fixed age $x$ is independent of the age at maturity. We simulated a change in the age at first reproduction by either shifting the fecundity column of the life table (Table 1) forward for earlier reproduction, or backward for later reproduction, without a corresponding shift in the survivorship column. An important consequence of treating age at first reproduction and prereproductive annual survival rates independently is that for either declining or increasing populations, earlier ages of first reproduction always cause the rate of population change to become more positive (Hoogendyk and Estabrook 1984).

The effect of age at first reproduction of 3 years on $\lambda$ is most pronounced for low values of s and high values of $s_0 s_1$ (Fig. 2). Under conditions of low preadult and high adult survival, the effects of delayed reproduction on $\lambda$ are very small. For example, the estimate of $\lambda$ from equation (6) with $T = 3$ is 0.96, which is equivalent to 2 significant digits to the value of $\lambda$ from equation (3).

## Senescence

The effects of a senescent decline in fecundity were explored by incorporating a maximum age, $w - 1$, beyond which no reproduction occurs (i.e., $b_x = 0$, $x \geq w$) (Mertz 1971, Nichols et al. 1980). The equation for population growth incorporating senescence is

$$\lambda^2 - s\lambda - bs_0s_1[1 - (s/\lambda)^{w-2}] = 0, \quad w \geq 2, \quad 0 < s \leq 1. \qquad (7)$$

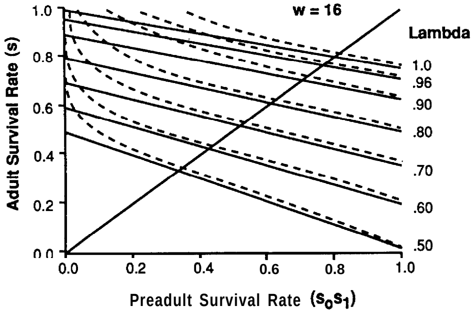

Fig. 4. Annual finite rate of increase ($\lambda$) with no senescence (solid isopleths) and senescence at age 16 years (dashed isopleths) for various values of adult ($s$) and preadult ($s_0s_1$) survival rates.

With truncation of the life table, $\lambda$ may be less than $s$.

The general characteristic equation for various ages of first reproduction ($T$) and ages of senescence ($w - 1$) is (Appendix)

$$\lambda^T - s\lambda^{T-1} - bs_0s_1s^{T-2}[1 - (s/\lambda)^{w-T}] = 0, \quad (8)$$

where $T \geq 1$, $w \geq 2$, $0 < s \leq 1$. The life span of spotted owls, and whether or not fecundity remains constant, are unknown. However, it is unlikely that the high estimates of $s$ would arise if spotted owls lived <15 years. The effects of a senescent decline in fecundity on $\lambda$ become progressively more pronounced as w decreases. The effects of senescence are most apparent for high s and low $s_0s_1$ and are pronounced at values of $\lambda \geq 0.7$ (Fig. 4). The effects of senescence at ages $\leq 21$ years for populations with values of $\lambda$ near 1.0 are dramatic (Fig. 4). Failure to account for senescent declines could result in a gross overestimate of $\lambda$. Conversely, incorporating se-

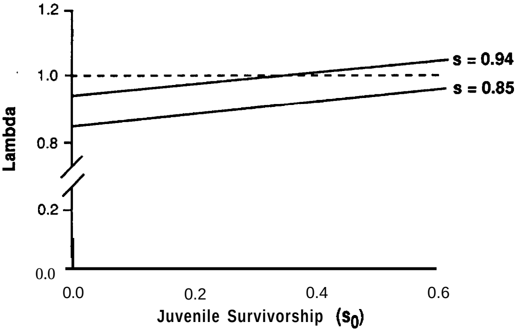

Fig. 5. Annual finite rate of increase ($\lambda$) as a function of the first year survival rate ($s_0$). The dashed line indicates a constant $\lambda = 1.0$.

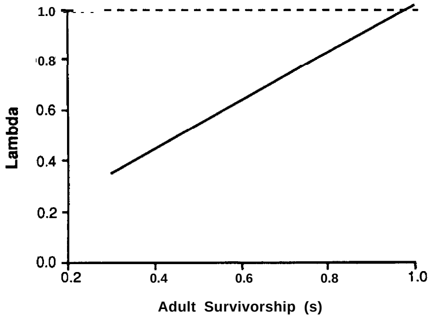

Fig. 6. Annual finite rate of increase (λ) as a function of the annual adult survival rate ($s$). The dashed line indicates a constant λ = 1.0.

