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## DEMOGRAPHY OF THE CALIFORNIA SPOTTED OWL IN NORTHEASTERN CALIFORNIA

JENNIFER A. BLAKESLEY<sup>1</sup>, BARRY R. NOON AND DANIEL W. H. SHAW<sup>2</sup>

*Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523*

**Abstract.** We estimated age-specific survival ( $\phi$ ), fecundity ( $b$ ), and the finite rate of population change ( $\lambda$ ) of California Spotted Owls (*Strix occidentalis occidentalis*) over a 10-year period (1990–1999). Two hundred nineteen juvenile and 200 subadult or adult owls were banded at 90 sites, with a combined total of 1080 captures. Least-squares mean estimates ( $\pm$  SE) of fecundity (# female fledglings per territorial female) over all years were  $0.065 \pm 0.066$  for subadults ( $n = 33$ ) and  $0.291 \pm 0.065$  for adults ( $n = 381$ ). Estimated annual apparent survival probability was  $0.333 \pm 0.055$  for juveniles and  $0.827 \pm 0.015$  for subadults and adults combined. Using these estimates to construct a four-stage projection matrix, the finite rate of population change,  $\hat{\lambda}$ , was  $0.910 \pm 0.025$ . This value of  $\lambda$  suggests an annual rate of decline in the territorial population of 9% per year over the period of study. Elasticity analyses showed  $\lambda$  to be most sensitive to variation in adult female survival. However, the standard deviation of  $\lambda$  was dominated by year-to-year variation in fecundity. Conservation guidelines should focus on management activities that increase the value of adult survival while minimizing its temporal variability.

**Key words:** *California Spotted Owl, demography, fecundity, Strix occidentalis occidentalis, survival.*

### Demografía de *Strix occidentalis occidentalis* en el Noreste de California

**Resumen.** Estimamos la supervivencia ( $\phi$ ) y fecundidad ( $b$ ) específicas por edad y la tasa discreta de crecimiento poblacional ( $\lambda$ ) de *Strix occidentalis occidentalis* en un periodo de 10 años (1990–1999). Marcamos 219 lechuzas jóvenes y 200 adultas y subadultas en 90 localidades, para un total combinado de 1080 capturas. La estimación de la media ( $\pm$  ES) de fecundidad (número de pichones hembras por hembra territorial) fue  $0.065 \pm 0.066$  en subadultos ( $n = 33$ ) y  $0.291 \pm 0.065$  en adultos ( $n = 381$ ). La probabilidad estimada de supervivencia aparente fue  $0.333 \pm 0.055$  para los jóvenes y  $0.827 \pm 0.015$  para subadultos y adultos combinados. Usando tales estimaciones para construir una matriz de proyección de cuatro etapas, se obtiene una tasa discreta de cambio en la población,  $\hat{\lambda}$ , de  $0.910 \pm 0.025$ . Este valor de  $\lambda$  indica una tasa anual decreciente del 9% en la población territorial durante el periodo estudiado. Los análisis de elasticidad indicaron que  $\lambda$  es más susceptible a la variación en la supervivencia de las hembras adultas. Sin embargo, la desviación medio de  $\lambda$  fue dominada por la variación interanual en la fecundidad. Las reglas de conservación deben concentrarse en actividades de manejo dirigidas a aumentar el nivel de supervivencia de hembras adultas y al mismo tiempo minimizar su variabilidad en el tiempo.

## INTRODUCTION

The California Spotted Owl (*Strix occidentalis occidentalis*) inhabits coniferous and hardwood

forests of the southern Cascades, western Sierra Nevada, and central and southern coastal mountains of California (Verner et al. 1992). Similar to the Northern Spotted Owl (*Strix occidentalis caurina*), the distribution of the California subspecies is associated with large, old trees and closed-canopy forests at both the nest and landscape scales (Gutiérrez et al. 1992, Hunsaker et al. 2001).

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<sup>1</sup> E-mail: jab@cnr.colostate.edu

<sup>2</sup> Present address: Forestry Sciences Laboratory, 2081 E. Sierra Ave., Fresno, CA 93710.

Management of national forests for the California Spotted Owl has been a major concern of the USDA Forest Service during the past decade (USDA 2001). In addition, a petition to list the subspecies under the Endangered Species Act has led the U.S. Fish and Wildlife Service to initiate a status review to determine if listing is warranted. Therefore, the results of our study are relevant to the pending listing decision and the development of a long-term management plan for public lands within the range of the California Spotted Owl.

