

Chapter 8

Estimates of Demographic Parameters and Rates of Population Change

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Detailed analyses of a species' life-history structure are essential to understand its population dynamics, provide insights to effective management, and also suggest directions for future research. In this chapter, we present analyses of available demographic data on the California spotted owl, using life-history and demographic information in an approach similar to that of Mertz (1971), Nichols et al. (1980), Noon and Biles (1990), and Thomas et al. (1990, appendix L). Our objectives were (1) to characterize the life-history structure of the California spotted owl, (2) to estimate values of the demographic parameters needed to compute rates of population change, (3) to test the sensitivity of the rate of population change to each of the demographic parameters, (4) to infer which parameters may be most influenced by management decisions, and (5) to suggest future research priorities, as indicated by the demographic analyses.

Methods

Demographic studies of spotted owls were conducted at five locations for periods ranging from 2 to 6 years—Lassen National Forest (NF), Eldorado NF, Sierra NF, Sequoia/Kings Canyon National Parks (NPs), and San Bernardino NF (table 8A). Density studies were conducted at four of those sites and at three additional sites (table 8B). The territorial behavior of spotted owls allows researchers to survey their populations by listening for and eliciting vocalizations. The usual procedure is to locate owls at night, then to follow up the next day with visual confirmation and, for demographic studies, to capture and uniquely

Table 8A—Summary information on the five demographic study areas.

Location	Approximate size (square miles)	Years of marking	Total individuals marked
Lassen National Forest	500	1990-91	130
Eldorado National Forest	136	1986-91	72
Sierra National Forest	160	1990-91	82
Sequoia/Kings Canyon National Parks	130	1988-91	62
San Bernardino National Forest	730	1987-91	367

Table 8B—Density estimates (owls per square mile) of spotted owls in California.

Study area	Size in square miles	Crude density ¹	Reference
Northern spotted owl			
Six Rivers National Forest	113	0.609	Franklin et al. 1990a
Simpson Timber Company	94	0.990	Diller 1989
California spotted owl			
Eldorado National Forest	137	0.259	Lutz 1992
Yosemite National Park	156	0.518	Roberts et al. 1988
Sierra National Forest	160	0.526	Verner et al. 1991
Sequoia/Kings Canyon National Parks	132	0.440	Roberts 1989; Verner et al. 1991
San Bernardino National Forest	207	0.347	LaHaye et al. in press
Mount San Jacinto	67	0.466	Gutiérrez and Pritchard 1990
Palomar Mountain	13	1.657	Gutiérrez and Pritchard 1990

¹Estimated number of owls/total study area. Much of the area included was not suitable habitat, and the proportion of unsuitable may have varied markedly from one study area to another.

color band each bird to allow individual identification in the field without recapture. The sex of adults was determined from their vocalizations, and reproductive status was determined by a protocol in which live mice were fed to the owls and they were then observed to determine whether they eventually carried a mouse to a nest site (Forsman 1983). Captured spotted owls can be placed into one of four age-classes: juvenile ($x < 1$), first-year subadults ($1 \leq x < 2$), second-year subadults ($2 \leq x < 3$), and adults ($x \geq 3$) based on plumage characteristics (Moen et al. 1991). Model structure, however, seldom has been based on all four age-classes because parameter estimates do not differ among classes, or because of insufficient data. Second-year subadults and adults are often collapsed into a single age-class (see below).

Parameter Estimation

Estimates of density (owls per square mile) assumed complete enumeration of all owls within a defined area. Usually when owls were counted, they were also color-banded to minimize the likelihood of double counting. Because territorial owls tended to vocalize regularly and to be spatially restricted within their home ranges, they were more likely to be detected than

nonterritorial owls (floaters). To the extent that many floaters occurred in an area, true density may have been underestimated.

Ideally, we would use precise and accurate estimates of three classes of parameters (s_x , b_x , and a) to compute the finite population growth rate, or λ :

1. s_x = probability of survival from age x to $x + 1$.

Previous demographic analyses of spotted owls generally assumed that s differed for at least three age-classes—juveniles (s_0), first-year subadults (s_1), and adults (s). The adult class, defined on the basis of age at first reproduction ($a = 2$ years), thus included second year subadults. The juvenile stage ends at the age of 1 year for spotted owls. In our analyses we did not partition juvenile survival rate into preand postdispersal probabilities, as done by Lande (1988). The subadult stage for the northern spotted owl covers the second year of life (age 1 to age 2) and is assumed to be an age interval in which the birds typically do not breed. The adult stage was thus anything older than 2 years (Noon and Biles 1990). Ideally, survival rates of these stages can be computed directly for each population modeled, using data from that population. Using program JOLLY (Pollock et al. 1990), we could estimate juvenile survival rate (s_0) only for the San Bernardino study area, because data were insufficient for the Eldorado and Sequoia study areas. Consequently, the San Bernardino value for s_0 was used as an approximation for the other two locations. It is similar to estimates of s_0 from several studies of northern spotted owls (Franklin 1992; USDI, FWS 1992), and λ is not especially sensitive to variations in s_0 . The true value of s_0 for these sites, however, is unknown.

Data were also insufficient to compute separate estimates of s_1 and s for the Eldorado and Sequoia/Kings Canyon study areas, and these two values were statistically indistinguishable for the San Bernardino study area. Therefore, in demographic analyses reported here, we used survival estimates for only two age-classes— s_0 (juvenile) and s ("nonjuvenile," combining subadult and adult age-classes). The probability of survival to age x was thus computed as $l_x = s_0 s^{x-1}$ (by definition $l_0 = 1.0$) (table 8C).

Table 8C—Spotted owl life history (age at first reproduction is 2 years).

x^1	l_x^2	b_x^3	$l_x b_x^4$
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	$s_0 s_1 s^{x-2} b$

¹ x denotes age in years.

² l_x denotes the probability that an individual aged 0 (a newly hatched bird) will survive to enter age class x .