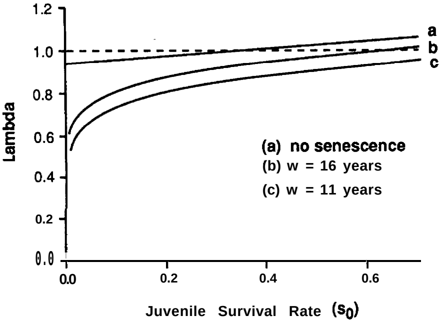

Fig. 7. Annual finite rate of increase (λ) as a function of first year survival rate ($s_0$) with senescence at 11 and 16 years as well as no senescence.

nescence when it does not occur can result in gross underestimates of λ. For example, using equation (7) and setting $w$ = 16, yields the estimate λ = 0.83, suggesting a 17% annual rate of population decline with a half-life <4.0 years. The dramatic effect of early senescence (Fig. 4), incorporated implicitly into several previous analyses, explains much of the variation in previous estimates of λ (Table 2).

## Juvenile and Adult Survival Rates

Even extensive variation in juvenile survival rate ($s_0$) yields a nearly constant estimate for λ (Fig. 5). The λ isopleth for $s$ = 0.94 lies very close to the line λ = 1.0 for all values of $s_0$ examined. The λ isopleth for $s$ = 0.85 also is close to the line λ = 1.0, but lies below it for all values of $s_0$ examined.

The value of λ is strongly dependent on adult survivorship (Fig. 6), particularly in comparison to its relationship with fecundity (Fig. 3) and juvenile survival rate (Fig. 5). Given the parameter estimates used in our study (Table 2), λ was ≥ 1.0 only at very high values of $s$ and attained a maximum value (at adult immortality $s$ = 1.0) of only λ =1.02. Further, values of $s$ < 0.85 suggest annual rates of decline exceeding 10%. However, errors in the estimation of s could yield quite different estimates of λ. For example, $s$ = 0.98 suggests a stable population (λ = 1.0), whereas s = 0.92 suggests a 6% annual rate of population decline (λ = 0.94).

## Juvenile Survival Rate and Senescence

We examined the relationship between variation in first year survival rate ($s_0$) and the estimate of λ under conditions of no senescence as well as senescence at ages 16 and 11 ($w$ = 16 and 11 in equation [7]). The latter analyses represent truncation of the life table (Table 2) at ages 15 and 10.

The effects of senescence are most pronounced for low values of $s_0$ (Fig. 7). For example, the estimate of λ assuming no senescence (equation [3]) is λ = 0.96, and the estimate with senescence at age 11 ($w$ = 11, equation [7]) is λ = 0.74. The first estimate suggests a 4% annual rate of population decline (population half -life ≅ 16 yr), whereas the latter suggests a 26% rate of decline (population half-life ≅ 2.3 yr).

# DISCUSSION

## Inferences from the Deterministic Analyses

The Forest Service (USFS 1986) and the Audubon Panel (Dawson et al. 1986) suggested that low preadult survivorship contributed most to low estimates of population growth (λ) with a significant additional effect attributable to low adult fecundity. Our analyses and Lande (1988) provide additional clarification by demonstrating, when parameters are considered separately, an extreme sensitivity of λ to variation in adult survival rate and a relative insensitivity to average fecundity or preadult survival rate. We also considered the sensitivity of λ to several joint variations of parameters. However, we found no further insights than those provided by varying parameters separately. For example, doubling $b$ or $s_0$ separately increased the estimate of λ by only 0.02; jointly doubling both $b$ and $s_0$ increased λ by 0.05.

Lande's (1988) and our demographic analyses differ from the analyses of Barrowclough and Coats (1985), the Forest Service (USFS 1986, 1988), Dawson et al. (1986), and Marcot and Holthausen (1987) in that we did not truncate the life table of the spotted owl. Truncation of life table at $x$ years is equivalent to a senescent decline in fecundity occurring at age $x + 1$. Presumably, the implicit incorporation of early senescence into previous analyses (USFS 1986, Marcot and Holthausen 1987) led to an incorrect emphasis on the importance of first year survival rate to rates of population change.

A frequent assumption is that birds do not experience senescent declines in fecundity and survival rates (Deevey 1947). However, an estimate of mean generation length (Caughley 1977: 124) without reproductive senescence suggests the unlikely average age of mothers at the birth pulse to be about 53 years. Invoking senescence at age 26 or 16 years yields more reasonable estimates of generation length of about 12 and 8 years, respectively. It is unlikely that reproductive senescence occurs much before 16 years; strong natural selection against the evolution of early senescence would be expected in a species with life history characteristics like the spotted owl.