Here we summarize demographic data from a 10-year capture-recapture study of California Spotted Owls in and around the Lassen National Forest in northeastern California. Our specific goals were to estimate age- and sex-specific survival, reproductive rates (nesting and nest success rates, productivity, and fecundity), and the annual finite rate of population change,  $\lambda$ , over the study interval for resident, territorial females. In addition, we were interested in exploring the sources of variation in  $\lambda$  and its sensitivity to variation in the vital rates using elasticity (de Kroon et al. 2000) and components of variance analyses (Burnham et al. 1987).

## METHODS

### STUDY AREA

The study area encompassed approximately 2200 km<sup>2</sup> of forested land in northeastern California (40°30'N, 121°00'W). We did not survey most private land nor some inaccessible areas within the study area boundaries. The majority of the study area is on the Lassen National Forest (LNF), with some overlap onto the Plumas National Forest (4 owl territories), private timber lands (8 territories), Lassen Volcanic National Park (1 territory), and Bureau of Land Management land (1 territory).

The study area lies at the southern end of the Cascade Geographic Province. However, it is included in the Sierra Nevada Province for Spotted Owl management purposes (e.g., USDA 2001), as it lies at the northern limit of the distribution of the California Spotted Owl. The majority of forested stands on the study area are classified as white fir-mixed conifer ("mixed conifer"). In addition, some stands are classified as white fir, red fir, or pine. All forest types are typical of the Sierra Nevada (Rundel et al. 1977). Mixed conifer stands include white fir (*Abies concolor*),

sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), incense cedar (*Calocedrus decurrens*), and Douglas-fir (*Pseudotsuga menziesii*). Red fir (*Abies magnifica*) and white fir stands are monocultures or contain occasional other firs. Pine stands consist of ponderosa pine and Jeffrey pine (*Pinus jeffreyi*). Elevations on the study area range from 1200 to 2100 m.

### SURVEY METHODS

We used standard methods to locate, identify, and capture Spotted Owls (Forsman 1983, Franklin et al. 1996). We located owls both day and night by imitating their calls. During daytime visits, we either captured and banded non-juvenile owls with unique color bands, or identified previously banded owls. Juvenile owls were banded after fledging with cohort-specific (non-unique) color bands. When these owls were later encountered as nonjuveniles, we replaced the cohort band with a unique color band. Each year we attempted to locate and identify all banded subadult and adult owls observed in at least 1 of the previous 2 years. We systematically searched for any owl not located for two consecutive field seasons, following a standardized protocol (G. Miller, unpubl.). The search entailed complete nighttime surveys of a 2.4-km-radius area centered around the nest or primary roost of the owl in question. For owls replaced at a site by another owl of the same sex, we conducted two complete surveys each year. For owls that had not been replaced, we made six visits to the site including four complete surveys each year (G. Miller, unpubl.). In addition, we continued to search most sites that were occupied during early years of our study with four complete surveys per year to determine how long these sites remained vacant.

When an owl was found, its reproductive status was determined based on its response to the presentation of live mice. In general, an owl belonging to a nesting pair will take mice to the nest; if fledged young are present, the parent will take mice to the young; if an owl is not nesting and no fledglings are present, the owl will eat or cache the mice (Forsman 1983). Field crews followed a strict protocol during the "mousing" procedure to eliminate observer bias in drawing conclusions about owl reproductive status (G. Miller, unpubl.; Franklin et al. 1996).

We delimited the approximate boundaries of owl sites based on the owls' behavior, move-

ment patterns, and the distribution of roost and nest locations. Sites roughly approximated owl territories; however, we did not determine territory boundaries. During capture and handling, we assigned owls to one of four age classes: juvenile (<1 year), first-year subadult (in their second year), second-year subadult (in their third year), and adult birds ( $\geq 3$  years) based on plumage characteristics (Forsman 1981, Moen et al. 1991).

#### DEMOGRAPHIC ANALYSIS

*Reproduction.* For statistical analysis, we defined territorial females as our sample population (Seamans et al. 1999). Productivity was defined as the mean number of female young fledged per female that produced fledglings. Fecundity ( $b_x$ ) was defined as the number of female young per female of age class  $x$ . The sex of fledglings was not determined and we assumed that one-half of the juveniles produced were female (Franklin et al. 1996). We computed least-squares mean estimates of age-specific fecundity using mixed models ANOVA under a maximum likelihood framework (Littell et al. 1996). Owl site and year were modeled as random effects.

