

**Ecology of the California Spotted Owl on the Lassen National Forest, 1990-2004; Final Report.**

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## **INTRODUCTION**

The California subspecies of the spotted owl (*Strix occidentalis occidentalis*) occurs in coniferous and hardwood forests of the southern Cascade Mountains of California, throughout the western slope of the Sierra Nevada, in the central and south coastal mountains of California, and into Baja California Norte, Mexico (Verner et al. 1992a, Gutierrez et al. 1995). The majority of California spotted owls occurs on public land in the Sierra Nevada and southern Cascades (Verner et al. 1992a).

This report summarizes fifteen years (1990-2004) of research on the California spotted owl on the Lassen National Forest. Our study was initially conducted through the U. S. Forest Service, Redwood Sciences Laboratory, in Arcata, CA (1990-1998). From 1999-2004, our study was conducted through Colorado State University, in Fort Collins, CO. As of 2005, this study became part of the California spotted owl module of the Plumas-Lassen Administrative Study, conducted jointly through Colorado State University and the U. S. Forest Service, Sierra Nevada Research Center, in Davis, CA.

Our original and primary objectives were to estimate demographic parameters including age-specific nesting and nest success rates, age-specific fecundity, age- and sex-specific survival rates, the finite rate of population change, and sex and age class structure of the population. Original objectives also included quantifying the spotted owls' diet through analysis of egested owl pellets, as well as characterizing nest trees and the composition and structure of vegetation surrounding nest trees. In 1998 we added two additional objectives to our study that were the subject of dissertation research by J. Blakesley: (1) Establish the relationship between demographic variation and variation in habitat structure and composition around spotted owl nest sites at multiple spatial scales (Blakesley 2003, Blakesley et al. In Press 2005), and, (2) Identify factors associated with spotted owl breeding dispersal probability and breeding dispersal distance and evaluate the consequences of breeding dispersal (Blakesley 2003, Blakesley et al. In Press 2006). In addition, we have documented the expansion of barred owls (*Strix varia*) and hybrid barred-spotted owls into northeastern California, and we have gathered data on external parasites of spotted owls. Finally, we collaborated on a study of spotted owl thermal ecology and energetics (Weathers et al. 2001).

### **Study Area**

The Lassen study area encompassed approximately 2200 km<sup>2</sup> of National Forest land in northeastern California. The majority of the study area occurred on the Almanor and Eagle Lake Districts of the Lassen National Forest (LNF), with three owl sites on the Hat Creek District of the LNF and five sites on the Plumas National Forest. In addition, some owls were found on land immediately adjacent to the LNF which was owned or administered by private timber companies (nine sites), the National Park Service (three sites), the Bureau of Land Management (one site), or private individuals (one site).

In 2001, in response to a change in the method used to estimate population change (see below), we delineated a bounded study area encompassing the majority of owl territories containing banded owls (hereafter, Density study area, or DSA). The DSA consists of the geographic core of the study area. We based the DSA boundaries on topographic features (watershed boundaries) and administrative

boundaries (e.g. between Forest Service and Private land). Sites not included in the DSA are located at the periphery of the Lassen study area, (e.g., in the northeast portion of the Eagle Lake Ranger District, on the Hat Creek Ranger District, on the north side of Lassen Volcanic National Park, and on the Plumas National Forest). Throughout this report, unless otherwise indicated, results are reported from throughout the greater Lassen study area.

Elevations on the study area ranged from 1200 to 2100 meters. Annual precipitation at the lower elevations averaged 141 cm in the west (Mineral, CA), 86 cm in the center (Chester, CA) and 36 cm just east of the study area (Susanville, CA). Most precipitation fell as snow between November and April. Average high temperatures in the center of the study area ranged from 6°C in January to 29°C in July. Average low temperatures ranged from -7°C in January to 7°C in July.

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 1993, 2001, 2004, Verner et al. 1992a), as it lies at the northern limit of the distribution of the California spotted owl. The majority of forested stands on the study area were classified as white fir-mixed conifer ("mixed conifer") or red fir; both are typical of the Sierra Nevada (Rundel et al. 1977). Mixed conifer stands included 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*) stands were monocultures or contained occasional white firs.

## **FIELD METHODS**

We followed standard techniques for locating, capturing, and banding spotted owls (Forsman 1983) and standard protocols for surveying large geographic areas, determining spotted owl reproductive status, and analyzing our data (Miller 1990, Franklin et al. 1996). Owls were initially located at night by vocally imitating their calls. When owls responded by calling back, we estimated each owl's location on a topographical map using one or more compass bearings taken from the observer to the calling owl. When an owl was detected, we conducted "walk-in" surveys to determine: (1) social status, i.e., whether the owl was single or paired with a mate, (2) reproductive status, and (3) identity of the owl. If an owl was unbanded or previously banded with a juvenile cohort band, we attempted to capture the owl and band it with a uniquely identifiable adult color band. In 1990 we began searching for owls at historic nest, roost, and nighttime detection locations, and added sites by surveying new areas.

We determined social status of non-juvenile owls (age  $\geq 1$  year old) on each visit; we made an overall determination of occupancy and social status for each site each year. In establishing pair status, a male and female owl had to be detected together on two or more occasions, with at least one pair detection occurring in the daytime (Franklin et al. 2004).

We determined owl reproductive status by following a standardized "mousing" protocol (Franklin et al. 2004) to eliminate observer bias in drawing conclusions about owl reproductive status. Mousing protocols are based on the owl's 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, a parent will take mice to the young; if an owl is not nesting and no fledglings are present, the owl will eat and/or cache the mice.

We determined owl sex based on the pitch of their calls. We captured owls and banded them with unique color bands, or, if already banded, we identified owls by observation of the color bands. Whenever possible, we determined the age class of each owl (juvenile [young of the year], first year subadult, second year subadult, adult) based on plumage characteristics (Forsman 1981, Moen et al. 1991). We banded juvenile owls with a cohort (year-specific color) band that identified them as juveniles fledged in a specific year. When we subsequently relocated a subadult or adult owl wearing a juvenile band, we made a concerted effort to recapture it and band it with a unique color band. Each year, we attempted to locate and identify all subadult and adult owls which had color bands during the previous year and to capture all unbanded owls.

We delimited owl sites on the basis of nest and roost locations and the owls' behavior. Sites roughly approximated owl territories; territory boundaries, however, could not be determined without the use of radio-transmitters. Owl site centers often fluctuated between years, and some owls exhibited breeding dispersal (Blakesley 2003, see below).

From 1991-2000, we searched for each previously banded owl which we could not find, by conducting complete nighttime surveys of a 1.5 mile radius area centered around the owl's last nest or roost location. If an owl was replaced at a site by another owl of the same sex, we conducted two complete searches each year, for two years. If the owl had not been replaced, we conducted six visits to the site including four complete surveys each year, for two years. After an owl was missing for two years, we no longer conducted complete searches for that owl. From 2001-2004, rather than survey site-centered circles, we completely searched the Density Study Area at least three times each year.

We collected spotted owl pellets below roost and nest trees during daytime surveys. We also collected pellets whenever we observed a pellet being egested. Pellets were dried, stored, and later dissected to identify prey remains and consequently infer composition of the spotted owl diet.

We measured vegetation and physiographic characteristics surrounding nest trees. We established sampling strip plots 10 m in width, beginning 5 m from the nest tree and extending 30 m in each of the 4 cardinal directions. We measured diameter at breast height (dbh) and height of all trees  $\geq 40$  cm dbh, all snags  $\geq 12$  cm dbh, and all logs  $\geq 25$  cm diameter within the entire plots. We measured dbh and height of trees  $< 40$  cm dbh in the central third of each plot. We estimated canopy cover 10 m and 25 m from the nest tree in each of the 4 cardinal directions using a spherical densiometer. In addition, we recorded nest type (top cavity, side cavity, platform); species, dbh, and height of the nest tree; nest height; tree condition (live tree or snag); slope; aspect; and elevation.