In both Forest Service analyses first year survivorship was increased to obtain an estimate of $\lambda \cong 1.0$ (Table 2). The rationale for changing parameter estimates, particularly $s_0$, was to match model-based estimates of $\lambda$ (equation [3]) with empirical estimates of A based on statewide inventories in Oregon (Forsman et al. 1984, 1987). It is not surprising that empirical estimates deviate from model-based estimates. The empirical estimate of $\lambda$ (i.e., $\lambda = N_t/N_{t-1}$) based on survey data does not directly account for the number of additions (births) and losses (deaths) a population may be experiencing. Thus, even a population whose death rate far exceeded its birth rate could remain relatively stable over the short term due to outside recruitment. This problem is highlighted because there are currently no reliable estimates of the size of discrete spotted owl populations. Estimates of $\lambda$ from demographic models, however, are functions of turnover events (the survival rates) and thus are capable of discriminating between the above scenario and one in which a population is stable due to a balance between birth and death rates. We believe it is inappropriate to judge the validity of model-based estimates of population change according to how well they agree with empirical estimates based on large-scale inventory data that are insensitive to turnover events.

### Limitations of the Current Analyses

Estimating the sensitivity of population growth to variation in individual demographic parameters, as we have done, can be misleading. Demographic parameters do not vary independently and thus should be considered simultaneously. Our analyses allowed us to identify the relative importance of various parameters, but we strongly encourage an integrative approach when designing spotted owl research and making management decisions. Decisions should be based on a perspective that encompasses the entire life history of the spotted owl and not just 1 or 2 life history attributes.

Further, 2 types of information are relevant to a species' population growth rate. One is the sensitivity of $\lambda$ to variation in life history characters as was explored in our paper. The other concerns life history attributes showing the most natural variation. Variations in growth rate ($\lambda$) might be associated more closely with attributes showing extensive variation than to attributes that are less variable but to which growth rate is more sensitive in a mathematical sense. Reliable information on the natural variation in demographic parameters of spotted owls is not yet available.

All of the life history parameters used in our analyses are subject to both estimation error and sampling variation, but we did not consider these sources of variation. Further, no natural population is exposed to purely deterministic forces. Thus, population dynamics of the spotted owl should be examined relative to both demographic and environmental stochasticity.

## RESEARCH PRIORITIES

Knowledge of demographic parameters that most significantly influence a species' population dynamics is useful to order research priorities. From our demographic analyses, we believe that studies of the relationship between habitat variation and variation in adult survival rate are a high priority. It may turn out that one of the major influences on adult survivorship is energy expenditure and vulnerability to predation during reproduction. In general, questions concerning the relation between demographic and habitat variation should be studied at both local and landscape scales.

Secondly, several poorly understood aspects of spotted owl life history need attention. For example, it is important to know whether spotted owls exhibit senescence in fecundity or survival. Our analyses show that estimates of $\lambda$ were strongly influenced by the age at which we invoked reproductive senescence. Without detailed information on the reproductive history of marked individuals, such relationships may go undetected.

Thirdly, factors contributing to the low and variable reproductive rates of spotted owls also need investigation. Whether the extensive annual variation in reproductive success is due to variable resource levels (prey base), variable environmental conditions, or some combination is not known. Whether reproductive rates or adult survival rates can be increased by direct management for prey populations is also an important research question.

Finally, as suitable spotted owl habitat becomes more fragmented, it will become increasingly important to estimate the dispersal capabilities of spotted owls and to identify factors that affect survival during dispersal. This includes influences on the survival of juvenile birds dispersing from their natal territories as well as adult birds displaced by habitat loss.

## MANAGEMENT IMPLICATIONS

The implications of these analyses to management concern the decisions that differentially affect adult and preadult birds. The life history pattern of the spotted owl suggests that it must have evolved in an environment stable with respect to adult survivorship. The much greater sensitivity of $\lambda$ to variation in adult rather than preadult survival rates suggests strong selection pressures to maintain low adult mortality rates. Further, a low fecundity rate suggests that recruitment may always have been variable, but given high adult survivorship, the spotted owl has been capable of persisting through long periods of low reproductive output. Low fecundity, however, precludes a rapid repopulation after a population decline. Thus, we contend that any management policy that lowers the survival rate of adults, particularly if coupled with reductions in population size, may greatly increase the likelihood of local extinctions.