*Survival.* We estimated apparent annual survival probability with contemporary capture-recapture methods using program MARK (White and Burnham 1999) and the model selection and testing procedures outlined in Franklin, Anderson et al. (1996). Data were summarized in a capture history matrix including information on the age and sex of each owl. We evaluated goodness-of-fit to the global Cormack-Jolly-Seber (CJS) model and estimated a variance inflation factor,  $\hat{c}$ , by simulating 1000 bootstrap replications of the capture history data in Program MARK, where

$$\hat{c} = \frac{\text{deviance}_{\text{observed}}}{\text{avg deviance}_{1000 \text{ reps}}}.$$

The variance inflation factor is used to adjust the variances and covariances of the maximum likelihood estimates in the case of overdispersion in the data. Overdispersion may arise, for example, when the fates of paired male and female owls are not independent.

We developed a set of *a priori* candidate models that allowed for modeling the effects of time, sex, age class, and interactions among these factors on apparent survival ( $\phi_i$ ) and recapture ( $p_i$ ) probabilities. We used Akaike's Information Cri-

terion, adjusted for small sample size and overdispersion (QAICc), to select the best model supported by our data (Lebreton et al. 1992, Burnham and Anderson 1998). Vital rate estimates are presented as mean  $\pm$  SE.

*Population trend.* Based on the results of the best-fit fecundity and survival models, we used a four-stage projection matrix model parameterized with average estimates of the demographic rates. Four stages were justified because both subadult age classes had significantly lower fecundity than adult owls (see below). The structure of the matrix elements was based on a post-birth-pulse survey of the population (Noon and Sauer 1992). We computed the dominant eigenvalue of this matrix as an estimate of  $\lambda$ , the annual finite rate of population change (Caswell 1989). Additional assumptions and details of the estimation procedures are discussed in Noon and Biles (1990) and Noon et al. (1992).

Our hypothesis of interest was whether the population was declining during our study period. Therefore, we tested  $H_0: \lambda \geq 1.0$  versus the alternative,  $H_a: \lambda < 1.0$  with a one-tailed Z-statistic (Franklin et al. 1996). The SE of  $\lambda$  was estimated based on sampling variances and covariances of the fecundity and survival estimates, using the Delta method (Oehlert 1992).

*Life history sensitivities.* We computed the partial derivatives and elasticities of each matrix element ( $a_{ij}$ ) and the elasticities of the vital rates comprising the matrix elements, the so-called lower-level elasticities (Caswell 1989). Lower-level elasticities directly measure the contribution of each survival and fecundity rate across all matrix elements ( $a_{ij}$ ) in which they occur. For a vital rate  $x$  that is one component of one or more matrix elements, chain-rule differentiation is used for each  $a_{ij}$  that contains  $x$  (Wisdom and Mills 1997). Lower-level elasticities are calculated on the same scale and can be directly compared. The elasticity of  $\lambda$  to a specific vital rate was computed as (Caswell 1989):

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

All matrix calculations were performed using Mathcad version 8.0 (MathSoft 1996).

*Variance components.* Our study provides us with a series of fecundity and survival estimates across time. However, the variance in this series includes true stochasticity in population growth

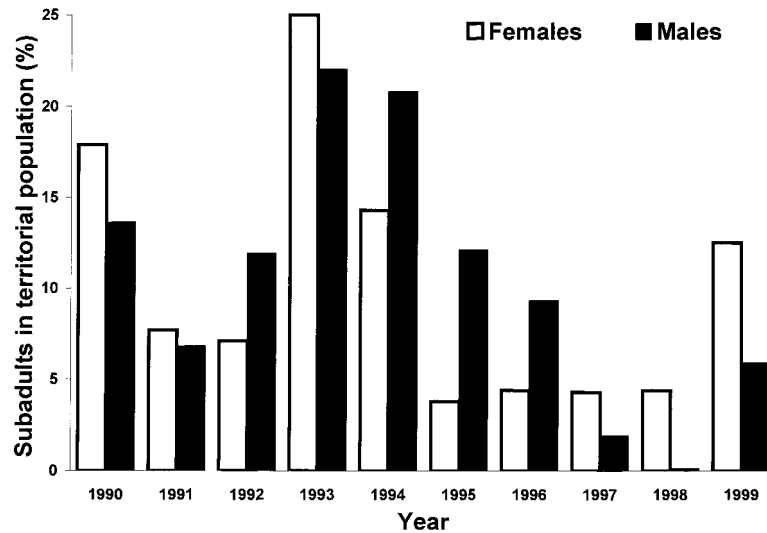


FIGURE 1. Percent of male and female territorial California Spotted Owls in the subadult age classes in northeastern California, 1990–1999.