³ b_x denotes the expected number of female fledglings produced by a surviving female aged x .

⁴ $l_x b_x$ denotes the net maternity function. At this time for the California spotted owl, $s_1 = s$.

2. b = fecundity, the expected number of female fledglings produced per female per year; b_x is the fecundity of a female of age x .

Fecundity values were calculated by halving the number of young fledged per territorial female, assuming an even sex ratio among fledglings. Because ages of females breeding, or attempting to breed, were seldom known, we assumed a constant reproductive rate for females of all ages: $b_x = b$ ($x \geq 2$ years).

3. a = age at first reproduction.

Apparently female spotted owls rarely breed when only 1 year old; most do not begin until at least 2 years old (Franklin 1992). Therefore, we used $a = 2$ years in demographic analyses reported here.

Estimates of age-specific survival rates from study areas with ≥ 4 years of data came from capture histories of marked birds using Program JOLLY (Pollock et al. 1990). Because some studies suggest that reproduction by spotted owls may be affected by radio transmitters attached with back-pack harnesses (Paton et al. 1991, Foster et al. 1992), estimates of survival and reproductive rates used in this demographic analysis were based solely on banded birds. To increase the precision of the estimates, we estimated the minimum number of parameters that adequately fit the data. When sufficient data were available, we tested for differences between adjacent age-classes to justify pooling of capture histories. In most cases, however, data were insufficient, so we pooled values for all individuals at least 1 year old to compute a survival rate for adults. Because the Lassen and Sierra studies have been underway for only 2 years, their data were insufficient for statistically reliable estimates of survival rates. For these sites, we simply estimated survival rates empirically, pooling data from all males and females at least 1 year old.

Analysis

Standard Lotka-Leslie methods (Leslie 1945, 1948; Lotka 1956) were applied to the estimates of vital rates (age-specific birth and death rates) to make inferences about rates of population change. In addition to assumptions identified above, we assumed (1) that reproduction was characteristic of a "birth-pulse" population—one with a single, well-defined, annual breeding period (Caughley 1977, p. 6), (2) a stable age (stage) distribution, and (3) no density dependence—a change in population density did not affect the values of the vital rates. This assumption was probably valid within the limits of the population densities modeled here. Preadult survival rate (l_2) was the probability of survival from fledging (age when leaving the nest) to age 2 and was given by the product of s_0 and s .

Estimates of all parameters needed for a completely age-specific Leslie matrix (Leslie 1945, 1948) were not available for any of the populations modeled. Often such data are limited for long-lived species, and estimates of all the age-specific parameters are impossible to attain or have large sampling variances because of small sample sizes. Repeated multiplication of imprecise estimates in fully age-specific models is likely to lead to uncontrolled error propagation (Dobson and Lyles 1989). The

Lefkovitch stage-projection matrix model (Lefkovitch 1965) is a useful approximation to an age-structured model. The dynamics of the two models are usually similar, but the Lefkovitch model is more tractable (Boyce 1987). A stage is simply a category (age-class) within which birth and death rates are assumed to be constant. Consequently, estimating the population dynamics of spotted owls with a stage matrix would yield misleading conclusions only if the birds manifest an age-related decline in reproductive rate (senescence) before about 15 years old (Noon and Biles 1990). Given the current high estimates of s , early senescence seemed unlikely.

Our application here of the Lefkovitch model uses only two stages juveniles (J) and nonjuveniles (NJ), as defined above. Time was expressed as an interbreeding interval of 1 year, and age at first reproduction was set at 2 years. Given that populations were based on census estimates corresponding to a period shortly after the breeding period, the Lefkovitch matrix had the following structure (details in Noon and Sauer 1992):

$$\begin{pmatrix} J_{t+1} \\ NJ_{t+1} \end{pmatrix} = \begin{pmatrix} 0 & sb \\ s_0 & s \end{pmatrix} \begin{pmatrix} J_t \\ NJ_t \end{pmatrix}$$

The location of s along the diagonal of the matrix reflects our assumption of constant adult survival and no senescence. The possibility of very old owls in the population had little effect on our estimate of λ assuming that adult survival was estimated, irrespective of adult age, from an unbiased sample of all adults in the population (Boyce 1987). We believe this assumption was valid for all populations modeled here.

The basic characteristic equation of the matrix is given by

$$\lambda^2 - s\lambda - s_0sb = 0. \quad (1)$$

The dominant, real-valued solution (λ_1) is an estimate of the annual, finite rate of change of the population. Vital rates suggest an increasing population if $\lambda > 1.0$, a stable population if $\lambda = 1.0$, and a declining population if $\lambda < 1.0$. We urge caution in using the computed estimates of λ to forecast future population sizes or to infer sizes of historical populations. Lambda estimated how the population was changing only during the period of study. Using the estimate of λ to project future population size would assume, unrealistically, that current estimates of vital rates are constant over time.

Hypothesis Tests of Lambda

We had estimates of fecundity and adult survival from three study areas and, in addition, an estimate of juvenile survival from one study. Based on these parameter estimates, and assuming s_0 to be equal at all locations, we computed λ from the Eldorado NF and Sequoia/Kings Canyon NPs in the Sierra Nevada Province, and from the San Bernardino NF in the Southern California Province. The sensitivities (partial derivatives) of λ with respect to individual life-history characteristics indicate which parameters most affect variation in population growth rate (Lande 1988, Noon and Biles 1990). In addition, sensitivi-

ties are needed to estimate the standard error of λ and to perform hypothesis tests. Sensitivities were computed by implicit differentiation of the characteristic equation (Goodman 1971, Lande 1988). Sensitivities for the two-stage Lefkovitch model are:

$$\begin{aligned} s_0: \partial\lambda/\partial s_0 &= sb/(2\lambda - s); \\ s: \partial\lambda/\partial s &= (\lambda + s_0b)/(2\lambda - s); \text{ and} \\ b: \partial\lambda/\partial b &= s_0s/(2\lambda - s). \end{aligned}$$

For all areas, change in population growth rate was most sensitive to variation in adult survival rate. It was much less sensitive to variation in first-year survival rate and fecundity; sensitivity to these two parameters was about equal.