We found $\lambda$ to be relatively insensitive to increases in $s_0$ and $b$; however, it would be incorrect to infer that these attributes should not be considered in management plans. Adult survival rate is already very high and may not be amenable to further increases. Assuming no reduction in adult survival rate, increases in first year survival or fecundity through direct management actions may be the most likely way to increase the growth rate of spotted owls. For example, silvicultural prescriptions that result in increases in the owl's preferred prey may be 1 way of ameliorating the effects of timber harvest.

Given the spotted owl's life history structure, an evaluation of management decisions in terms of persistence likelihoods is only possible when viewed over the long term (50-100 yr). With its very high adult survival probability and apparent longevity, the species may be able to persist over the short term even in the face of extensive reductions in the amount of suitable habitat. Thus, there may be a significant time lag in the response of spotted owl population size to decreases in environmental carrying capacity.

Rapid rates of population decline in either deterministic or stochastic analyses are not surprising when $\lambda$ is $< 1.0$. In our deterministic analyses, we have simply demonstrated exponential rates of population change. Most natural populations presumably demonstrate density-dependence in 1 or more life history parameters. As the subspecies' preferred habitat continues to decline and becomes more fragmented, we believe northern spotted owls may actually experience a decline in survival and fecundity rates at low population densities. As the northern spotted owl increasingly takes on a metapopulation structure (Levins 1970, Shaffer 1985) due to habitat fragmentation, the uncertainty of successful dispersal will become progressively more relevant to the subspecies' long-term population dynamics and likelihood of persistence.

## LITERATURE CITED

BARROWCLOUGH, G. F., AND S. L. COATS. 1985. The demography and population genetics of owls, with special reference to the conservation of the spotted owl *(Strix occidentalis).* Pages 74-85 in R. J. Gutierrez and A. B. Carey, eds. Ecology and management of the spotted owl in the Pacific Northwest. U.S. For. Serv. Gen. Tech. Rep. PNW-185.

BARROWS, C. W. 1985. Breeding success relative to fluctuations in diet for spotted owls in California. Pages 50-54 in R. J. Gutiérrez and A. B. Carey, eds. Ecology and management of the spotted owl in the Pacific Northwest. U.S. For. Serv. Gen. Tech. Rep. PNW-185.

CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York, N.Y. 234pp.

DAWSON, W. R., J. D. LIGON, J. R. MURPHY, J. P. MYERS, D. SIMBERLOFF, AND J, VERNER. 1986. Report of the advisory panel on the spotted owl. Audubon Conserv. Rep. 7. National Audubon Society, New York, N.Y.

DEEVEY, E. S., JR. 1947. Life tables for natural populations of animals. Q. Rev. Biol. 22:283-314.

DIXON, K. R., AND T. C. JUELSON. 1987. The political economy of the spotted owl. Ecology 68: 772-776.

FORSMAN, E. D., C. R. BRUCE, M. A. WALTER, AND E. C. MESLOW. 1987. A current assessment of the spotted owl population in Oregon. Murrelet 68:51-54.

———, E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the spotted owl in Oregon. Wildl. Mongr. 87:1-64.

FRANKLIN, A., J. P. WARD, AND R. J. GUTIÉRREZ. 1986. Population ecology of the northern spotted owl *(Strix occidentalis caurina)* in Northwestern California: preliminary results. Unpubl. rep. submitted to the Calif. Dep. Fish and Game, Sacramento. 38pp.

GUTIÉRREZ, R. J., AND A. B. CAREY. 1985. Ecology and management of the spotted owl in the Pacific Northwest. US. For. Serv. Gen. Tech. Rep. PNW-185. Portland, Oreg. 119pp.

HOOGENDYK, C. G., AND G. F. ESTABROOK. 1984. The consequences of earlier reproduction in declining populations. Math. Biosci. 71:217-235.

KEYFITZ, N. 1968. Introduction to the mathematics of populations. Addison- Wesley, Reading, Mass. 450pp.

LANDE, R. 1988. Demographic models of the northern spotted owl *(Strix occidentalis caurina).* Oecologia 75:601-607.

LEVINS, R. 1970. Extinction. Pages 77-107 *in* M. Gerstenhaber, ed. Some mathematical questions in biology. Vol. II. Am. Math. Soc. Providence, RI.

MARCOT, B. G., AND R. HOLTHAUSEN. 1987. Analyzing population viability of the spotted owl in the Pacific Northwest. Trans. North Am. Wildl. Nat. Resour. Conf. 52:333-347.