## **SITE OCCUPANCY**

Lassen National Forest personnel began surveying for spotted owls in 1981. Between 1981 and 1989, owls were detected at approximately 50 sites within the Lassen study area. We subsequently

detected territorial owls at 115 sites from 1990 through 2004, including 78 territories within the Density study area (Tables 1 and 2).

Owl pairs occurred at 70 sites in the DSA and at an additional 26 sites in the Lassen study area in at least one year from 1990-2004 (Tables 1 and 2). Among the 78 sites within the DSA in which territorial owls were observed (Table 1), we compared site occupancy in 1991-1994 with site occupancy in 2001-2004. We observed declines between early years of our study and later years of our study, whether we compared the number of sites with any owl detection, at least one resident owl detection, or a pair detection (Table 3). These declines occurred despite more extensive surveys in 2001-2004 than in 1991-1994. Four spotted owl territories were abandoned following timber harvest within the nest stand (CARIBO, RUFFAR) or within approximately 0.5 km of the nest stand (GURNSE, COPPER). In addition, one territory (KAYTSA) was abandoned two years after the Storrie wildfire, even though the KAYTSA spotted owls nested in a charred snag the year following the Storrie fire.

Outside of the DSA, many sites where owls were found in earlier years were not surveyed in subsequent years because no owls were banded at those sites. Therefore, changes in the total number of sites where owls were found each year outside the DSA (Table 2) should not be interpreted as changes in spotted owl site occupancy over time.

## **REPRODUCTIVE RATES**

Fecundity is defined as the number of female offspring per female owl  $\geq 1$  yr old. Productivity is the number of female offspring per female owl that produced young. We assumed  $\frac{1}{2}$  of all young were female.

Nesting rates were generally higher for adult than subadult female owls (Table 4). All measures of reproductive output showed considerable annual variation (Table 4). The proportion of female owls nesting ranged from 0.11 to 0.97. The proportion of nesting females that successfully fledged young ranged from 0.25 to 0.91. Fecundity of adult female spotted owls ranged from 0.07 to 1.09. Productivity of spotted owls ranged from 0.56 to 1.15. Estimated overall fecundity appears under "Fecundity, Survival and Population Change", below.

The proportion of females nesting, productivity, and consequently fecundity were all higher in 1992 than in any other year. Over half of the broods observed in 1992 were composed of triplets, 7 sets of triplets were observed in 2002, and only one set of triplets was observed in the remaining years. The high reproductive output in 1992 and 2002 was reflected in increased recruitment in subsequent years -- a greater proportion of subadults were observed in 1993 and 2003 than in other years (Figure 2). The lowest number of subadults observed in the population, 2 in 1998, followed the year with the lowest fecundity--1997.

## **FLEDGING DATES**

We observed 248 different broods of fledgling spotted owls in 1990-2004 (broods consisted of 1-3

young). Most fledging occurred in June, although fledglings were observed as early as 16 May, ( $n = 4$  fledging events in May) and other nests were known to fledge from 1-17 July ( $n = 13$ ). Of 128 nests known to be active  $\leq 21$  days before fledging was first observed, 90% fledged by 8 July (Figure 1).

## **FECUNDITY, SURVIVAL, AND POPULATION CHANGE – summary of peer-reviewed publications.**

### **Analytical Methods**

We analyzed spotted owl demographic rates from 1990-1999, including fecundity, age-specific apparent survival, and the finite rate of population change ( $\lambda$ ; Blakesley et al. 2001). We estimated fecundity using mixed models ANOVA under a maximum likelihood framework (Littell et al. 1996), with owl site and year modeled as random effects. We estimated apparent annual survival probability using program MARK (White and Burnham 1999) and used QAICc in an information-theoretic framework to select the best model of survival probability (Franklin et al. 1996). We estimated  $\lambda$  using a four-stage projection matrix model ( $\lambda_{PM}$ ; Caswell 1989, Franklin et al. 1996). We also conducted elasticity analyses to evaluate the contribution to  $\lambda$  of each fecundity and survival rate (Caswell 1989).

Projection matrices were used to estimate  $\lambda$  in three earlier meta-analyses of the northern spotted owl, *S. o. caurina* (USDI 1990, Forsman et al. 1996, Franklin et al. 1999), in two other studies of the California spotted owl (LaHaye et al. 1992, Seamans et al. 2001), and one study of the Mexican spotted owl, *S. o. lucida* (Seamans et al. 1999).

Projection matrix methods for estimating  $\lambda$  are based on several assumptions, including geographical closure (neither emigration nor immigration occurs) and a stationary population (average survival and fecundity rates occur each year). With respect to geographical closure, new owls are added to a projected population only through internal recruitment (using fecundity estimates), whereas owls are lost from the projected population through both death and permanent emigration from the study area (reflected in owl capture histories). Emigration is most likely to occur through natal dispersal. With respect to average vital rates,  $\lambda_{PM}$  is an asymptotic value that does not incorporate annual variation in survival and fecundity (see Franklin et al. 2004:17 and 53-54 for further discussion of the use of projection matrix population models with spotted owl data). It should be noted that the projection matrix method was the best available method for estimating  $\lambda$  during the time it was used by both northern and California spotted owl studies.

In July 2001 we participated in the first meta-analysis of demographic rates of California spotted owls, in Fort Collins, CO (Franklin et al. 2004). At this time, a new analytical method was available for estimating  $\lambda$  (Pradel 1996), referred to as the reparameterized Jolly-Seber method, or Pradel's model, and denoted as  $\lambda_{RJS}$  or  $\lambda_t$ . Pradel's model estimates  $\lambda$  directly from capture-recapture data, does not require the assumption of a stationary population and allows for time-specific estimation of  $\lambda$ . In a 1998 meta-analysis of the northern spotted owl,  $\lambda$  was estimated by both the projection matrix and Pradel methods (Franklin et al. 1999). Although the Pradel model was considered to be exploratory during the 1998 meta-analysis (Franklin et al. 1999), it was used exclusively in the 2004 northern spotted owl meta-

analysis (Anthony et al. 2004) because it was considered to be more appropriate for spotted owl mark-recapture data (Franklin et al. 2004).

Estimates of  $\lambda_{PM}$  and  $\lambda_t$  differ in their interpretation:  $\lambda_{PM}$  reflects whether the population of territorial female owls within a study area *are replacing themselves* (through internal recruitment) if the system was geographically closed, whereas  $\lambda_{RJS}$  reflects whether the population of territorial female owls *had been replaced*, from internal recruitment and/or immigration (Franklin et al. 1999, Franklin et al 2004). In both cases,  $\lambda < 1$  indicates a declining population, and  $\lambda > 1$  indicates an increasing population.

At the 2001 California spotted owl meta-analysis, we estimated fecundity using mixed models ANOVA under a maximum likelihood framework, with owl site and year modeled as random effects. We modeled even-odd year effects (alternating years of relatively higher and lower fecundity), linear effects of time (e.g., steady downward trend in fecundity over the years) and quadratic time effects (non linear trends in fecundity) and the combination of even-odd year effects and a linear trend. We estimated age-specific apparent annual survival probability in a meta-analysis, and  $\lambda_t$  for individual study areas and in a meta-analysis, using program MARK (Franklin et al. 2004). We used AICc and QAICc in an information-theoretic framework to model selection for selecting the most appropriate models of fecundity, survival, and population trend (Franklin et al. 2004).

Because a second meta-analysis of demographic rates for California spotted owls is scheduled for January 2006, we do not present new demographic analyses here.