Sensitivities of λ appear in the formula that approximates the sampling variance of the estimate of λ (Lande 1988, p. 602):

$$\sigma^2_{\lambda} = \sum (\partial\lambda/\partial p)^2 \sigma^2_p \quad (2)$$

where p represents each of the parameters and σ^2_p their sampling variance. The variances of juvenile and nonjuvenile rates were estimated according to the methods of Jolly (1965) and Seber (1965). Variance of annual fecundity was based on variance among females across the years of study, divided by the appropriate sample size. For the power analyses (see below), we assumed the survival probability to have a binomial sampling distribution.

Equation (2) is based only on sampling variance, but the data include both sampling and temporal variance. Also, equation (2) neglects possible covariances among the demographic parameters and fails to account for between-year changes in vital rates. Year-to-year changes, estimated by factoring out the temporal component of variation from the total variance estimates of the vital rates and λ cannot yet be estimated for the California data.

Components of the sampling variance of λ were computed by using equation (2), based on the sensitivities and estimates of the vital rates. The standard error of λ , computed as the square root of the variance, was used to construct a confidence interval around λ . For example, the 95 percent confidence interval on λ was computed as: $\lambda \pm 1.96 \sigma_{\lambda}$. An estimate of λ and its standard error also allowed tests of hypotheses. Of most interest, relative to concern for the species' persistence, was whether λ was significantly < 1.0 . We tested the null hypothesis: $H_0: \lambda \geq 1$, versus the alternative hypothesis: $H_A: \lambda < 1$. The appropriate test statistics followed a Z-distribution, given by: $Z = |(\lambda - 1)/\sigma_{\lambda}|$. Tests were one-tailed with a specified probability of a type-I error = 0.05 (only a 5 percent chance of concluding a decline when none actually occurred).

Power of the Tests on Lambda

When a test fails to reject the null hypothesis (H_0), it is important to estimate the power of the test, which is the probability that H_0 will be rejected when a particular alternative hypothesis (H_A) is true. Failure to reject a false H_0 (that is, the popula-

tion is in decline) is known to statisticians as a type-II error. To estimate the power of the test when H_0 was not rejected, we used a method outlined by Taylor and Gerrodette (in press). The method involves estimating two sampling distributions, one based on a specified value of λ for H_A , the other on the value of λ for H_0 ($\lambda = 1.0$). Under H_A we specified a $\lambda = 0.95$, that is, a 5 percent annual rate of population decline. This rate of decline would result in a loss of >40 percent of the population over a decade. If the two distributions are completely disjoint, the power of the test is 1.0. If the two distributions are coincident, the power is 0. Power increases as the difference between the specified value of λ and the hypothesized λ value (for example, $\lambda = 1.0$) increases, or as the variance of the distributions decreases. The probability of a type-II error (β) is estimated as a function of the overlap between these two distributions. The power of the test is then $1 - \beta$. To estimate power, we generated simulated distributions of λ under each hypothesis (H_A and H_0) based on 16,000 randomizations.

Results

Density Estimates

Estimates of crude density (number of owls/total acreage of study area) were available from seven areas within the range of the California spotted owl, four in the Sierra Nevada Province

and three in the Southern California Province (table 8B). Densities varied from a high of 1.657 owls per square mile on Palomar Mountain to a low of 0.259 owls per square mile on the Eldorado NF. Overall, estimates of crude density for the California spotted owl tended to be slightly lower than those for the northern spotted owl (table 8B; see also Bart and Forsman in press).

Comparison of Demographic Study Areas

Demographic studies were done at five locations widely spaced over the range of the California spotted owl. Two studies have collected data for only 2 years, and the longest study has been in place for only 6 years (table 8D). All studies, however, are planned to continue for 3-5 more years. Some significant highlights from a comparison of the demographic attributes in the five areas (table 8D) include extensive among- and within-site variation in the proportion of nesting pairs and mean fecundity, and pronounced among-site variation in pair turnover rates (proportion of banded adults and subadults that are replaced on their territory by another bird) and nonjuvenile survival rates. Components that contributed to the observed variance in annual fecundity at a given site arose from variation in both the proportion of females nesting and in their productivity. Among-site variation in survival rates of nonjuvenile owls was particularly relevant, as even small changes in survivorship of adult females greatly affect rates of population change (Noon and Biles 1990).

Table 8D-Summary of demographic attributes of California spotted owls.

Attributes	Lassen National Forest	Eldorado National Forest	Sierra National Forest	San Bernardino National Forest	Sequoia/Kings Canyon National Parks
Years of banding	2	6	2	5	4
Mean proportion of pairs nesting ¹	0.52	0.31	0.65	0.59	0.51
Range of proportion of pairs nesting	0.38-0.70	0.0-1.0	0.63-0.67	0.50-0.76	0.18-0.80
Mean total fecundity ^{1,2}	0.48	0.94	1.02	0.59	0.53
Range of total fecundity ^{1,2}	0.36-0.64	0.37-1.50	0.75-1.22	0.35-0.80	0.08-1.50
Mean subadult turnover rate	0.57	0.14 ³	0.75	0.28 ³	--
Mean adult turnover rate	0.21	0.14 ³	0.19	0.28 ³	0.24
Mean empirical survival rate of subadult females	0.33	0.73	0.50	0.72 ^{2,3}	0.80 ^{2,3}
Mean empirical survival rate of adult females	0.84	0.73	0.74	0.72 ^{2,3}	0.80 ^{2,3}
Mean nonjuvenile survival	*	0.83 ^{2,3}	*	0.75 ^{2,3}	0.89 ^{2,3}

¹ Weighted by yearly sample size.

² Males and females combined.

³ Subadult and adult age-classes combined.

* Inadequate sample.