(process variation) and stochasticity in estimating the birth and survival rates of the population (sampling variation) (White 2000). To estimate the process component of variance in a time series requires that the sampling variance first be removed from the total observed variance. We used procedures explained in Burnham et al. (1987) and a computer program described in White (2000) to estimate the temporal components of variance in the adult fecundity and survival probability.

We also computed the relative contributions of temporal variation in fecundity and survival to the standard deviation in  $\lambda$ ,  $SD(\lambda)$ . The effects of temporal variation in a vital rate  $x$  on  $SD(\lambda)$  were computed by using a first-order Taylor series expansion (Caswell 1989):

$$SD(\lambda) \approx \sqrt{\left(\frac{\partial \lambda}{\partial x}\right)^2 \text{Var}(x)}$$

## RESULTS

### CAPTURE AND MOVEMENT

We detected owls at 117 sites from 1990–1999. Owl pairs were present during one or more years in at least 100 distinct sites. It is possible that some of the remaining sites were occupied by owl pairs, but we did not verify social status at these sites. Based on thorough surveys of all sites where owls had been banded, some occupied sites were subsequently unoccupied.

From 1990–1999, 219 juvenile owls and 200 adult and subadult owls were captured and banded at 90 distinct sites. First and second-year subadults accounted for 4% (1998) to 24% (1993) of the territorial owls observed each year (Fig. 1). Thirty-seven nonjuvenile (subadult and adult) territorial owls moved between sites (19 females and 18 males). Distances moved ranged from 1.2 to 32.7 km (mean = 11.0 km, median = 8.9 km). The majority of these movements involved individuals that were not previously part of the breeding population. First and second-year subadults accounted for at least 35% (13) of all nonjuvenile movements. Of the remaining birds that moved, 22% (8) were owls that nested at the sites they moved to but were never observed to nest at their initial site, 14% (5) involved single males that were never observed to breed, and 5% (2) moved back to their original sites the following year and successfully nested. Of the nonjuvenile owls that moved between sites, over 25% moved from just 5 initial sites. None of these 5 sites supported any nesting attempts after 1992, the year in which 97% of our sites checked for reproduction were successful.

Forty-four owls banded as juveniles were sighted in subsequent years (24 females and 20 males). Thirty-one of these owls were recaptured and given unique color bands. Straight-line distances from natal sites to points of recapture

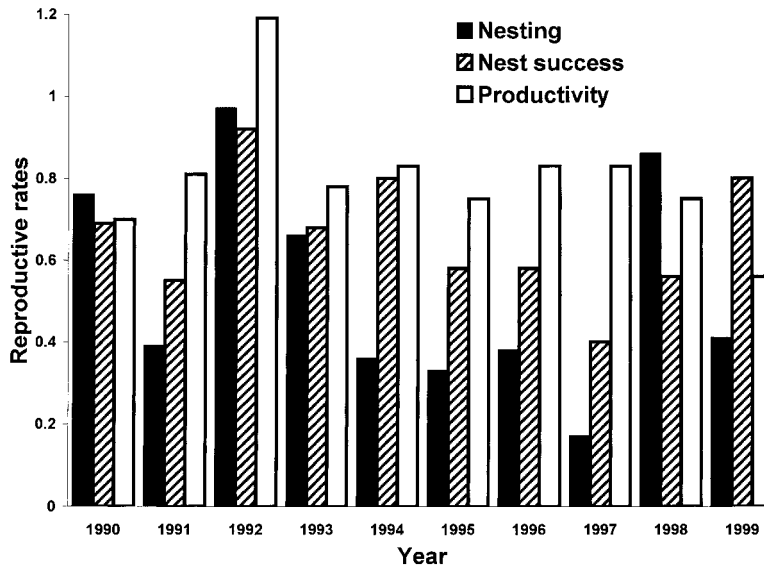


FIGURE 2. Estimated nesting rate, nest success rate, and productivity of adult (age  $\geq 3$  years) female California Spotted Owls in northeastern California, 1990–1999. Nesting rate is the proportion of owls nesting; nest success rate is the proportion of all nests that fledged young; productivity is the number of female young fledged per successful nest, assuming that half of the young fledged were female.

ranged from 4.2 to 76.4 km (mean = 27.9 km, median = 23.1 km).