## **Results**

### *Fecundity*

Least-squares mean estimates ( $\pm$  SE) of fecundity from 1990-1999 on the Lassen study area were  $0.065 \pm 0.066$  for subadults ( $n = 33$ ) and  $0.291 \pm 0.065$  for adults ( $n = 381$ ; Blakesley et al. 2001). Yearly effects accounted for 47% of the random variation in fecundity. In 2001, we were only able to compare models of fecundity among adult owls ( $n = 418$ ). The best model of fecundity for the Lassen study area had an even-odd year effect ( $\hat{\beta} = 2.96 \pm 0.141$ ) indicating higher fecundity in even-numbered years. This model was twice as likely as the next best model. Estimated mean fecundity across years (1990-2000) for adult spotted owls on the Lassen study area was  $0.336 \pm 0.083$  (Franklin et al. 2004).

### *Apparent Survival Probability*

We banded 219 juvenile and 200 subadult or adult owls at 90 sites, with a combined total of 1080 captures from 1990-1999. Estimated annual apparent survival probability ( $\hat{\phi}$ ) was  $0.333 \pm 0.055$  for juveniles and  $0.827 \pm 0.015$  for subadults and adults combined (Blakesley et al. 2001). In the 2001 meta-analysis, we estimated survival for adult owls only, 1990-2000 ( $n = 223$ ). The best model produced a combined estimate of apparent survival probability for the Lassen, Eldorado, Sierra, and San Bernardino study areas,  $\hat{\phi} = 0.819 \pm 0.008$  (Franklin et al. 2004). From the best model that provided separate

estimates for the Lassen study area ( $\Delta\text{QAICc} = 5.53$ ),  $\hat{\phi} = 0.829 \pm 0.015$ .

### *Population Trend*

Using estimates of fecundity and apparent survival probability from 1990-1999,  $\hat{\lambda}_{PM}$  was  $0.910 \pm 0.025$ , indicating an annual rate of decline in the territorial spotted owl population of 9% per year (Blakesley et al. 2001). Elasticity analyses revealed that  $\lambda$  was most sensitive to changes in survival of adult owls. However, the 43% of the variance in  $\lambda$  was due to variation in fecundity, and 28% due to variation in first year survival.

In the meta-analysis of  $\lambda_t$  we included capture histories of 191 adult and subadult spotted owls from 1992-2000, within a subset of the greater Lassen study area roughly equivalent to the current DSA described in the Field Methods of this report. The best model for the Lassen study area yielded  $\hat{\lambda}_t = 0.985 \pm 0.026$  (Franklin et al. 2004). Due to constraints of the  $\lambda_t$  method, this estimate applied only to 1994-1999. Although there was no evidence for time-specific effects or time trends in  $\lambda_t$  when the Lassen data were considered alone, the top model from the meta-analysis of  $\lambda_t$  indicated annual variation in  $\lambda_t$  (Franklin et al. 2004).

Franklin et al. (2004:36) provided an important caveat in understanding  $\lambda_t$ :

“Estimates of  $\lambda_t$  also should not be interpreted as numbers of birds; these are annual estimates of rates of change in the number of birds. For example, the periodic estimates of  $\lambda_t$  that are  $<1$  in the SIE and LAS study areas represent a decrease in the number of birds. The intervening values  $>1$  do not indicate that the population was restored to the original numbers at the beginning of the study; they only indicate that numbers increased relative to numbers in the preceding year. Thus, a cyclic pattern in  $\lambda_t$  can exist that ultimately results in losses of birds over time. However, this should be somewhat balanced in the estimates of mean  $\lambda_t$  over time.”

In an effort to understand how  $\lambda_t$  affected changes in abundance, Franklin et al. (2004) estimated “realized population change” as the product of the annual estimates of  $\lambda_t$ . The resulting population trajectory for the Lassen study area showed a decline in abundance of spotted owls from 1994-1999; however, 95% confidence intervals were very large, indicating a fairly stationary population (Franklin et al. 2004).

### **Discussion**

The even-odd year trend in fecundity among spotted owls in the Lassen study may be a characteristic of spotted owl populations in the Cascade geographic province; the even-odd trend was observed on all of the study areas in the Oregon and Washington Cascades (Franklin et al. 1999). This trend was also evident in the Lassen study area during the four years following the meta-analysis (Table 4).

Franklin et al. (2004:64) suggested that “the high reproductive output observed in 1992 may have affected rates of population change for several years following this event. If California Spotted Owl

population dynamics were largely driven by such events, then continued monitoring of these populations will be necessary to capture these relatively rare events.” We now have 4 additional years of site occupancy and fecundity data from the Lassen study area since the first California spotted owl meta-analysis. In 2002, we observed high reproductive output similar to that of 1992 (Table 4). However, site occupancy by resident owls in the Lassen study area did not rebound in the two years following this reproductive burst (Table-3).

Survival probability of adult California spotted owls on the Lassen and other National Forests was lower than survival probability of northern spotted owls where northern spotted owl populations were declining (Franklin et al. 1999).

Estimated  $\lambda_t$  from 1994-1999 (Franklin et al. 2004) was higher than estimated  $\lambda_{PM}$  from 1990-1999 (Blakesley et al. 2001) for spotted owls in the Lassen study area. Several explanations may account for the differences between the two estimates of  $\lambda$  from the Lassen study area, and these explanations are not mutually exclusive. First, recalling the differences in interpretation of the two estimates, the Lassen population may not be replacing itself but may be sustained by immigration from outside the study area. Second, the population may have declined more steeply from 1990-1994 than from 1994-1999. Third, the Lassen study was designed to use the  $\lambda_{PM}$  method and we did not completely survey the entire study area until 2001. This may have violated the assumption of equal capture probability of banded and unbanded birds required for estimation of  $\lambda_t$ . If this assumption was violated, it would have positively biased the estimate of  $\lambda_t$  (Franklin et al. 2004). Finally,  $\lambda_{PM}$  may have been underestimated due to an underestimate of first year survival caused by emigration of juvenile owls from the study area. However, we believe the rate of juvenile emigration was relatively small because the Lassen study area is large relative to dispersal distances of spotted owls and our estimated apparent survival probability of juvenile owls ( $0.333 \pm 0.055$ ) was similar to that of an insular population of California spotted owls ( $0.344 \pm 0.052$ ; LaHaye et al. 1994).

## **DIET**

We analyzed the contents of 3273 spotted owl pellets collected from 1990-2002. We estimated the biomass of each prey item consumed following standard methods employed for estimating spotted owl diet (e.g., Forsman et al. 2004). For this report, we estimated the average proportion of 10 prey categories across sites within each year, and then averaged the proportions across years.

Northern flying squirrels (*Glaucomys sabrinus*) accounted for 61% of prey biomass consumed. The remainder of the spotted owl diet was fairly evenly distributed among voles (8%; *Microtus spp.* and *Clethrionomys californicus.*), pocket gophers (8%; *Thomomys spp.*), woodrats (5%; *Neotoma spp.*), mice (5%; *Peromyscus spp.* and *Reithrodontomys megalotis*), birds (5%), diurnal squirrels (4%; *Sciurus griseus*, *Spermophilus lateralis*, *Tamiasciurus douglasii*, and *Tamias sp.*), shrews and moles (2%; *Scapanus latimanus*, *Sorex spp.*, and *Neurotrichus gibbsii*), lagomorphs (2%; *Sylvilagus bachmani* and, possibly, hares), insects (<1%). Pellets also contained 7 bats, 2 lizards, and 1 snake.

The diet composition of owls throughout the Lassen study area in 1990-1992) was very similar to that reported for a smaller sample (geographically and temporally) from the Lassen study area reported in Verner et al. (1992b).

### **NEST TREES AND NEST STANDS**

We measured nest stand characteristics for 132 spotted owl nests used on 174 occasions from 1990-2000 in the Lassen study area. Spotted owl nests occurred primarily in cavities of large live pines and firs (Table 5). Mean canopy cover in the immediate vicinity of the nest was consistently >80%. Nest tree dbh ranged from 38-219 cm; however, 90% of nest trees were  $\geq 76$  cm dbh. The number of hardwood stems was highly variable because very few sites contained a measurable hardwood understory, in contrast to some parts of the range of the California spotted owl (Verner et al. 2002a).