Hypothesis Tests on Lambda (λ)

Eldorado National Forest

This study has been underway for 6 years, with estimates of nonjuvenile survival rates based on capture histories of 72 birds >1 year old, and fecundity estimates based on reproductive performances of 66 territorial females (table 8E). The estimate of λ (equation 1) was 0.947, suggesting about a 5 percent annual rate of population decline during the period of study (1986-91). This value was not significantly <1.0 ($\alpha = 0.05$, $P = 0.1271$), so the statistical test did not reject the null hypothesis that the population is not declining ($H_0: \lambda \geq 1.0$). The test, however, had a power of only 0.30, setting the probability of a type-II error at about 0.70. The low power of the test was a result of a relatively small number of marked birds, and the large standard errors of parameter estimates (table 8E).

Sequoia/Kings Canyon National Parks

This study has been underway for 4 years, with estimates of nonjuvenile survival rates based on capture histories of 45 birds >1 year old, and fecundity estimates from the reproductive performances of 45 territorial females (table 8F). The estimate of λ was 0.969, suggesting about a 3 percent annual rate of population decline during the period of study (1988-91). As in the Eldorado study, the statistical test ($\alpha = 0.05$, $P = 0.2709$) failed to reject the null hypothesis ($H_0: \lambda \geq 1.0$). In this case, the test had a power of only 0.30, with an 70 percent probability of failing to detect a real decline of this magnitude. The very low power of the test was a consequence of the small number of marked birds and, to a lesser extent, the standard errors of parameter estimates (table 8F).

San Bernardino National Forest

This study, underway for 5 years, was unique among demographic studies of spotted owls in sampling, almost in its entirety, an insular population (LaHaye et al. 1992). It provides an estimate of juvenile survival rate of 0.296, based on capture histories of 130 owls banded shortly after fledging (table 8G). The estimate of nonjuvenile survival rate is based on capture histories of 184 birds > 1 year old, and the fecundity estimate comes from reproductive histories of 328 territorial females. Lambda was estimated at 0.827, suggesting about a 17 percent annual rate of population decline during the period of study (1987-91). The statistical test ($\alpha = 0.05$, $P \leq 0.0001$) strongly rejected the null hypothesis ($H_0: \lambda \geq 1.0$) of a nondeclining population.

Table 8E--Estimates of the annual finite rate of population change (λ) for the California spotted owl in the Eldorado National Forest, with test statistics and P value for the test of the null hypothesis that $\lambda \geq 1.0$ vs. $\lambda < 1.0$.

Parameter	Estimate	Sample size	Standard error	P
Juvenile survival (s_0) ¹	0.296	130	0.055	--
Nonjuvenile survival (s) ²	0.826	72	0.039	--
Fecundity (b) ³	0.470	66	0.054	--
Population change (λ)	0.947	--	0.046	0.1271

¹ LaHaye (pers. comm.).

² Combined estimate for males and females, adults and subadults.

³ Number of female young per territorial female.

Table 8F--Estimates of the annual finite rate of population change (λ) for the California spotted owl in Sequoia/Kings Canyon National Parks, with test statistics and P value for the test of the null hypothesis that $\lambda \geq 1.0$ vs. $\lambda < 1.0$.

Parameter	Estimate	Sample size	Standard error	P
Juvenile survival (s_0) ¹	0.296	130	0.055	--
Nonjuvenile survival (s) ²	0.895	45	0.047	--
Fecundity (b) ³	0.267	45	0.059	--
Population change (λ)	0.969	--	0.051	0.2709

¹ LaHaye (pers. comm.).

² Combined estimate for males and females, adults and subadults.

³ Number of female young per territorial female.

Table 8G--Estimates of the annual finite rate of population change (λ) for the California spotted owl in the San Bernardino National Forest, with test statistics and P value for the test of the null hypothesis that $\lambda \geq 1.0$ vs. $\lambda < 1.0$.

Parameter	Estimate	Sample size	Standard error	P
Juvenile survival (s_0)	0.296	130	0.055	--
Nonjuvenile survival (s) ¹	0.747	184	0.024	--
Fecundity (b) ²	0.297	328	0.087	--
Population change (λ)	0.827	--	0.035	0.0000

¹ Combined estimate for males and females, adults and subadults.

² Number of female young per territorial female.

Discussion

Owl Densities

Because we were able to estimate only crude density for most study areas at this time, interpretations of results are tentative. This is true because crude density does not adjust for the amount of unsuitable habitat in a study area. If one area has a higher proportion of unsuitable habitat than another, but the amounts are unknown, estimates of crude density for the two areas are not comparable. With this caution in mind, density estimates at least suggest some questions that need to be resolved.

The Eldorado study area is mostly forested. The apparent low density of spotted owls there may result from the fact that much of the area is in classic, alternate-section, checkerboard ownership between NF and private timberlands that have been intensively managed for timber production. For example, Bias and Gutiérrez (1992) reported that most roost sites and all nest sites in the Eldorado study area were on public lands. The private lands have not been generally clearcut, however, so owls probably forage in much of the private ownership.

Various hypotheses can be advanced to account for the apparent high density of owls on Palomar Mountain: (1) Crude density may have been overestimated. We know from other studies, for example, that density estimates of spotted owls are affected by the size of the study area, with positively biased estimates in study areas <40 square miles (Franklin et al. 1990b). Based on a regression equation and a proportional adjustment from the asymptotic density in Franklin et al. (1990b, fig. 4), the density estimate for Palomar Mountain should be adjusted downward to about 1.1 owls per square mile. But this is still higher than estimates for all other areas. (2) An extensive fire destroyed much owl habitat on Palomar Mountain in 1987, 1 year before the density survey (Gutiérrez and Pritchard 1990). Several previously occupied owl sites were lost in the fire and an unknown number of additional birds may have been displaced. As a result, densities may have increased temporarily from packing by displaced birds into remaining habitat. (3) Home-range sizes of spotted owls in much of southern California are considerably smaller than they are in conifer forests of the Sierra Nevada or in the San Bernardino Mountains (Chapter 6). Over much of the owls' distribution in southern California, however, suitable habitat tends to be concentrated in small, relatively isolated ravines and canyons; most of the intervening habitat is unsuitable. The crude density of owls there could be similar to that where home ranges are larger but where suitable habitat is more continuous. This is the case, for example, between the foothill woodland and conifer forest segments of the Sierra NF study area (Verner et al. 1991). If suitable habitat is more continuously distributed on Palomar Mountain, but owl home ranges there are relatively small (for example, because the owls specialize on woodrats as a prey source), the observed high

density at Palomar could be a real difference from all other density studies of the California spotted owl.