REPRODUCTION

The proportion of territorial females nesting ranged from 0.14 in 1997 to 0.97 in 1992 ( $n = 25$  to 38; Fig. 2). The proportion of nesting females that fledged young ranged from 0.40 in 1997 to 0.89 in 1992 ( $n = 5$  to 37; Fig. 2). The

proportion of all females that fledged young ranged from 0.07 in 1997 to 0.91 in 1992 ( $n = 38$  to 53). Productivity of Spotted Owls ranged from 0.56 in 1999 to 1.15 in 1992 ( $n = 3$  to 48). Fecundity of adult Spotted Owls ranged from 0.07 in 1997 to 1.09 in 1992 ( $n = 38$  to 53; Fig. 3). Fecundity rates estimated by least-squares means over all years were  $b_1 = 0.065 \pm 0.066$  for first and second-year subadult females ( $n = 33$ ) and  $b_2 = 0.291 \pm 0.065$  for adult females ( $n = 381$ ). Based on mixed model ANOVA, annual and site effects accounted for 47% and 0%, respectively, of the random variation in fecundity.

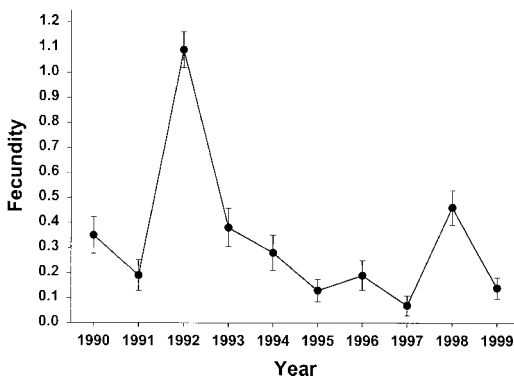


FIGURE 3. Estimated fecundity ( $\pm$  SE) of adult (age  $\geq 3$  years) female California Spotted Owls checked for reproduction in northeastern California, 1990–1999. Fecundity is defined as the mean number of female young fledged per female and assumes that half of the young produced were female.

SURVIVAL

The capture history data contained slight overdispersion ( $\hat{c} = 1.323$ ), indicating lack of independence in the data. Based on the QAICc-selected model, estimates of apparent survival probabilities were  $\phi_0 = 0.333 \pm 0.055$  for juvenile owls and  $\phi = 0.827 \pm 0.015$  for nonjuvenile owls. This model estimated common survival and recapture rates for subadult and adult owls of both sexes across time and an increasing trend over time in the recapture probability of owls first captured as juveniles. Four closely competing models ( $\Delta QAICc < 2$ ; Burnham and

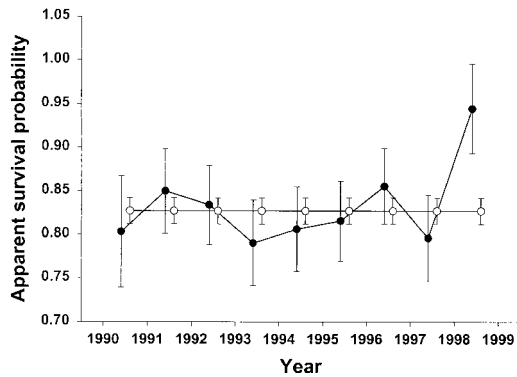


FIGURE 4. Estimated apparent survival ( $\pm$  SE) of nonjuvenile owls in northeastern California, 1990–1999. Unfilled circles are from the lowest AIC model. Filled circles are annual estimates for purposes of examining sources of variation.

Anderson 1998) were identical to the lowest QAICc model except for one additional parameter each. Additional parameters were  $\phi$  first-year subadults,  $\phi$  second-year subadults, a log-linear time trend in nonjuvenile  $\phi$ , and  $p$  second-year subadults. However, the slope estimates for all of these additional parameters overlapped zero; therefore, these were not considered to be parsimonious models.

Although year-specific survival rates were not supported by model selection, we estimated annual survival probabilities of nonjuvenile Spotted Owls for the purpose of examining components of variation (Fig. 4).

POPULATION TREND

The age-specific survival and fecundity estimates resulted in a projection matrix ( $A$ ) with the following structure:

$$A = \begin{bmatrix} \phi_0 b_1 & \phi b_1 & \phi b_2 & \phi b_2 \\ \phi_0 & 0 & 0 & 0 \\ 0 & \phi & 0 & 0 \\ 0 & 0 & \phi & \phi \end{bmatrix}$$

The estimate of  $\lambda$  from 1990–1999 for our study population was  $0.910 \pm 0.025$ . This estimate was significantly different from a stationary population (1-tailed  $Z = 3.6$ ,  $P < 0.001$ ), and suggests the territorial female owl population declined 9% annually from 1990–1999.