### **SITE OCCUPANCY, APPARENT SURVIVAL AND REPRODUCTION OF CALIFORNIA SPOTTED OWLS IN RELATION TO FOREST STAND CHARACTERISTICS – summary of peer-reviewed publication.**

We evaluated the relationships between spotted owl demographic parameters and forest stand characteristics within spotted owl home ranges (Blakesley et al. In Press 2005). These analyses were predicated on the owls having selected home ranges within a landscape, and therefore reflect a finer scale of habitat selection than studies that compare habitat used with habitat available at a landscape scale.

Our objectives were to determine (1) whether variability in spotted owl site occupancy, apparent survival probability, or reproduction were related to forest cover and stand structure; (2) whether such relationships were stronger at the scale of home range core areas or at the scale of smaller nest areas; (3) which characterization(s) of high quality habitat best explained variation in site occupancy, apparent survival probability and reproduction; and (4) whether forest cover type, nest tree characteristics, and/or local nest stand measures were related to nesting success (Blakesley et al. In Press 2005).

### **Methods**

We used vegetation classification maps for 67 spotted owl sites on and near the Almanor Ranger District of the Lassen National Forest, within roughly the western 2/3 of the Lassen spotted owl study area. Spotted owl data were collected as part of the Lassen spotted owl demography study. Measurement of vegetation and physiographic characteristics was described in Field Methods, above.

We defined spotted owl core areas (814 ha) following Bingham and Noon (1996). Core areas were empirically estimated regions within spotted owl home ranges that received concentrated use. Nest areas represented the area assumed to be used exclusively by a single owl pair. We defined nest areas (230 ha) based on one half the minimum distance between adjacent owl territories.

We modeled site occupancy as a function of habitat classes using logistic regression with an ordered multinomial response: no owls (0), single owl (1), owl pair (2) ( $n = 273$ ). We used spotted owl

capture history data from the demographic study to model the effects of vegetation covariates on apparent survival probabilities in program MARK (White and Burnham 1999). We modeled reproduction of adult female owls as a function of habitat classes using binomial logistic regression (no juveniles produced, including no breeding attempt and breeding failure [0], 1-3 juveniles produced [1]). We used logistic regression to model nest success as a function of nest tree and nest stand characteristics, habitat class of the nest stand, and year ( $n = 122$  reproductive outcomes; 89 successes, 33 failures). For all analyses, we used an information-theoretic approach to model selection.

## **Results**

Seventy-eight percent of the owl core areas and 83% of nest areas were composed of forested stands dominated by trees  $\geq 30$  cm dbh and with  $\geq 40\%$  canopy cover. Site occupancy was positively associated with the amount of the nest area dominated by large trees with high canopy cover within the nest area. Site occupancy was negatively associated with the amount of non-forested areas and forest cover types not used for nesting or foraging, and with medium-sized trees with high canopy cover within the nest area. Site occupancy also decreased over time and with increasing elevation. Apparent survival probability varied annually and was positively related to the area of each habitat class multiplied by the quotient proportion used/proportion available for each type, at both the nest and core scales. Reproductive output was negatively related to elevation and non-habitat within the nest area. Nest success was positively associated with the presence of large remnant trees within the nest stand (Blakesley et al. In Press 2005).

## **BREEDING DISPERSAL – summary of peer-reviewed publication.**

Although spotted owls are generally philopatric, we observed breeding dispersal in 7% of inter-annual observations of banded individuals ( $n = 54$  of 743 occasions; Blakesley et al. In Press 2006). We made a priori predictions about the factors associated with breeding dispersal probability, breeding dispersal distance, and the consequences of dispersal based on ecological theory and published literature.

## **Methods**

We used logistic regression to model breeding dispersal probability as a function of sex, age class, reproduction, social status, territory quality, and interactions between territory quality and age class, territory quality and social status, and sex and reproduction. We used general linear models to model breeding dispersal distance as a function of age class, social status, sex, pre-dispersal territory quality and post-dispersal territory quality. In analyses of breeding dispersal probability and dispersal distance, we used an information-theoretic approach to model selection. We compared the quality of each owl's pre-dispersal territory with its post-dispersal territory. We compared the subsequent pair status of single owls that dispersed with single owls that did not disperse, using a  $X^2$  test. Similarly, we compared the pair status of owls that lost their mates and dispersed with owls that lost their mates and did not disperse (Blakesley et al. In Press 2006).

## **Results**

As predicted, breeding dispersal probability was higher for younger owls, single owls, paired owls which lost their mates, owls at lower quality sites, and owls which failed to reproduce in the year preceding dispersal. Breeding dispersal of northern spotted owls occurred at a similar rate (8%) and decreased with increasing age of the owls (Forsman et al. 2002). Sex had little effect on breeding dispersal probability in California spotted owls (Blakesley et al. In Press 2006), but was higher for female than male northern spotted owls (Forsman et al. 2002).

Breeding dispersal distance was similar for female and male California spotted owls (median = 7 km, range = 1-33; Blakesley et al. In Press 2006). In contrast, median breeding dispersal distances for northern spotted owls were approximately 14 km for males and 23 km for females (Forsman et al. 2002). We found no strong relationships between dispersal distance and any of the conditions that were associated with dispersal probability in California spotted owls (Blakesley et al. In Press 2006), whereas breeding dispersal distance was greater for younger than older northern spotted owls (Forsman et al. 2002).

Breeding dispersal resulted in improved territory quality in 72% of cases for California spotted owls, indicating that breeding dispersal is adaptive (Blakesley et al. In Press 2006).

## **NATAL DISPERSAL**

Sixty-one owls banded as juveniles on the Lassen study area were reobserved in subsequent years, recaptured and given unique color bands (28 females and 33 males). Additionally, 12 owls with juvenile cohort bands were detected but were not recaptured. Straight line distances moved from natal sites to points of recapture ranged from 3 to 77 km (median = 25 km), with no differences observed between the sexes. Similarly, median natal dispersal distances of northern spotted owls were 25 km for females and 15 km for males (Forsman et al. 2002).

## **BARRED OWLS**

A recent review of the status of the northern spotted owl thoroughly detailed the invasion and potential future threats of a close relative, the barred owl (Courtney et al. 2004). This report documented the rapid expansion of the range of the barred owl southward from Washington to include most of the historic range of the northern spotted owl. The report also documented negative interspecific interactions between barred owls and northern spotted owls including territory displacement, competition for food and space, and hybridization. Courtney et al. (2004) concluded that, although they were convinced that barred owls were negatively impacting northern spotted owls, additional data was necessary to address the extent of current and future potential impacts.

The first barred owl detection in California was in 1981 (Evens and LeValley 1982) and the range expansion since has been rapid (Dark et al. 1998). Although there are currently relatively few barred owl detections in the Sierra Nevada Mountains, the range is expanding (Courtney et al. 2004). Three barred

owls have been detected on the Lassen study area. One was detected on a single occasion in 2001 and not captured. The other two occurred together during 2002 in the middle of a spotted owl territory that had successfully fledged three young. A female spotted owl was heard aggressively calling back and forth with a pair of barred owls on one occasion. Neither the adult spotted owls nor their young could be relocated later in 2002, despite numerous visits. We do not know if the spotted owls were silent or temporarily displaced. The same pair of adult spotted owls occupied the territory in 2003 and the barred owls have not been detected since.

