

# Demography of the California Spotted Owl in the Sierra National Forest and Sequoia/Kings Canyon National Parks<sup>1</sup>

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## Abstract

Nine years (1990–1998) of demographic data on California spotted owls (*Strix occidentalis occidentalis*) in two study areas on the western slopes of the Sierra Nevada—one in the Sierra National Forest (SNF), the other in Sequoia/Kings Canyon National Parks (SNP)—are summarized. Numbers of territorial owls fluctuated from 85 to 50 in SNF and 80 to 58 in SNP over the period from 1990 to 1998, and demographic parameters indicate significantly declining populations in both study areas during the same period. Owl densities in conifer forests, reproductive performance, and survival rates did not differ significantly between the two study areas. These results suggest that factors influencing population trends may be more than local in scope, such as weather and/or prey populations. Local forest management may compound the regional variation, however, as may be reflected in the lower adult/subadult survival rates in the SNF study area compared to the SNP study area. Continual timber harvest has occurred in SNF since the late 1800's, but SNP has had little harvesting activity. Prescription burning and recreation continue to occur on both sites. Declining trends in owl numbers also reflect poor breeding success from 1995 through 1998, apparently attributable to unseasonal storms during the breeding period, especially during the incubation and nestling phases. Results suggest the hypothesis that spotted owls are “pulse” breeders that exhibit unusually successful reproduction only at intervals of several years, when all conditions are favorable. Continuation of these studies as part of the Kings River Sustainable Forest Ecosystems Project within boundaries of SNF will provide opportunities to explore relations among spotted owl demographics and timber harvest, weather, and prey availability.

California spotted owls (*Strix occidentalis occidentalis*) in the western Sierra Nevada show a close association with dense forest and woodland ecosystems and their nesting/roosting stands typically have much “decadence” in the form of standing dead trees (snags), diseased and/or deformed live trees, and decaying wood on the forest floor. Pairs in Sierra conifer forests use home ranges that average about 3,400 acres during the breeding period and about 9,700 acres during the nonbreeding period (Verner and others 1992). Consequently, maintenance of sufficient habitat to assure viability of the Sierra population represents a substantial cost in allowable timber volume. The California spotted owl is not currently listed as a threatened or endangered species, although major environmental organizations are poised to petition the U.S. Fish and Wildlife to list the subspecies.

Nests are typically in large trees—mean of about 45 inches in diameter at breast height (dbh)—with broken tops and cavities large enough to accommodate a female owl and two or three young (Steger and others 1997b). Nesting in the southern Sierra Nevada is intermittent, involving from none to as many as 95 percent of pairs in any given year (50 percent of pairs nesting is regarded as a

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“good” year). Details of the structure and composition of owl habitat in relation to successful breeding are still uncertain.

The California spotted owl uses a diverse array of vegetation types, from riparian hardwood forests in the western Sierra Nevada foothills to red fir forests at high elevations. A recent technical assessment of the current status of the California spotted owl (Verner and others 1992) concluded that research is needed to distinguish levels of habitat quality for the birds by relating forest structure and composition to owl population parameters.

This paper provides information on the California spotted owl’s adult survival rates, population turnover rates, reproductive rates, site fidelity, mate fidelity, and other population characteristics on two study sites under different management regimes, and it assesses the effects of management at landscape scales.

The specific objectives of this study were to:

- Estimate spotted owl density and territorial occupancy status by area.
- Estimate vital rates (reproduction, mortality) by age class.
- Assess site fidelity among individual spotted owls.
- Estimate turnover rates (annual replacement of vacancies in occupied territories).
- Estimate lambda ( $\lambda$ ), the finite rate of population change under the null hypotheses, the population of resident owls is stable ( $\lambda = 1$ ) in all study areas; and vital rates (age at first reproduction, reproductive rate, and survival rate) do not differ among years, between sexes, or between study sites.
- Quantify the distribution of vegetation types within each study area.