LIFE HISTORY SENSITIVITIES

The partial derivatives of the matrix elements with respect to  $\lambda$  measure the absolute change in  $\lambda$  given an infinitesimal absolute change in matrix element  $a_{ij}$  (de Kroon et al. 2000). Because these measures are scale-dependent they do not allow a direct comparison of element sensitivities. However, the elasticities of the elements measure the proportional change in  $\lambda$  resulting from an infinitesimal proportional change in  $a_{ij}$  and do permit a direct comparison of elements. The relative values of the matrix elasticities clearly indicate that the value of  $\lambda$  is most sensitive to incremental changes in the survival rate of owls  $\geq 3$  years of age (Table 1).

Because survival rates are also embedded in both the subdiagonal and top row elements of the projection matrix, the lower-level elasticities provide a direct measure of the effect of one-at-a-time, proportionate, and small changes in each individual life-history component on changes in population growth rate. As is apparent from Table 1, the elasticity of adult survival rate is approximately an order of magnitude larger than the next largest elasticity.

TABLE 1. Estimated partial derivatives and elasticities of the matrix elements and lower-level elasticities for the vital rates for California Spotted Owls in northeastern California, 1990–1999.  $b_x$  = age-specific fecundity;  $\phi_x$  = age-specific survival.  $\phi_1$ ,  $\phi_2$ , and  $\phi_3$  correspond to nonjuvenile survival,  $\phi$ , in the matrix, above.

Matrix element	Partial derivative	Elasticity	Vital rate	Lower-level elasticity
$\phi_0 b_1$	0.081	0.002	$b_1$	0.003
$\phi_1 b_1$	0.030	0.002	$b_2$	0.014
$\phi_2 b_2$	0.027	0.010	$\phi_0$	0.081
$\phi_3 b_2$	0.266	0.070	$\phi_1$	0.079
$\phi_0$	0.216	0.079	$\phi_2$	0.077
$\phi_1$	0.085	0.077	$\phi_3$	0.763
$\phi_2$	0.077	0.070		
$\phi_3$	0.763	0.693		

#### VARIANCE COMPONENTS

The persistence of a population depends, in part, on the inherent variation in its vital rates (Dennis et al. 1991). To estimate variation arising from demographic and environmental stochasticity, we partitioned the total variance in our series of estimates of adult survival and adult fecundity into its process and sampling components. For adult survival, we found that almost all the observed variation was due to sampling error. In contrast, for adult fecundity about 95% of the total variance was attributable to year-to-year process variance.

We computed the contribution of each matrix element to the total variation in  $\lambda$  as the product of the square of their partial derivatives with respect to  $\lambda$  and their total variance (Caswell 1989). Based on this analysis, 43% of the year-to-year variance in  $\lambda$  was attributable to variation in fecundity (the top row of the matrix) and 28% to variation in first-year survival rate.

#### DISCUSSION

Our estimates of demographic rates allow inference about the population of territorial owls on the Lassen study area, 1990–1999.

#### REPRODUCTION

All measures of reproductive success showed extensive annual variation. Our estimate of mean adult fecundity ( $0.291 \pm 0.065$ ) was comparable to estimates from other Spotted Owl populations. For example, recent estimates for the California Spotted Owl in other parts of its range include  $0.400 \pm 0.010$  from the Eldorado National Forest (Seamans et al. 2001),  $0.316$  from the Sierra National Forest and  $0.300$  from Sequoia-Kings Canyon National Park (G. Steger, unpubl. data). Our adult fecundity estimate fell in the middle third of estimates from 16 Northern Spotted Owl study areas (range  $0.103$ – $0.568$ ) and was similar to the mean estimated adult fecundity across the 16 study areas ( $0.321 \pm 0.030$ ; Franklin et al. 1999). Adult fecundity estimates from two populations of Mexican Spotted Owls were  $0.494 \pm 0.043$  and  $0.380 \pm 0.037$  (Seamans et al. 1999).

The proportion of female owls nesting, the proportion of young fledged, and fecundity were all greater in 1992 than any other year. Over half of the broods observed in 1992 were composed of triplets; only one set of triplets was observed in all other years. As a result, the point estimate

for fecundity in 1992 was 2–8 times greater than in any other year. The exceptional reproductive output in 1992 was reflected in increased recruitment the subsequent year (Fig. 1). Forty percent of all resighted juvenile banded birds and 13 percent of all 1999 territory holders were from the 1992 cohort. Annual variation in reproductive output of California Spotted Owls, with a strong peak in 1992, has also been reported from demographic studies on the Sierra National Forest, Sequoia and Kings Canyon National Parks (G. Steger, unpubl. data), and the Eldorado National Forest (Seamans et al. 2001). Apparently, conditions favorable to reproduction were synchronous throughout the Sierra Nevada in 1992. The environmental conditions responsible for this reproductive peak are unknown.