Sources of Bias in Estimates of Lambda

Juvenile Survival

"Estimates of juvenile survival rate can be biased low if some juveniles leave the study area, survive a full year, and never return. To the extent that these three events occur, juvenile survival rate is underestimated and the estimates of λ are too low" (USDI, FWS 1992, appendix C). If emigrating juveniles do not survive their first year, or if they survive but are subsequently detected, then no bias occurs. To provide a statistically reliable estimate, we estimated s_0 using the maximum-likelihood procedure from Program JOLLY (Pollock et al. 1990) for the San Bernardino study (LaHaye pers. comm.). We believe the estimate from that study is reliable. First, it was based on a sample of 130 owls banded as fledglings. Second, the study area covers almost the entire San Bernardino Mountain Range, and the population was largely isolated from other owl populations (LaHaye et al., 1992). Consequently, the area covered by dispersing juveniles was more restricted and the entire area was surveyed each year. These factors greatly increased the likelihood of reobserving banded juveniles. Finally, the estimate of s_0 (0.296) is nearly the same as that for the five northern spotted owl study areas ($s_0 = 0.311$) (USDI, FWS 1992) based on longer-term studies.

Nonjuvenile Survival

As for estimates of juvenile survival, nonjuvenile survival rate would be underestimated if many banded birds permanently left a study area and survived at least 1 year. Thomas et al. (1990, appendix L) investigated this potential bias by computing the number of emigrations per bird-year in studies of radio-tagged, adult spotted owls. A bird-year was defined as one adult bird tracked for one calendar year. From radio-tracking studies near Roseburg, Oregon, only one permanent emigration occurred in >100 bird-years. Similarly, in northwestern California, one permanent emigration occurred in 60 bird-years. These findings suggest that estimates of adult survival rate for the northern spotted owl were essentially unaffected by permanent emigration from study areas. Although we lack comparable data from the California spotted owl, we have no reason to believe that permanent emigration by adults would be more common for that subspecies.

Senescence

The effects of age-related decline in reproductive potential of spotted owls have been explored by Noon and Biles (1990). Failure to account for senescent declines could result in a significant overestimate of λ . Conversely, incorporating senescence when it does not occur can result in significant underestimates of λ . We do not know the life span of spotted owls or whether fecundity remains constant through life. The high, observed

estimates of s would not likely arise, however, if spotted owls lived <15 years. If reproductive senescence occurs at earlier ages, the decline in λ would be increasingly pronounced.

Researchers often assume that birds do not experience senescent declines in fecundity and survival rates (Deevey 1947). An estimate of mean generation length (Caughley 1977, p. 124) without reproductive senescence and assuming $s = 0.92$, however, suggests the unlikely average age of mothers at the birth-pulse = 53 years. Given the magnitude of this estimate, we believe that senescent declines must occur in reproduction and/or adult survival rate. Invoking reproductive senescence at ages of 16 or 26 years yields more reasonable estimates of generation length ($\cong 8$ and $\cong 12$ years, respectively), but it lowers the estimates of λ . Reproductive senescence is not likely to occur much before 16 years; rather, we would expect strong natural selection against the evolution of early senescence in a species with life-history characteristics like the spotted owl's.

Stable Stage Distribution

Calculation of λ from equation (1) assumes a stable stage distribution. If the vital rates are constant, the convergence to a stable distribution is asymptotically exponential (Caswell 1989, p. 70). If the vital rates vary stochastically, or are time-dependent, then the assumption of a stable stage distribution is invalid. At this time we have insufficient data to estimate the degree of stochasticity in the vital rates for the spotted owl, or to determine if the year-to-year differences among projection matrices represent time-dependency or simply sampling variation. In the absence of this information, we assumed mean values for the vital rates. We can, however, examine the likelihood of introducing a bias into the estimate of λ by assuming constant vital rates, and thus a stable stage distribution.

If the growth of a given population is time-dependent, then the growth of that population is described by the product of a sequence of projection matrices. In the special case of independent matrices (that is, independent environments), population growth rate is equivalent to the dominant eigenvalue (λ) of the projection matrix based on the mean values of the vital rates (Tuljapurkar 1982). Unfortunately, under stochastic conditions, the growth rate of the average population may be a misleading indicator of population stability. This occurs because the distribution of population sizes from stochastic projection matrices is approximately lognormal (Tuljapurkar and Orzack 1980). A property of lognormal distributions is that the modal or most likely population size will always be smaller than that based on mean values of the vital rates (Gerrodette et al. 1985). Under conditions of stochasticity, the realized trajectory of any single population is simply one of an infinite number of possible outcomes. Thus, the actual growth rate of any single population with stochastic vital rates is always less than or equal to the growth rate estimated from mean values of the projection matrix (Cohen et al. 1983).

The likely consequence of our assumption of a time-invariant, mean projection matrix, therefore, was to overestimate the growth rate (λ) experienced by any given population, unless the environmental variability was negligible. In general, as the environmental variability becomes small, the average growth rate of

a stochastic population approaches (from below) that described by the dominant eigenvalue of the mean projection matrix (Caswell 1989, p. 222). There are some exceptions to this general rule. For example, in nonstochastic, periodic environments, Tuljapurkar (1989) found that variation can increase population growth rate if the period of the environmental oscillation is roughly equivalent to the generation length of the organism being modeled. We emphasize that this is an unlikely outcome for any climatically induced variation in the vital rates of a given species (see, for example, figs. 8A and 8B). The general observation that, in stochastic environments, a probability of extinction exists even when the mean growth rate, λ , is >1.0 (Lande and Orzack 1988) should temper any overly optimistic interpretation of λ values.