## Study Areas

The two study areas were selected for their proximity and vegetative similarities. The Sierra National Forest (SNF) study area, located in the southern Sierra Nevada about 30 mi east of Fresno, California, covered 160 mi<sup>2</sup> from 1990 to 1993, when the area was enlarged to 265 mi<sup>2</sup> as the Kings River Sustainable Forest Ecosystems Project began. The additional 105 mi<sup>2</sup> was labeled the New Sierra (NS) study area. The 132-mi<sup>2</sup> Sequoia and Kings Canyon National Parks study area (SNP) was also in the southern Sierra Nevada, about 50 mi east of Visalia, California. All three study areas included three habitat zones:

- The oak-woodland type, at the lowest elevation—1,000 to 4,000 ft—had a canopy dominated by blue oak (*Quercus douglasii*), live oak (*Quercus wislizenii*), and foothill pine (*Pinus sabiniana*). Various foothill chaparral species were abundant.
- The mid-elevation coniferous forest—4,000 to 8,000 ft—made up the majority of each study area. Vegetation was dominated by ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), and black oak (*Quercus kelloggii*). Sites nearer to 8,000 ft had inclusions of Jeffrey pine (*Pinus jeffreyi*) and red fir (*Abies magnifica*). Nearly all of the SNF and NS sites had been logged since 1880, and only small, scattered patches of old-growth forest remain. Forest regeneration programs are in place on both public and private lands. Nearly all logging was some form of selective cutting; the little clear cutting that occurred was in scattered patches, typically smaller than 20 acres. The SNP included large stands of giant sequoia (*Sequoiadendron giganteum*) and large tracts of old-growth,

mixed-conifer forest. Some logging occurred in the late 1800's and early 1900's, but most stands were in mature or old stages of growth.

- The high-elevation coniferous forest—8,000 to 9,600 ft—was dominated primarily by red fir, lodgepole pine (*Pinus contorta*), and western white pine (*Pinus monticola*).

## Methods

These demographic studies involved surveying, banding, determining age and reproductive success, and rechecking owls on an annual basis from 1990 to 1998. Data from a few birds in the SNF study area included the period from 1987 through 1989, when we were studying movements, home ranges, and vegetation types used by radio-tagged spotted owls. In addition, we have added information to the SNP database from birds studied in 1988 and 1989 by Roberts (1990) within boundaries of our SNP study area. Spotted owls were located by night and day surveys, by observers imitating calls of owls to elicit responses. Surveying included point, leapfrog road, walking cruise, and walk-in methods (Forsman 1983). Survey period and the duration of surveys have been described by Steger and others (1993).

Owl surveys in all study areas began in the first week of March each year and ended on 30 September. Changes in survey effort that occurred over time usually resulted from poor weather conditions or inability to access sites. Several changes in survey effort occurred in 1997 and 1998 because of budget constraints. We chose a system that provides survey priority to pair sites, then sites with past owl detections, and finally sites with no previous owl detections. Surveys continued from March through September or until funding was exhausted.

Birds were captured with either a noose pole or mist net (Forsman 1983). All individuals were banded with a U.S. Fish and Wildlife Service leg band and a colored, plastic band on the opposite leg. A colored vinyl tab 0.8 inches long was attached to each color band (Franklin and others 1987), allowing hundreds of unique combinations. Sex and age classes of owls were determined following Forsman (1981, 1983). Fledgling, subadult, and adult age classes were recognized.

Owls were assessed for social status, reproductive status, and turnover (replacement) on sites using standard techniques (Miller 1990). Protocols for determining these attributes were described by Steger and others (1993).

Vegetative sampling was used to determine if nest sites differed in canopy cover, species composition, and size class between study areas. Nest trees were located from 1990 to 1998 using methods described by Forsman (1983), and sampled using methods described by Steger and others (1997a, 1997b).

Data were analyzed by using a variety of statistical tests (Sokal and Rolf 1981, Zar 1984). Annual survival rates (the probability of surviving from age  $x$  to  $x + 1$ ) were calculated for subadults and adults combined as one age class using the Jolly-Seber (J-S) capture-recapture model for open populations (Jolly 1965; Seber 1965, 1982), which allows for losses and gains to the population between sampling periods. A sampling period was defined as one field season, for example from March 1 to September 30. The J-S model assumes that all individuals in the population have equal probabilities of survival, capture, and recapture (resighting in this case); that emigration is permanent, although the model partially adjusts for emigration vs. mortality using the rate at which emigrants return to the study area in later years; and that the sampling period is instantaneous (Nichols and others 1981, Seber 1982). A small percentage of our color-banded owls are more difficult to resight (read their band colors) than most banded owls because they tend to remain more concealed, and few have lost their colored bands. We consider these to be a minor violation of the first assumption. The second assumption is probably violated a few times because

not all emigrants from the study area are likely to return in later years. Finally, the third assumption is probably violated to a small degree because of the relatively long, 7-month sampling interval, although the very low mortality rate during this period mitigates this effect (Nichols and others 1981).