#### SURVIVAL

The apparent survival probability of nonjuvenile owls ( $>1$  year old) from our study is similar to those reported for California Spotted Owls in the Eldorado National Forest ( $0.795 \pm 0.012$ ; Seamans et al. 2001) and Mexican Spotted Owls in Arizona and New Mexico ( $0.814 \pm 0.050$  and  $0.832 \pm 0.029$ , respectively; Seamans et al. 1999). It is also comparable to that estimated from a meta-analysis of 15 studies of Northern Spotted Owls ( $0.850 \pm 0.005$ ; Franklin et al. 1999). The apparent survival probability of juvenile owls from our study is higher than estimates for Mexican Spotted Owls in Arizona and New Mexico ( $0.179 \pm 0.081$  and  $0.109 \pm 0.041$ , respectively; Seamans et al. 1999) and higher than the mean estimate from 16 studies of the Northern Spotted Owl ( $0.281 \pm 0.032$ ; Franklin et al. 1999).

*Possible sources of bias.* Open population capture-recapture models provide estimates of apparent survival rather than true survival (White and Burnham 1999). That is, survival probability estimates include data from animals that died between sample periods, as well as those that emigrated from the study area, survived  $\geq 1$  year, and were never resighted (Burnham et al. 1994, 1996, Franklin et al. 1996). Because juvenile owls may permanently move beyond the bounds of the study area before their fates can be determined, estimates of first-year survival probability may be biased low.

The magnitude of bias in our estimate of juvenile survival due to permanent emigration is unknown, but several lines of evidence suggest

it is small. First, our estimate of juvenile survival is similar to that of a geographically isolated population of California Spotted Owls in the San Bernardino Mountains of southern California ( $0.344 \pm 0.052$ ; LaHaye et al. 1994).

Second, assuming that adult survival probability and fecundity rates are accurate, for our population to show a stable trend from 1990–1999 ( $\lambda = 1.0$ ) would require a first-year survival probability of 0.790. Our population would demonstrate this rate of survival only if juveniles had an annual permanent emigration rate of 0.578. Estimates of juvenile emigration rates from three Northern Spotted Owl dispersal studies using radio-telemetry ranged from  $0.295 \pm 0.044$  to  $0.579 \pm 0.113$ , with a combined average of  $0.364 \pm 0.039$  (Franklin et al. 1999). These estimates represent the rate of emigration of birds in their first year of life and were used to correct juvenile Spotted Owl survival estimates from the three study areas (Franklin et al. 1999). This correction assumes that first-year emigration is permanent, and does not account for juvenile-banded owls recaptured outside of the study areas. Similar estimates of juvenile emigration rates do not exist for California Spotted Owls.

Of the juvenile-banded birds we relocated, 61% were sighted 2 or more years after banding. These birds either temporarily emigrated off the study area, temporarily occupied areas that were not normally surveyed within our study area, or simply went undetected because they were floaters and did not respond to vocalizations (Franklin 1992, Thraillkill et al. 1996). Similarly, of 145 Northern Spotted Owls first banded as juveniles on four study areas and later recaptured, 60% were first relocated 2 or more years after banding (Raphael et al. 1996).

There are several reasons why we believe that the level of juvenile emigration from our study area is relatively small. First, to date we have relocated 21% of all birds that have been banded as juveniles, a rate significantly higher than the 12% relocation rate for four Northern Spotted Owl study areas (Raphael et al. 1996). Second, vast expanses of unsuitable habitat bound our study area to the east (Great Basin) and to the west (Central Valley). Areas to the north are characterized by forested buttes capable of supporting few pairs of owls. Finally, our study area is large; banded juvenile owls can disperse >70

km and still be within the bounds of our study area.

Estimates of survival probability from nonjuvenile age classes are also subject to a negative bias if owls emigrate, survive  $\geq 1$  year, and are never recaptured. However, the likelihood of owls permanently emigrating once they have held territories in the study area is probably very low (Burnham et al. 1996). Estimated movement rates of adult and subadult Northern Spotted Owls were low: Franklin et al. (1996) reported a nonjuvenile movement rate of 6.6%; Wagner et al. (1996) reported a nonjuvenile movement rate of approximately 1.5%; Thraillkill et al. (1996) reported an adult movement rate of 4%. We observed a nonjuvenile movement rate of 6.2%. All of these estimates are potentially biased low due to the possibility of owls moving out of study areas without detection. Because the median detected distance moved by adult and subadult owls on our study area was small in comparison to the study area size, we believe the undetected emigration rate of adults and subadults is very low.