We have also detected and banded three spotted owl/barred owl hybrids. Hybrid owls have not been detected in great numbers as the barred owl has expanded its range across the western United States and Canada (Courtney et al. 2004). Of 9000 *Strix* owls banded in Washington and Oregon, only 47 were confirmed hybrids (Kelly and Forsman 2004). One hypothesis is that hybrids occur mainly where barred owls are uncommon and finding a barred owl mate is difficult (Kelly and Forsman 2004).

The three hybrid owls we detected, two males and one female, have paired with spotted owls. None have successfully nested. All had plumage characteristics and vocalizations intermediate between spotted and barred owls, similar to previous descriptions of hybrids (Hamer et al. 1994). The first male hybrid detected was resident at an established spotted owl territory in 1999 and 2000 and was not detected after 2000. This male was observed on several occasions aggressively chasing and diving at the male and female spotted owls of a neighboring territory. Both the long-time resident female spotted owl where the male hybrid was present and the female spotted owl at the neighboring territory vacated their territories between the 1999 and 2000 field seasons, but returned after the hybrid male was gone. The second hybrid male was resident at an established spotted owl territory in 2001 but not detected after 2001. The female hybrid, the largest owl with the longest wing chord measured on our project, was first detected in 2001 and has been resident at three different established spotted owl territories in four years. This female was observed aggressively chasing a subadult female spotted owl that vacated the territory. The long-time resident female spotted owl formerly at the most recent territory used by the hybrid female owl later occupied a neighboring territory. Given overall low rates of breeding dispersal (see above), it is likely that the spotted owl was displaced by the hybrid owl. We believe that our observations support the idea that barred owls, and hybrids, aggressively displace spotted owls. Our study has the unique opportunity to examine the impacts of a potential invasion of the barred owl given a decade of pre-invasion information for comparison.

## **EXTERNAL PARASITES**

Hippoboscids are a common ectoparasite on spotted owls (Young et al. 1993, Hunter et al. 1994) and can serve as vectors for pathogenic organisms (Baker 1967), including West Nile Virus (Gancz et al. 2004). With the recent arrival of West Nile Virus in North America and the possible susceptibility of spotted owls to West Nile disease, hippoboscids warrant increased attention by owl researchers and managers (Courtney et al. 2004).

Young et al. (1993) found that handling of spotted owls during capture was 95% efficient in detection of hippoboscids, and reported 17% of northern spotted owls in northwest California were infested with hippoboscids. We have observed hippoboscids on 2.3% of owls captured (n = 689). Only two juveniles that we captured had hippoboscids (n = 353). Young et al. (1993) also found that juveniles had a much lower rate of infestation than adults and noted that this may be due to lack of protection from preening in juvenile plumage. Young et al. (1993) did not compare infestation rates of subadult and adult spotted owls; however, we found subadults had a 7.3% infestation rate (n = 96) whereas 2.3% of adult owls were infested (n = 216).

We have not taxonomically identified the hippoboscids from the Lassen study area but we have collected and preserved the majority of hippoboscids encountered. We have not observed any other external parasites on spotted owls in the Lassen study area.

### **THERMAL ECOLOGY AND ENERGETICS – summary of peer-reviewed publication.**

We collaborated on a study of the thermal ecology and ecological energetics of California spotted owls (Weathers et al. 2001). The study measured spotted owl resting metabolic rates using open-circuit respirometry in the laboratory, and field metabolic rate using the doubly labeled water technique. Results indicated that spotted owls have a basal metabolic rate of  $10.13 \pm 0.46$  J/g/hr and a thermoneutral zone of 18-35°C. The basal metabolic rate was only 82% of that predicted allometrically. Estimated field metabolic rate of adult spotted owls with dependent young averaged  $249 \pm 60$  kJ/day, only 34% of that predicted for similarly sized non-passerine birds (Weathers et al. 2001).

Resting metabolic rate of spotted owls at temperatures above 35 °C increased 1.5 times faster than predicted allometrically, supporting the hypothesis that spotted owls prefer structurally complex, older forests because of the forests' favorable microclimate (Weathers et al. 2001).

### **SUMMARY**

In 15 years of research, we have provided insight into many aspects of California spotted owl ecology, including demographic rates and trends, relationships between demographic parameters and forest stand characteristics, causes and consequences of breeding dispersal, diet, competitors, parasites, and energetics. We have published 5 peer-reviewed papers; readers are encouraged to read our publications for more complete understanding of our analyses and results.

Key findings of our research include:

- Several lines of evidence suggesting the spotted owl population in the Lassen study area declined from 1990-2004. The number of sites occupied by territorial owls declined, two estimates of population change ( $\lambda$ ) were  $< 1$ , and models of site occupancy in relation to habitat included a declining trend over time. There is no evidence that the spotted owl population on the Lassen study area increased from 1990-2004.

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- Site occupancy and apparent survival of California spotted owls were enhanced in core and nest areas that contained habitat features known to be selected by the owl at the landscape scale. Reproductive output decreased as the amount of non-habitat within the nest area increased.
- Diet of spotted owls in the Lassen study area is dominated by a single prey species, the northern flying squirrel.
- Breeding dispersal probability was higher for younger owls, single owls, paired owls which lost their mates, owls at lower quality sites, and owls which failed to reproduce in the year preceding dispersal. Breeding dispersal resulted in improved territory quality for most owls.
- Barred owls and hybrid barred x spotted owls were rare on the Lassen study area through 2004. However, barred and hybrid owls appeared to displace territorial spotted owls.

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Table 1. Social status<sup>a</sup> of California spotted owls within the Lassen Density study area, 1990 through 2004.

Site	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
ALDERC	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
BATTLE	NS	NS	NS	NS	NS	NS	PAIR	MRFP	PAIR	PAIR	PAIR	MRFP	0	0	0
BENKNO	MR <sup>b</sup>	MR <sup>b</sup>	MP	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRFP	PAIR	PAIR	PAIR
BENNER	PAIR	PAIR	PAIR	PAIR	PAIR	MRFR	FP	PAIR	MP	0	0	0	0	0	0
BENSPR	0	0	0	FR	0	0	MR	0	MR	0	0	PAIR	PAIR	PAIR	PAIR
BLULED	NS	NS	NS	MRFR	NS	MRFR	PAIR	MRS	MRFP	MRFR	MPFP	0	0	0	0
BOGARD	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
BUTTCR	PAIR	MRFR	PAIR	PAIR	MRFR	PAIR	PAIR	MRFP	PAIR	MRFR	0	MRS	MRFP	MRFP	PAIR
BUTTMN	PAIR	PAIR	PAIR	PAIR	PAIR	MRFR	PAIR	PAIR	PAIR	MPFR	0	0	0	0	MP
BUTTMW	PAIR	PAIR	PAIR	PAIR	MRFP	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
CAIRNN	PAIR	PAIR	PAIR	PAIR	MRFP	0	MRFP	0	0	0	FP	0	MP	MP	PAIR
CARIBO	PAIR	PAIR	PAIR	0	0	NS	0	0	0	0	0	0	0	0	0
CARTER	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	FRS	0
COLD CR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	0
CONELA	NS	MR	NS	0	0	MP	0	0	0	0	0	0	0	0	0
COPPER	PAIR	PAIR	PAIR	PAIR	0	MPFP	0	0	NS	0	FRS	MP	0	MRS	0
CRAZYH	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	0	PAIR	PAIR	PAIR	PAIR
CUMMIN	PAIR <sup>b</sup>	MPFP <sup>b</sup>	FP <sup>b</sup>	MP	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR	MRFR	PAIR	PAIR	PAIR
DOEMTN	NS	NS	NS	NS	NS	NS	PAIR	MPFR	NS	FP	NS	NS	FR	MRFP	PAIR
DOMING	NS	NS	NS	NS	NS	MR	NS	NS	NS	NS	NS	NS	0	0	0
DYERMT	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	FRS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
EAGLER	NS	MRFP	PAIR	NS	NS	NS	NS	NS	NS	NS	NS	NS	0	0	0
ELAMCR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR

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Site	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
ELAMEA	NS	NS	PAIR	PAIR	MRFR	MRFR	0	0	0	0	0	0	0	0	0
ELAMWE	NS	NS	NS	NS	NS	MR	0	0	0	0	0	0	0	0	0
FANANI	MRFP	PAIR	MRS	PAIR	MPFP	0	NS	NS	0	NS	NS	NS	0	0	MRFP
FANSOU	NS	NS	NS	PAIR	MPFR	PAIR	MPFR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
FLEISH	PAIR	MR	PAIR	MRFP	PAIR	PAIR	PAIR	MRS	0	MRFP	MRS	0	0	0	0
GRIZZL	PAIR	PAIR	PAIR	MPFP	NS	NS	NS	MPFP	NS	NS	NS	NS	MPFP	NS	NS
GURNSE	NS	MRFP	PAIR	PAIR	PAIR	0	0	0	NS	0	0	0	0	0	0
HAMILT	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRFP	PAIR	PAIR	PAIR
HAMPTO	MPFP	MP	NS	NS	NS	NS	NS	MP	NS	NS	NS	NS	0	MP	0
HAZENF	NS	NS	NS	NS	NS	NS	MP	NS	NS	NS	NS	NS	PAIR	PAIR	MRS
HOLEGR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	PAIR	PAIR	PAIR	PAIR
JENNIE	PAIR <sup>b</sup>	PAIR <sup>b</sup>	PAIR	MRFR	MRFP	MPFP	PAIR	PAIR	PAIR	0	PAIR	PAIR	PAIR	PAIR	PAIR
KAYTSA	PAIR	PAIR	PAIR	PAIR	MPFR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	0
LASTCR	NS	MR	PAIR	PAIR <sup>b</sup>	MRFR	MRFR	PAIR	PAIR	0	0	0	0	0	FP	0
LCSPRS	NS	NS	NS	NS	NS	NS	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
LGRIZC	NS	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	MRS	MRS	PAIR	PAIR	0	PAIR	MRS	MRFP
LOCHER	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
LONGVI	NS	PAIR	PAIR	PAIR	PAIR	MRFP	0	0	0	MP	0	0	0	0	0
LOSTTO	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	MRS	0	MP	0	0	0	MPFP	0
MARNOR	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR
MARTIN	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MPFR	PAIR	PAIR	PAIR	PAIR
MILLCR	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	FP	PAIR	PAIR	PAIR
MILLER	MP	MP	MR	MRFR	PAIR	MRS	0	0	MRFP	MRS	0	MP	0	0	0
MOONPA	PAIR	PAIR	NS	0	NS	NS	NS	NS	NS	NS	NS	PAIR	PAIR	PAIR	0

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Site	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
MORGAN	MRFP	PAIR	PAIR	PAIR	MR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
MOSQUI	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
MUDCRE	PAIR	PAIR <sup>b</sup>	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	0	0	0	0	0
PEAPTN	MRFR	MRFR	NS	NS	MR	NS	MR	0	0	0	0	0	0	MRS	0
PEGLEG	PAIR	MRFP	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	0	PAIR	FP
PINECR	NS	NS	NS	MRFR	MRS	PAIR	MRS	MP	NS	0	0	FP	PAIR	MRS	MP
RICECR	MP	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
ROCKCR	PAIR <sup>b</sup>	MRFP <sup>b</sup>	PAIR	PAIR	MPFR	PAIR	FP	NS	FP	PAIR	FP	0	0	MRS	FP
ROCKPT	PAIR	PAIR	PAIR	PAIR	MRFP	PAIR	MRFP	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
RUFFAR	NS	MRFP	0	NS	NS	NS	NS	PAIR	PAIR	PAIR	0	MRS	0	0	0
SCENIC	PAIR	PAIR	PAIR	MRFR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	PAIR	PAIR	PAIR	PAIR
SHANGH	MRFP	MRFR	0	0	NS	0	MP	NS	0	NS	NS	NS	0	0	0
SHANOR	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MRFR	PAIR	PAIR	PAIR	PAIR	PAIR
SMBUTT	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	0	MPFP	0
SOLDIE	NS	NS	NS	NS	NS	MRFP	MP	MP	NS	NS	NS	NS	0	MP	0
SPENCE	NS	NS	NS	NS	NS	0	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	0	0	0
STARBU	PAIR <sup>b</sup>	PAIR <sup>b</sup>	PAIR <sup>b</sup>	PAIR <sup>b</sup>	MRFP <sup>b</sup>	MR <sup>b</sup>	NS	NS	NS	NS	NS	NS	0	FP	0
SUSNRN	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
SWAINM	NS	NS	NS	NS	NS	NS	PAIR	PAIR	MPFP	0	0	0	0	0	0
TURNER	MR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MPFR	PAIR	PAIR	FRS
TWINTS	PAIR	MRFR	PAIR	MPFR	PAIR	PAIR	PAIR	PAIR	MRS	0	MPFP	MPFR	0	0	0
UPDEER	NS	NS	NS	NS	NS	MRFR	FP	NS	NS	NS	PAIR	NS	MPFP	PAIR	PAIR
UPSTEP	PAIR	FP <sup>b</sup>	NS	PAIR	MRS	PAIR	0	0	MRFP	MRS	MRS	PAIR	0	0	0
UPYELL	PAIR	PAIR	PAIR	PAIR	MRS	PAIR	PAIR	PAIR	PAIR	PAIR	MRFR	PAIR	PAIR	MPFR	PAIR

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Site	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
WARNER	MRFR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	0	MRFP	MRS	MP	0	0
WARVAL	NS	NS	NS	NS	PAIR	0	0	NS	NS	NS	NS	NS	0	0	0
WILDCM	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	0	NS	0	0	0	0	0	MP
WILLAR	MPFP	MPFP	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	PAIR	MRFP	PAIR
WILLKS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
WILLOW	PAIR	PAIR	PAIR	PAIR	PAIR	MPFR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
WILSON	MPFR	PAIR	PAIR	MRFR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
CLOVER <sup>c</sup>												0	0	FP	0
FEATHE <sup>c</sup>				MP								0	0	0	0
JONESVA <sup>c</sup>						MP						0	0	0	0
LTFRED <sup>c</sup>												0	0	MP	0
MILRES <sup>c</sup>												0	0	FP	UP
SLATEC <sup>c</sup>												0	0	FP	0

<sup>a</sup> Key: M = Male; F = Female  
R = Owl Resident (detected at least 2 times, separated by one week)  
P = Owl Present  
PAIR = Male and Female Resident, found together at least twice  
S = Resident owl is confirmed to be single (no owl of the opposite sex detected after 6 visits)  
NS = Not Surveyed completely  
0 = Surveyed completely and no owls detected  
UK= Owl of Unknown sex detected (did not vocalize)

<sup>b</sup> One or more owls carrying a radio transmitter; not used for demographic estimates.

<sup>c</sup> Owl observed on only one occasion/yr; not an established territory.

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Table 2. Social status<sup>a</sup> of California spotted owls within the greater Lassen study area but outside of the Density study area, 1990 through 2004.