We could not estimate juvenile survival rates for our study areas because of insufficient data. Instead, we have used 0.3278 as our estimate of juvenile survival rate, based on data from a similar demographic study of spotted owls in the San Bernardino Mountains, where probably few if any juveniles leave the study area (LaHaye and others 1997).

Fecundity was calculated as the number of female offspring produced per territorial female checked for reproduction (Noon and others 1992). Turnover rates were calculated as the proportion of marked adults and subadults that were replaced annually on their territory by another owl.

*Lambda* ( $\lambda$ ) was calculated using the Lefkovich stage-projection matrix model (Lefkovich 1965). Population trends were considered to be increasing if  $\lambda > 1.0$ , stable if  $\lambda = 1.0$ , and in decline if  $\lambda < 1.0$ . An estimate of  $\lambda$  and its standard error allowed the tests of hypotheses:  $H_0: \lambda \geq 1$ , versus the alternative  $H_a: \lambda < 1$ . The appropriate test statistics followed a Z-distribution, given by:  $Z = |(\lambda - 1) / \lambda_{se}|$ . We followed the method adopted by Noon and others (1992) in testing the significance of  $\lambda$  values, in which the appropriate test statistics followed a Z-distribution, and the specified probability of a Type I error = 0.05.

## Results

Estimates of abundance, productivity, and population change, in most instances, were similar in the three study areas (*table 1*), although we consider the data for the NS study area to be marginal because it has been under study only since 1994. The numbers of territorial owls increased from 1991 through 1994 in SNF and 1991 through 1995 in SNP, but they have since declined in all areas. Densities in the conifer forest zones (3,400-7,600 ft in SNF; 3,600-8,000 ft in SNP) did not differ significantly between SNF and SNP ( $t = 0.02$ ;  $P = 0.98$ ) but was considerably lower in NS. Productivity (young/pair) was marginally higher in SNF than in SNP, but turnover rates were lower in SNP (suggesting higher survival there). Although the average percentage of territorial birds disappearing each year was slightly higher in SNF than in SNP, the net loss of territorial birds (loss minus replacement rates) was essentially the same in those study areas.

We have color banded 256 of 289 young owls known to fledge from the three study areas over the 9 years of study (129 of 140 fledglings in SNF, 108 of 128 in SNP, and 19 of 21 in NS). Of 242 fledglings banded prior to 1988, 42 (17 percent) have been recaptured within study area boundaries, another seven have been resighted but not recaptured, for an observed return rate of 20 percent. The fledgling sex ratio of 72:50 (male:female), determined from blood samples of 122 birds from 1993 to 1998, was significantly different from a ratio of 1:1 ( $P = 0.0284$ , binomial test). (Note: the fledgling sex ratio in 1999 was 13:30, bringing the overall total to 85:80—not significantly different from 1:1.)

Reproduction differed markedly among years. The percent of pairs fledging young averaged at least 45 percent in 1990-1994 in all study areas but less than 16 percent in 1995-1998 (*table 2*). Generally, however, reproductive performance differed little among the study areas—when it was a “good” year in one area, it was good in all and, when it was a “bad” year in one area, it was bad in all. In most instances, poor reproduction was associated with unseasonably stormy weather in March, April, and/or May (North, “Environmental Factors Associated with Spotted Owl Reproduction,” this volume).

Cumulative rates of population change ( $\lambda$ ) from 1988 to 1998 were significantly less than 1 in all populations (*table 1*), indicating that all were