#### POPULATION TREND

Our estimates of demographic rates provide an estimate of  $\lambda$  with a 95% confidence interval less than 1.0. (0.862–0.959). This  $\lambda$  estimate suggests that the territorial population of owls in the Lassen study area declined at an average of 9% per year from 1990–1999. In comparison,  $\lambda$  for the Northern Spotted Owl, based on an average from 15 study areas throughout its range, was estimated to be  $0.917 \pm 0.013$  (95% CI = 0.889–0.945) from 1985–1998 (Franklin et al. 1999).

Valid estimates of  $\lambda$  from the analysis of projection matrices are subject to a number of strict assumptions. Among these are a stable age (or stage) distribution and unbiased parameter estimates. The significance of these assumptions, relative to inferences to Spotted Owl population dynamics, is discussed in detail in Noon et al. (1992). Given these assumptions, if the true rate of change were as low as 4% per year (upper 95% CI of  $\lambda = 0.959$ ) and the demographic rates remained at their current mean values, we would project the population to decline by one-half within 20 years. This inference would be valid only if the conditions operative during our study were to remain constant. Given our uncertainty of the underlying causes for the observed means

and variances of the birth and survival probabilities, projecting population trends beyond the period of study must be done with great caution.

#### LIFE HISTORY SENSITIVITIES AND VARIANCE COMPONENTS

The elasticity of the adult survival rate was significantly larger than the mean elasticities of the fecundity rates. This pattern of differential life-history sensitivities is common to many long-lived bird species (Saether and Bakke 2000). Low fecundity rates, coupled with delayed attainment of full reproductive potential, suggest strong natural selection to maintain high adult survival probabilities. Small declines in adult survival will have large effects on population growth rate.

If we assume that fecundity and first-year survival rate retain their current values, the survival probability of all female owls  $\geq 1$  year old would have to increase to  $\geq 0.92$  to produce a stable population. Such an increase would obviously require a substantial reduction in subadult and adult female mortality. Elasticities associated with the fecundity parameters were small, but the rates themselves were variable across years, suggesting that recruitment is often highly uncertain. Thus, high adult survival in Spotted Owls may allow population persistence through long periods of low reproductive success.

The major source of variation in our mean estimate of  $\lambda$  arose from process variation in adult fecundity. Thus, variation in the population rate of change from 1990–1999 was primarily a consequence of variable reproductive success arising from some combination of temporal, spatial, and individual variation in reproduction within our study population. The Spotted Owl population in Lassen National Forest may be similar to populations of Northern Spotted Owls in northern California where climatic variation explained most of the variation in life history traits (Franklin et al. 2000).

In contrast, little of the observed variance in  $\lambda$  was attributable to process variation in adult survival even though it had the largest elasticity. This result is consistent with Saether and Bakke (2000) who found in a comparative study of avian taxa that the variance in  $\lambda$  is most strongly influenced by the vital rate with the highest temporal variability rather than by the vital rate with the largest elasticity.

In both their among and within-species com-

parisons, Saether and Bakke (2000) commonly found an inverse relationship between the sensitivity of a vital rate and its temporal variation. They suggest that a reduction in the variance of a sensitive vital rate would be favored by natural selection. Such a pattern could be interpreted as a bet-hedging strategy among long-lived species to spread the risk in reproductive investments over several breeding seasons (Franklin et al. 2000, Saether and Bakke 2000).

#### CONSERVATION IMPLICATIONS

The inverse relation between process variation and sensitivity in the fecundity and adult survival rates has important management implications for the California Spotted Owl. First, population size should not be allowed to become too small, because low fecundity precludes rapid recovery from population declines. Thus, once a Spotted Owl population becomes small, it will remain vulnerable for a long period to the risks of extinction known to affect small populations. Second, any management actions which further reduce the survival probabilities of adult female owls will have disproportionately large and negative effects on population growth rate. Finally, all management practices which increase the temporal variance in a vital rate with high sensitivity (e.g., adult survival) will have a serious effect on population viability because this will lead to a significant reduction in the mean population growth rate (Lande 1993, Saether and Bakke 2000).

Given the current trend in California Spotted Owl populations, the most positive step that can be taken to reverse the apparent decline is to improve adult survival probabilities. Owl studies to date suggest that this will occur with increased retention and recruitment of large trees and retention of closed-canopy conditions throughout the Sierra Nevada (Gutiérrez et al. 1992, Verner et al. 1992, Hunsaker et al. 2001).

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