Tests on Lambda

Although the null hypothesis of a stable population was not rejected for either the Eldorado or the Sequoia/Kings Canyon study area, we could not correctly conclude that these populations were stable during the periods of study. The power of our statistical tests was disturbingly low for both areas, and there was a high likelihood of failing to detect real annual declines of 5 percent or less. The greater uncertainty that accompanied a smaller sample of banded birds and a shorter time series of capture histories is clearly illustrated by comparison with the northern spotted owl. The estimate of λ for the northern spotted owl on lands managed by the Bureau of Land Management near Roseburg, Oregon, was nearly identical to that for the Eldorado study area ($\lambda = 0.941$ vs 0.947 , respectively). In the Roseburg study, however, the null hypothesis of a stable population was strongly rejected (probability of a type-I error <0.0005-USDI, FWS 1992, appendix C). In contrast to the Eldorado study, the Roseburg study was based on a larger sample of birds (589 vs 72) and a longer time series (7 years vs 6 years).

Given the high likelihood of accepting false null hypotheses of stable populations in the Sierra Nevada studies, the correct inference to draw from the statistical tests is that, at this time, we are uncertain about true trends of the Eldorado and Sequoia/Kings Canyon populations during the periods of study.

If the California spotted owl has experienced gradual declines in habitat quality in the Sierra Nevada, these effects may be subtle and, therefore, more difficult to detect than those experienced by the northern spotted owl. With the exception of the mid-1980s, very little clearcut logging was practiced in the Sierra Nevada. Even the heavy cutting that occurred on private timberlands near mills and railroad lines usually left some large trees standing that could eventually serve as nest sites in regenerating stands. In contrast, within the range of the northern spotted owl, most logging has been by clearcutting, and most of the decline in suitable owl habitat has been compressed into the interval since about 1950 (Murphy and Noon 1992). As a result, the landscape pattern for northern spotted owls is coarse-grained, with clear distinctions between suitable and unsuitable habitat. Selective logging of the largest trees from the most productive sites in the Sierra Nevada has resulted in significant changes in diameter distributions and produced a more fine-grained landscape pattern for the California spotted owl (Chapter 11).

The effects of changes in forest structure and landscape pattern on owl demographics are unknown. If changes in habitat quality accompany selective logging methods, however, it seems obvious that they would produce less pronounced declines in the vital rates than clearcut logging. As a result, only very long-term studies involving a large number of banded birds would be able to detect such effects.

We do not know the reason(s) for the significant decline of about 17 percent in numbers of territorial owls in the San Bernardino study area from 1987 to 1991. Much logging occurred there in the 1960s, but we doubt whether that disturbance can explain the current decline. A more plausible hypothesis involves either direct or indirect effects of the drought in southern California. For example, precipitation from 1987 through 1990 averaged about 60 percent below normal at a weather station at the western end of Big Bear Lake, in the San Bernardino Mountains (fig. 8A) and 67 percent of normal at the east end (fig. 8B). Rainfall in 1991 was above normal at both of these sites, but almost all of it occurred in March, after the owls would have initiated breeding. One working hypothesis is that dusky-footed woodrats, the primary prey of the owls in the San Bernardino Mountains (Chapter 4; LaHaye pers. comm.), have experienced marked population declines as a result of the drought. For example, Linsdale and Tevis (1956) and Spevak (1983) reported depressed woodrat populations in California during droughts, although Kelly (1989) failed to find a decline in woodrats during a drought at Hastings Natural History Reservation in Monterey County in the late 1980s.

If the recent drought has contributed in some way to the decline of the owl population in the San Bernardino Mountains, it suggests that the population is subject to high levels of environmentally induced variation in its demographic parameters. As the population declines, individuals may be lost from marginal habitats, where survival and reproduction are possible only

during "good" times (for example, see O'Connor 1986). Individuals that survive, and even reproduce, during the decline may be those that occupy better, more stable habitats, as where more mesic conditions prevail (for example, riparian areas). Such refuges would be particularly important to the species' long-term persistence, and any destabilization of them-by logging, water diversion, depression in ground water levels, or excessive development of recreational activities-could pose a significant threat to the species' survival.

Future Research Needs

Based on a three-stage model, estimates of parameter sensitivities from all three study areas suggest that λ values were most sensitive to estimates of adult survival rate (s), distantly followed by first- and second-year survival rates (s_0, s_1) and fecundity (b) (fig. 8C). The sensitivity coefficient associated with age at first reproduction was small (Noon and Biles 1990). The much steeper slope for adult (≥ 2 years) survival rate demonstrates the importance of precise estimates of adult survival to produce precise estimates of λ . Introducing senescence at age 16 increases the slopes for fecundity and prereproductive survival rates, but s is still most important (fig. 8D). For a fixed recapture probability, more precise estimates of s can be attained only by having a larger sample of banded birds.

A comparison of figures 8C and 8D indicates that it may be important to know whether spotted owls exhibit senescent decline in fecundity or survival. Noon and Biles (1990) showed that estimates of population growth rate (λ) were strongly influenced by the age at which reproductive senescence was assumed. Without detailed information on reproductive histories of marked individuals, insights into senescent declines in the owl's vital rates cannot be detected.