**Table 1**—Measures of owl abundance, productivity, and population change on the three study areas

Measure	Sierra National Forest	New Sierra	Sequoia/Kings Canyon National Parks
Most territorial owls (year)	85.00 (1990)	37.00 (1994)	80.00 (1995)
Fewest territorial owls (year)	50.00 (1998)	24.00 (1998)	58.00 (1998)
Mean number of pairs	28.30	12.80	27.50
Mean number of owls/mi <sup>2</sup>	0.44	0.29	0.50
Mean number of young/year	15.00	3.80	13.20
Mean number of young/pair	0.62	0.33	0.58
Mean survival rate of banded males	0.80	0.81	0.88
Mean survival rate of banded females	0.80	0.87	0.86
Mean annual percent of territorial owls moving to new territory in the study area	6.00	3.00	3.00
Mean loss rate (percent) of territorial owls	20.00	18.00	14.00
Mean turnover rate (percent) of territorial owls <sup>1</sup>	17.00	8.00	11.00
Highest lambda value <sup>2</sup> (year)	1.00 (1993)		1.04 (1993)
Lowest lambda value <sup>2</sup> (year)	0.90 (1998)		0.95 (1998)

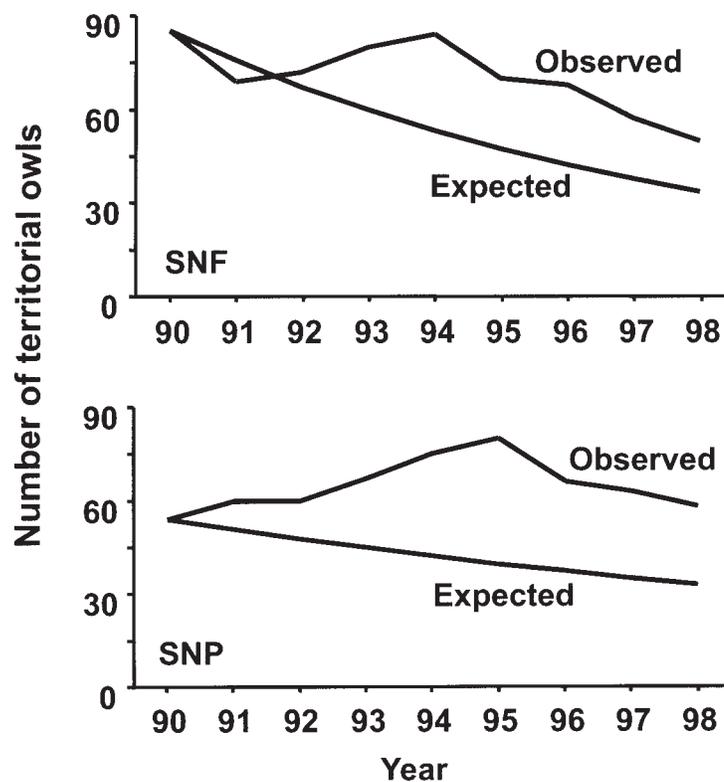
<sup>1</sup> Turnover rate is the annual replacement rate of vacancies in territories.

<sup>2</sup> Too few years in the New Sierra study area to compute these values.

**Table 2**—Percent of pairs sampled to established protocols that fledged young in the three study areas

Year	Sierra National Forest	New Sierra	Sequoia/Kings Canyon National Parks
1990	72	—	88
1991	38	—	8
1992	87	—	85
1993	42	—	44
1994	42	45	48
1995	4	7	6
1996	12	8	7
1997	24	20	22
1998	10	20	27

**Figure 1**—Observed numbers of territorial California spotted owls compared to projected numbers, based on the numbers expected each year from 1990 through 1998 if the estimate of *lambda* ( $\lambda$ ) is correct for the Sierra National Forest study area ( $\lambda = 0.90$ ) and the Sequoia/Kings Canyon National Parks study area ( $\lambda = 0.95$ ).



declining. Projected rates of decline of the SNF and SNP populations, using the  $\lambda$ -values through 1998, exceeded those based on the known numbers of territorial birds in each population (fig. 1).

Observed survival rates of banded males and females did not differ significantly ( $t = 1.96, P = 0.079$ ; and  $t = 0.98, P = 0.35$ ) between SNF and SNP. Among adult owls in the three study areas, males in SNF had the lowest mean annual survival rate (0.80 percent), and males in SNP had the highest (0.88 percent) (table 1). These survival rates suggest that an original cohort population of 100 males in SNF might have a single individual survive to age 20; similarly a cohort of 100 males in SNP might have one surviving representative after 34 years. In fact, some of the owls in our study areas are at least as old as the studies. A male banded as an adult in SNF in 1987 was still occupying a territory in 1998, giving it a minimum age of 14 years (an unbanded bird classified as an adult would be at least 3 years old), and a pair banded by Roberts (1990) as adults in SNP in 1989 were still in their territory in 1998, at a minimum age of 12 years.