MERTZ, D. B. 1971. The mathematical demography of the California condor population. Am. Nat. 105:437-453.

MILLER, G. S., S. K. NELSON, AND W. C. WRIGHT. 1985. Two-year old female spotted owls breed successfully. West. Birds 16:93-94.

NICHOLS, J. D., G. L. HENSLER, AND P. W. SYKES, JR. 1980. Demography of the Everglade kite: implications for population management. Ecol. Modelling 9:215-232.

SALWASSER, H. 1987. Spotted owls: turning a battleground into a blueprint. Ecology 68:776-779.

SHAFFER, M. L. 1985. The metapopulation and species conservation: the special case of the northern spotted owl. Pages 86-99 *in* R. J. Gutiérrez and A. B. Carey, eds. Ecology and management of the spotted owl in the Pacific Northwest. U.S. For. Serv. Gen. Tech. Rep. PNW-185.

SIMBERLOFF, D. 1987. The spotted owl fracas: mixing academic, applied, and political ecology. Ecology 68:766-772.

U.S. FOREST SERVICE. 1986. Draft supplement to the environmental impact statement for an amendment to the Pacific Northwest regional guide. Two volumes. U.S. For. Serv., Portland, Oreg. 390pp.

———. 1988. Final supplement to the environmental impact statement for an amendment to the Pacific Northwest regional guide. Two volumes. U.S. For. Serv., Portland, Oreg. 897pp.

VERNER, J. 1978. California condors: status of the recovery effort. U.S. For. Serv. Gen. Tech. Rep. PSW-28. Berkeley, Calif. 30pp.

*Received 13 January 1989.*
*Accepted 26 September 1989.*
*Associate Editor: Crawford.*

## APPENDIX

Let N,(t) denote the number of female fledglings at time *t*. Then, in terms of the parameters introduced in Table 1,

$$\begin{aligned} N,(t) = {} & b_1 s_0 N_0(t-1) + b_2 s_0 s_1 N_0(t-2) \\ & + b_3 s_0 s\ _1 s N_0(t-3) \\ & + b_4 s_0 s_1 s^2 N_0(t-4) \\ & + \ldots + b_{w-1} s_0 s_1 s^{w-1-2} N_0 \\ & \cdot (t - w - 1), \end{aligned}$$

where $b_x = 0$ for $x < T$ and $b_x = b$ for $x \geq T$; *i.e.*,

$$N,(t) = b s_0 s_1 \sum_{x=T}^{w-1} s^{x-2} N_0(t \quad x). \tag{9}$$

If we assume a stable age distribution,

$$\begin{aligned} N,(t) &= \lambda N_0(t-1) = \lambda^2 N_0(t-2) \\ &= \lambda^3 N_0(t-3) = \ldots = \lambda^x N_0(t-x). \end{aligned}$$

Therefore,

$$N_0(t \quad x) = \lambda^{-x} N_0(t). \tag{10}$$

Substituting (10) into (9),

$$N_0(t) = bs_0s_1 \sum_{x=T}^{w-1} s^{x-2}\lambda^{-x}N_0(t)$$

or

$$\begin{aligned} 1 &= [(bs_0s_1)/s^2] \sum_{x=T}^{w-1} (s/\lambda)^x \\ &= [(bs_0s_1)/s^2] \sum_{x=0}^{w-1-T} (s/\lambda)^{x+T} \\ &= [(bs_0s_1)/s^2](s/\lambda)^T \sum_{x=0}^{w-1-T} (s/\lambda)^x. \qquad (11) \end{aligned}$$

Recall, in general

$$\sum_{k=0}^{n} x^k = (1 - x^{n+1})/(1 - x).$$

Incorporating this relationship into (11),

$$\begin{aligned} 1 = {} & [(bs_0s_1)/s^2](s/\lambda)^T \\ & \div [1 - (s/\lambda)^{(w-1-T)+1}] \\ & \div [1 - (s/\lambda)]. \qquad (12) \end{aligned}$$

Expressing (12) in terms of λ and setting it equal to 0,

$$\lambda^T - s\lambda^{T-1} - bs_0s_1s^{T-2}[1 - (s/\lambda)^{w-T}] = 0. \qquad (13)$$

Equation (13) is equivalent to equation (8). Letting $w$ be undefined and setting $T = 2$ gives equation (7). Letting $w = \infty$ and $T = 2$ in equation (13) gives equation *(3)*.