Site	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
ALDCAM	NS	NS	NS	NS	NS	NS	MRFP	PAIR	PAIR	MRFR	MRS	PAIR	MPFP	MPFP	NS
ASHURS	MRS	NS	NS	NS	NS	MR	NS	NS	NS	NS	NS	NS	NS	NS	NS
BATHTU	NS	PAIR	NS	NS	NS	NS	MRFP	PAIR	MP	NS	NS	NS	NS	NS	NS
BATHTW	NS	NS	NS	NS	NS	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MP	NS
BAXTER	PAIR	PAIR	PAIR	PAIR	PAIR	MP	NS	NS	NS	NS	NS	NS	NS	NS	NS
BEARFL	NS	MRFP	0	FP	0	0	NS	NS	NS	NS	NS	NS	NS	NS	NS
BIGBEN	MPFP	FP	NS	NS	NS	NS	NS	PAIR	MRFR	MRFR	PAIR	MR	NS	NS	NS
BLACKS	NS	NS	NS	NS	MPFP	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
CAMPBE	NS	NS	NS	NS	NS	NS	MR	MR	NS	PAIR	MRS	MRS	NS	NS	NS
CANDAM	NS	NS	NS	NS	NS	NS	NS	NS	PAIR	NS	NS	NS	MP	NS	NS
CHRISH	FRS	0	PAIR	MR	MP	MR	MP	PAIR	NS	NS	NS	NS	MRFR	0	0
CRATER	NS	NS	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR	MRS	0	0	PAIR	PAIR	PAIR
CUBCRE	MR	PAIR	MPFP	MRFP	MRFP	MRFR	FP	NS	NS	MPFP	MPFP	0	0	MP	NS
FANLAV	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	PAIR	NS	NS
GOLDRU	PAIR	PAIR	PAIR	PAIR	0	MP	MP	0	NS	0	0	0	0	0	NS
GRAYSF	NS	NS	NS	NS	NS	MR	NS	NS	MP	NS	NS	NS	NS	NS	NS
HEARTL	PAIR	PAIR	MR	MRFP	NS	NS	NS	NS	NS	NS	NS	NS	MPFP	NS	NS
HUMBOL	MRFP	0	NS	MPFP	NS	NS	NS	NS	NS	MR	NS	MP	NS	NS	NS
JENNCR	NS	NS	NS	NS	NS	NS	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR
KEDRTS	PAIR	PAIR	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

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Site	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
KEDSOH	NS	MPFP	NS	NS	NS	NS	NS	NS	MPFP	NS	NS	NS	NS	NS	NS
LASTCH	NS	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	0	NS	NS
LCWEST	NS	NS	NS	NS	NS	MPFP	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	0	NS	NS
LIGHTS	NS	NS	NS	NS	MRFR	NS	NS	NS	NS	MP	NS	MR	NS	MPFR	NS
LOGANM	MRFR	NS	NS	NS	NS	NS	NS	PAIR	PAIR	PAIR	PAIR	0	0	FRS	NS
MONTPT	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	FP	MRFP	MRFR	PAIR
MOSRID	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	MPFP	PAIR	PAIR	PAIR	NS
MUDBUT	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	PAIR	PAIR	PAIR
MUDSOU	NS	NS	NS	FR	0	0	NS	NS	NS	NS	0	0	0	0	0
PCTRAI	MPFP	MPFR	PAIR	MRFR	PAIR	FP	FP	0	0	NS	NS	NS	0	0	0
PEASOH	PAIR	MRFP	PAIR	MPFR	MRFR	MR	MR	MR	0	MRS	FRS	0	0	0	MP
PHILBR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	PAIR	MPFR	MRFP	NS	NS	NS
REESEF	MPFP	MRFP	MP	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ROOPMT	NS	NS	PAIR	MRFP	PAIR	PAIR	PAIR	MRFP	0	0	0	NS	NS	NS	NS
SODARI	MP	MRFP	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
SODRAV	NS	NS	NS	NS	NS	NS	MRFP	MR	MR	MRFP	PAIR	PAIR	PAIR	NS	NS
WHEEL	NS	NS	PAIR	0	0	0	NS	NS	NS	NS	NS	FP	NS	NS	NS
COLBYC <sup>c</sup>	NS	NS	NS	NS	NS	FP	NS	NS	NS	NS	NS	NS	NS	NS	NS
HOMERL <sup>c</sup>	MP	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
LNPSTA <sup>c</sup>	NS	NS	NS	NS	NS	FP	NS	NS	NS	NS	NS	MP	NS	NS	NS
MARSPR <sup>c</sup>	NS	NS	NS	NS	NS	NS	NS	NS	MP	NS	NS	NS	NS	NS	NS

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Site	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
MOONPK <sup>c</sup>	NS	NS	NS	NS	NS	MP	NS	NS	FP	NS	NS	NS	NS	NS	NS
SQUIRR <sup>c</sup>	NS	MP	NS	FP	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

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 R = Owl Resident (detected at least 2 times, separated by one week)  
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 PAIR = Male and Female Resident, found together at least twice  
 S = Resident owl is confirmed to be single (no owl of the opposite sex detected after 6 visits)  
 NS = Not Surveyed completely  
 0 = Surveyed completely and no owls detected  
 UK= Owl of Unknown sex detected (did not vocalize)

<sup>c</sup> Owl observed on only one occasion/yr; not an established territory.

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Table 3. Changes in spotted owl site occupancy over time on the Lassen Density study area (DSA). These data are derived from Table 1.

<u>Number of sites among 78 established territories in the DSA</u>	<u>1991</u>	<u>1992</u>	<u>1993</u>	<u>1994</u>	<u>2001</u>	<u>2002</u>	<u>2003</u>	<u>2004</u>
Pair detected	40	49	45	36	30	38	33	34
At least 1 resident owl detected	53	51	54	52	41	40	44	38
Any owl detected	58	53	56	53	45	44	51	43

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Table 4. Reproductive rates of California spotted owls on the Lassen study area, 1990-2004. Fecundity is the number of female offspring per female owl  $\geq 1$  yr old. Productivity is the number of female offspring per female owl that produced young. We assumed one half of all young were female.

Year	Female Ageclass	Females nesting		Nests successful		Fecundity		Productivity	
		Proportion	n	Proportion	n		n		n
1990	Adult	0.76	21	0.69	16	0.35	30	0.70	15
	Subadult	0	4		0	0	4		0
	Unknown		0		0	0.50	4		2
	Total	0.64	25	0.69	16	0.33	38	0.74	17
1991	Adult	0.39	28	0.55	11	0.19	35	0.81	8
	Subadult	0	1		0	0	2		0
	Unknown	0	1		0	0	1		0
	Total	0.37	30	0.55	11	0.17	38	0.81	8
1992	Adult	0.97	37	0.92	36	1.09	49	1.19	45
	Subadult	1.00	1	0	1	0.33	3	0.50	2
	Unknown		0		0	0.50	1		1
	Total	0.97	38	0.89	37	1.04	53	1.15	48
1993	Adult	0.66	29	0.68	19	0.38	33	0.78	16
	Subadult	0.17	6	1.00	1	0.06	9	0.50	1
	Unknown		0		0	0	1		0
	Total	0.57	35	0.70	20	0.30	43	0.76	17
1994	Adult	0.36	28	0.80	10	0.28	36	0.83	12
	Subadult	0	5		0	0	6		0
	Unknown	0	2		0	0	3		0
	Total	0.29	35	0.80	10	0.22	45	0.83	12
1995	Adult	0.33	36	0.58	12	0.13	46	0.75	8
	Subadult		0		0	0	1		0
	Unknown		0		0		0		0
	Total	0.33	36	0.58	12	0.13	47	0.75	8
1996	Adult	0.38	32	0.58	12	0.19	40	0.83	9
	Subadult	0	1		0	0	1		0
	Unknown		0		0		5		2
	Total	0.36	33	0.58	12	0.20	46	0.82	11
1997	Adult	0.17	30	0.40	5	0.07	36	0.83	3
	Subadult	0	2		0	0	3		0
	Unknown	0	4		0	0	6		0
	Total	0.14	36	0.40	5	0.06	45	0.83	3
1998	Adult	0.86	21	0.56	18	0.47	37	0.76	23
	Subadult	0.33	3	1.00	1	0.17	3	0.50	1
	Unknown	1.00	2	0	1	0	2		0
	Total	0.81	26	0.55	20	0.43	42	0.75	24