## Discussion

### Population Trend

The general picture emerging to date from the demographic studies of these spotted owl populations in the southern Sierra Nevada is puzzling and certainly warrants further study. The poor reproductive performance in 1995-1998 appeared to result primarily from late seasonal storms that probably reduced the ability of males to deliver prey to their mates as they incubated eggs or brooded young. This interpretation is supported by the fact that reproductive failures occurred not only in SNF and NS but also in SNP, where owl habitats have not been altered by logging, and North (personal communication) found no difference between mean annual reproduction in SNF and SNP study areas.

Further support comes from the fact that 9 of 11 owl pairs nesting in 1998 failed after an unusually powerful storm in May.

In other years with unseasonal storms late in the winter or early spring, even when our sampling to full protocols indicated no nesting by a pair, we sometimes observed that the female had a brood patch, indicating that she had been incubating but deserted her nest. Because males provide food for the incubating female, and for her and the nestlings during the early part of the nestling period, a marked decline in his ability to capture and deliver prey to the nest site could force the female to leave the nest and forage for herself, thus jeopardizing the eggs or nestlings.

It is a troubling fact that both the demographic data ( $\lambda$ ) and the actual numbers of territorial birds indicate that all three study populations are declining. We believe, however, that our estimates of  $\lambda$  are negatively biased because permanent emigration of banded adults from a study area would lead to an underestimate of adult survival rate, and because our estimate of yearling survivorship also may be less than the true value. Consequently, we would expect population trajectories based on  $\lambda$ -values to be too steep, as we see in the comparison between those and empirical trajectories based on numbers of territorial birds (*fig. 1*). The difference in  $\lambda$ -values between study areas is attributable to higher adults/subadult survival rates in SNP than in SNF.

Following the highly productive breeding season in 1992, the number of territorial owls increased in both SNF and SNP, reaching peak counts in 1994 and 1995, respectively. This rise is consistent with the fact that most newly fledged spotted owls take 2-3 years to enter the territorial population. Declining numbers since then reflect the poor breeding years from 1995 to 1998. We should expect the number of territorial birds to increase markedly after the next productive nesting season. In this sense, we hypothesize that California spotted owls, at least in the southern Sierra Nevada, are "pulse" breeders, characterized by intermittent periods of unusually successful reproduction when all determining factors are favorable, but we would expect only moderate to poor success between pulses, depending on the mix of determining factors. This hypothesis not only fits our observations to date but also is consistent with the owl's life history strategy, in particular its relatively low reproductive rate, its relatively long life span, and usually a delay in its age at first attempted reproduction.

## **Relationship to Management**

Twenty-eight territories of California spotted owls are located within boundaries of the study area for the Kings River Sustainable Forest Ecosystems Project, and each has a protected activity center of about 300 acres set aside to protect the core area used by the owls. Over the course of the project, we expect to learn how these owls respond to the various silvicultural treatments within the two 32,000-acre watersheds that comprise the study area. Controls for these "experimental" treatments will be available in the remaining 105,000 acres within boundaries of the demographic study areas in SNF and NS. An additional level of control is available in the 83,200-acre study area in SNP, where timber management is absent but prescribed fire and recreation occur. This study thus may provide some answers to some fundamental questions about the responses of spotted owls to timber harvesting and prescribed fire within their home ranges.

Our current operating hypothesis is that successful breeding by the owls depends to a major extent on favorable weather conditions during the early stages of nesting—egg laying, incubation, and early nestling periods. Because we have experienced only 1 year (1992) when most pairs of owls in our study area nested, and the last 4 years (1995-1998) were poor for breeding by the owls, it may require a decade or two to fully understand the nature of the interacting factors needed to assure a self-sustaining population of spotted owls in ponderosa pine and mixed-conifer forest of the southern Sierra Nevada.

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Temporary field crews too numerous to name here have dedicated themselves to hard work in steep terrain at night, often during severe weather conditions, to help collect the data reported here. The study would have been impossible without their able and dedicated assistance over the past 9 years. Gordon I. Gould, Jr., and Jared Verner provided constructive reviews of the draft manuscript. We deeply appreciated the contributions made by all of these persons.

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