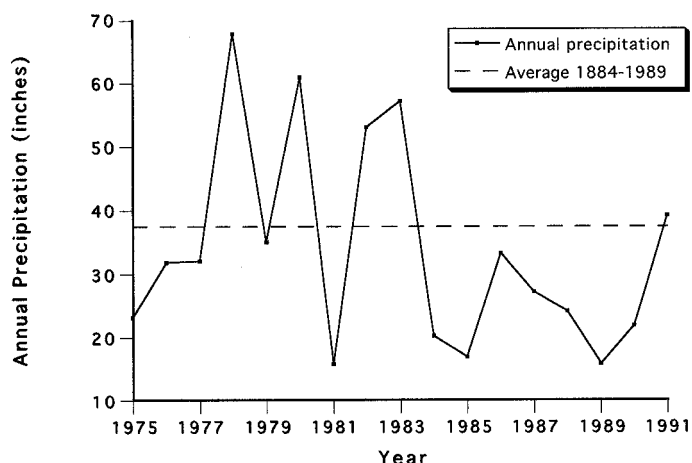


Figure 8A-Annual precipitation (inches) from 1975-91 as measured at the western end of Big Bear Valley, in the San Bernardino Mountains (Lundy pers. comm.).

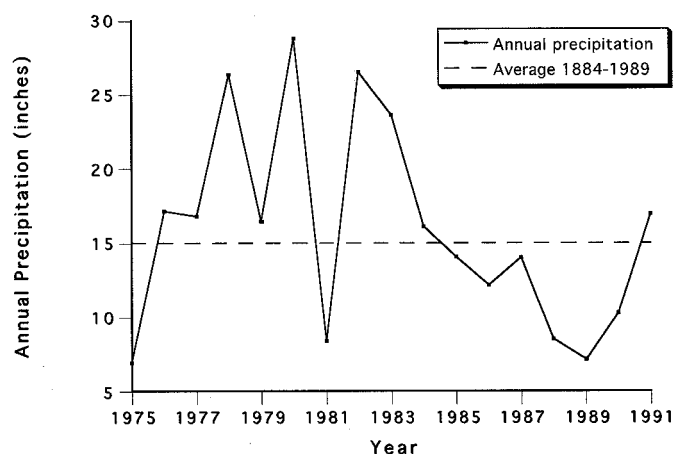


Figure 8B-Annual precipitation (inches) from 1975-91 as measured at Big Bear City, in the San Bernardino Mountains, 7 miles east of the weather station for results reported in figure 8A (Lundy pers. comm.).

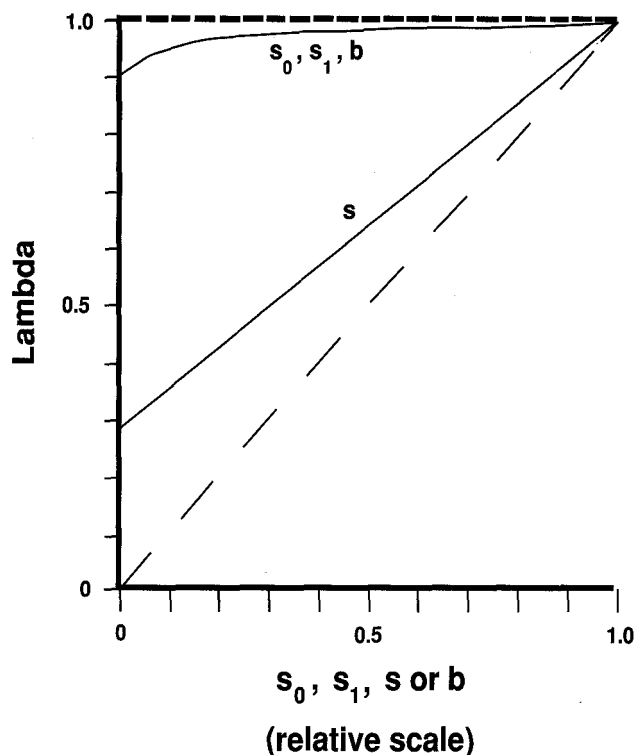


Figure 8C-Population growth rate (lambda) for a stage-structured model of the California spotted owl. The figure shows the effects on lambda (λ) of a proportional decline in a specific demographic rate, with all others held constant. Empirical estimates of mean survival rate have been scaled by $1/\lambda$ to yield an initial starting point of $\lambda = 1.0$ on the abscissa.

Two sources of information are relevant to a species' rate of population change (λ). One is the sensitivity of λ to variation in the vital rates as reflected in coefficients of parameter sensitivity. The other concerns those life-history attributes that show the most natural variation. Variation in population growth rate (λ) may be more closely associated with attributes that are naturally more variable than with attributes that are less variable but to which growth rate is mathematically more sensitive. We cannot yet estimate the magnitude of natural variation in demographic parameters of California spotted owls. Estimates that confound sampling error and true annual variation from the five demographic study areas (table 8D), however, indicate that fecundity exhibits the greatest annual variation. Fecundity combines two important components: productivity per breeding female and the proportion of females ≥ 2 years of age that breed. The latter is particularly variable (table 8D).

Factors contributing to the low and variable reproductive rates of spotted owls also need investigation. We do not know whether the extensive annual variation in reproductive success is due to variable resource levels (prey base), variable climatic conditions, or some combination. Nor do we know whether reproductive rates or adult survival rates can be increased by direct management for prey populations; this is also an important research question.

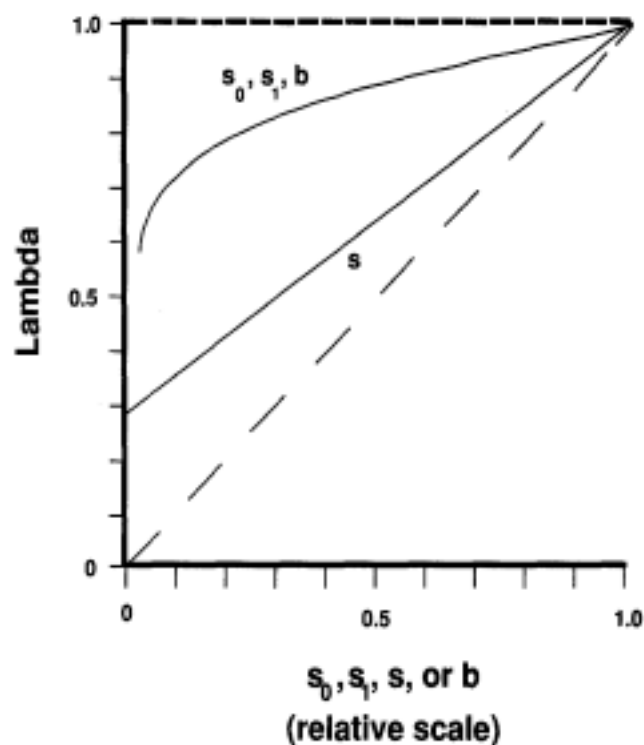


Figure 8D-Population growth rate (lambda) for an age-structured model of the California spotted owl. The figure shows the effects on lambda (λ) of a proportional decline in a specific demographic rate, with all others held constant. Empirical estimates of mean survival rate have been scaled by $1/\lambda$ to yield an initial starting point of $\lambda = 1.0$ on the abscissa.

Finally, as suitable spotted owl habitat becomes more fragmented, it will become increasingly important to estimate dispersal capabilities of California spotted owls (Chapter 4) 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

Implications of the demographic results for management involve decisions that may differentially affect adult and pre-adult 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 λ to variation in adult than preadult survival rates indicates strong natural selection to maintain low adult mortality rates. Further, the low fecundity rate suggests that recruitment may always have been variable. In spite of this, high adult survivorship has allowed the

spotted owl to persist through long periods of low reproductive output. A consequence of this trade-off is of great concern when considering management for spotted owls. Namely, low fecundity precludes rapid recovery from a population decline. Any management action that lowers adult survival rate, particularly when coupled with a reduction in population size, markedly increases the likelihood of local extinction.

Although λ is relatively insensitive to changes in s_0 and b (figs. 8C and 8D), we cannot infer that these attributes are unimportant when developing management plans. Adult survival rate is relatively high and may not be amenable to further increases. Assuming no reduction in adult survival rate, increasing first year survival or fecundity by direct management activity may be the most feasible way to increase the growth rate of spotted owl populations. For example, certain silvicultural prescriptions may increase the availability of the owl's preferred prey and somewhat ameliorate the otherwise negative effects of logging. But these prescriptions are still unknown and untested.

Given the spotted owl's life history structure, an evaluation of management decisions in terms of persistence likelihoods are possible only when viewed over the long-term (50-100 years). With a high adult survival rate and an apparently long life span, the Spotted Owl may be able to persist over the short-term even in the face of extensive reduction in the amount of its suitable habitat. Thus, significant time lags may occur in responses of spotted owl populations to declining environmental carrying capacity. By themselves, therefore, short-term survey results, even those including observations of breeding owls, are insufficient to allow inferences about population viability.

Rapid rates of population decline in either deterministic or stochastic analyses are not surprising when the finite rate of increase (λ) is <1.0 . Leslie-Lefkovich projection matrices and life table models yield simple exponential models of population growth or decline (see discussion in Noon and Sauer, 1992). For this reason, it is inappropriate to use estimates of λ to project future population size without strict qualifications. Most natural populations presumably demonstrate density-dependence in one or more life history parameters. Many examples exist of bird species shown to exhibit density-dependent effects on vital rates. These include the gray partridge (Blank et al. 1967), the mallard (Hill 1984), the tawny owl (Southern 1970), and the European sparrowhawk (Newton 1988). No empirical data for spotted owls presently indicate a relation between population density and values of vital rates. Nevertheless, on the basis of a simple nonspatial model, Boyce (1987) argued that spotted owl populations at low densities should exhibit density-dependent increases in survival and reproduction that could stabilize the populations. Very different inferences are drawn, however, from models that include the additional reality of spatial structure, such as the

uncertainties of successful dispersal and mate finding in spatially structured populations. Lande (1987) and Lamberson et al. (in press) found that owls at low population densities may experience negative effects of low densities that further depress survival and fecundity. In fact, their models indicate that if population densities are very low, or the amount of suitable habitat is greatly reduced, a threshold point exists beyond which the owl populations collapse to extinction.

We believe there are implications for the management of California spotted owls. Future management activities, for example, must not increase the mean nearest-neighbor distances among suitable pair sites. Subtle factors that uniformly decrease habitat quality, or increase fragmentation, will act to reduce population density and incrementally increase the uncertainties associated with successful dispersal and mate-finding. Habitat-induced changes in vital rates, such as declines in first-year survival and in the proportion of breeding females, will lead to declines in population growth rate. If suitable habitat is allowed to decline and become fragmented, as for the northern spotted owl, the uncertainty of successful dispersal will become progressively more relevant to the subspecies' long-term population dynamics and likelihood of persistence. Should this pattern ensue for the California spotted owl, then the most effective way to assure its long-term persistence may be to create a connected network of habitat conservation areas (HCAs) as was proposed for the northern subspecies (Thomas et al. 1990). Large HCAs provide stable areas of high population density that promote a balance between pair turnover and colonization of pair sites, either through internal recruitment of dispersing juveniles or the emigration of owls from neighboring HCAs. Implementing such a strategy, however, would risk an increasing threat of stand-destroying fires in areas maintained primarily for the owls.

Finally, it is important to recognize that rates of population change (λ) and the values of the owl's vital rates are ultimately determined by habitat quality at both local and landscape scales. For example, habitat quality at the scale of the home range may determine the survival and birth rates for an individual pair of owls. At a larger scale, the number of suitable pair sites and their spatial arrangement may determine the persistence of local populations. And, at a regional scale, providing habitat for a large number of local populations distributed widely across the landscape will increase overall persistence of the subspecies by decreasing the likelihood of populations simultaneously experiencing negative environmental effects. Thus, to ensure stable owl populations in the Sierra Nevada and Southern California Provinces will require specific management prescriptions, implemented at local to regional scales, to retain the amount and spatial pattern of habitat that will provide for a long-term balance between birth and death rates.

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