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Year	Female Ageclass	Females nesting		Nests successful		Fecundity		Productivity	
		Proportion	n	Proportion	n		n		n
1999	Adult	0.41	27	0.80	10	0.14	36	0.56	9
	Subadult	0	2		0	0	4		0
	Unknown		0		0	0	1		0
	Total	0.38	29	0.80	10	0.12	41	0.56	9
2000	Adult	0.77	30	0.82	22	0.50	33	0.87	19
	Subadult	0	1		0	0.50	3	0.75	2
	Unknown	1.00	1	0	1	0.33	3	1.00	1
	Total	0.75	32	0.78	23	0.49	39	0.86	22
2001	Adult	0.09	23	1.00	2	0.08	30	0.83	3
	Subadult	0.33	3	0	1	0	4		0
	Unknown	0	1		0	0	1		0
	Total	0.11	27	0.67	3	0.07	35	0.83	3
2002	Adult	0.97	32	0.89	28	0.79	33	0.93	28
	Subadult	0.67	6	1.00	3	0.50	7	1.17	3
	Unknown	1.00	1		0		0		0
	Total	0.92	39	0.90	31	0.74	40	0.95	31
2003	Adult	0.46	26	0.27	11	0.09	32	0.83	3
	Subadult	0.50	2	0	1	0.14	7	0.50	1
	Unknown	0	1		0	0	1		0
	Total	0.45	29	0.25	12	0.10	40	0.75	4
2004	Adult	0.70	33	0.90	21	0.55	32	0.92	18
	Subadult	0	1		0	0	1		0
	Unknown	1.00	2	1.00	2	0.50	3	0.75	2
	Total	0.69	36	0.91	23	0.53	36	0.90	20

Table 5. Nest tree and nest stand structural variables around California spotted owl nest trees in northeastern California, 1990-2000. After Blakesley et al (In Press 2005).

Nest tree or nest stand attribute	Unique nests ( $n = 132$ )		Nest uses ( $n = 174$ ) <sup>a</sup>	
	Mean	CV	Mean	CV
Nest tree diameter at breast height (cm)	117	0.29	118	0.28
Percent slope above and below nest tree	25	0.55	27	0.48
Nest tree elevation (m)	1714	0.09	1701	0.08
Number of conifer stems/ha 13-40 cm dbh	140	0.92	156	0.92
Number of hardwood stems/ha 13-40 cm dbh	13	3.51	16	3.18
Percent canopy cover 10 meters from nest tree	82	0.14	83	0.13
Percent canopy cover 25 meters from nest tree	81	0.16	81	0.16
Log volume ( $m^3/ha$ ) <sup>b</sup> of logs >25 cm diameter	25.25	0.74	26.08	0.69
Basal area ( $m^2/ha$ ) <sup>c</sup> of trees >61 cm dbh	5.42	0.55	5.36	0.59
Basal area ( $m^2/ha$ ) <sup>c</sup> of snags >61 cm dbh	1.17	1.00	1.38	0.95
Summary				
Nest tree condition: live (L), snag (S)	L = 97, S = 35		L = 134, S = 40	
Nest type: platform (P), top cavity (T), side cavity (S)	P = 21, T = 45, S = 66		P = 22, T = 65, S = 87	
Nest tree species: fir (F), pine (P), other (O)	F = 63, P = 54, O = 15		F = 79, P = 83, O = 12	
Aspect of slope at nest tree: N, E, S, W	N = 45, E = 35, S = 22, W = 30		N = 59, E = 35, S = 31, W = 49	

<sup>a</sup> Many nests were used by owls in more than 1 year, yielding a greater sample size than the number of unique nests

<sup>b</sup> To convert  $m^3/ha$  to  $ft^3/acre$ , multiply by 87.3.

<sup>c</sup> To convert  $m^2/ha$  to  $ft^2/acre$ , multiply by 26.6.

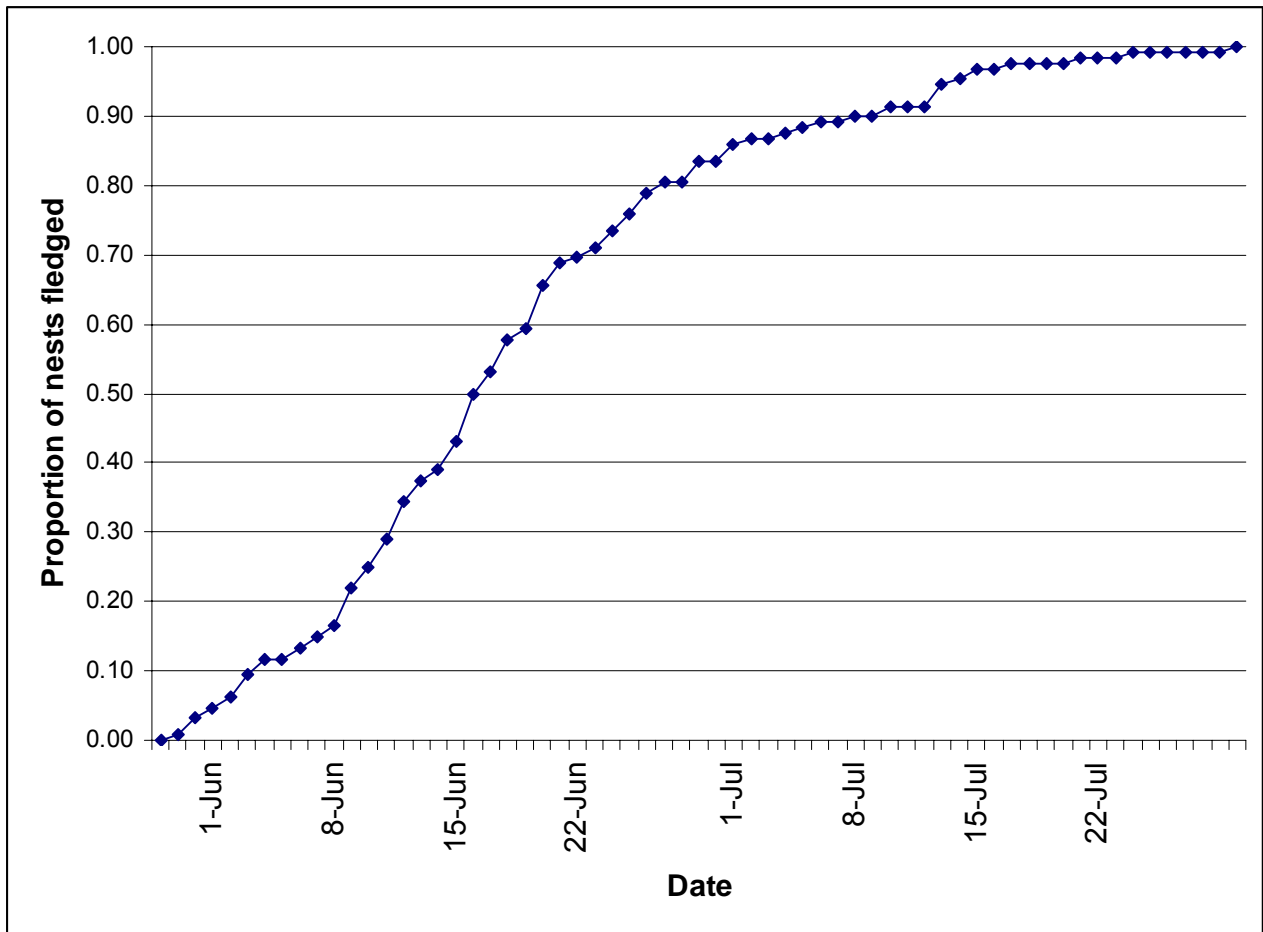


Figure 1. Cumulative distribution of California spotted owl fledging dates, 1990-2004 ( $n = 128$  nests known to be active  $\leq 21$  days previous to the date fledglings were first observed).

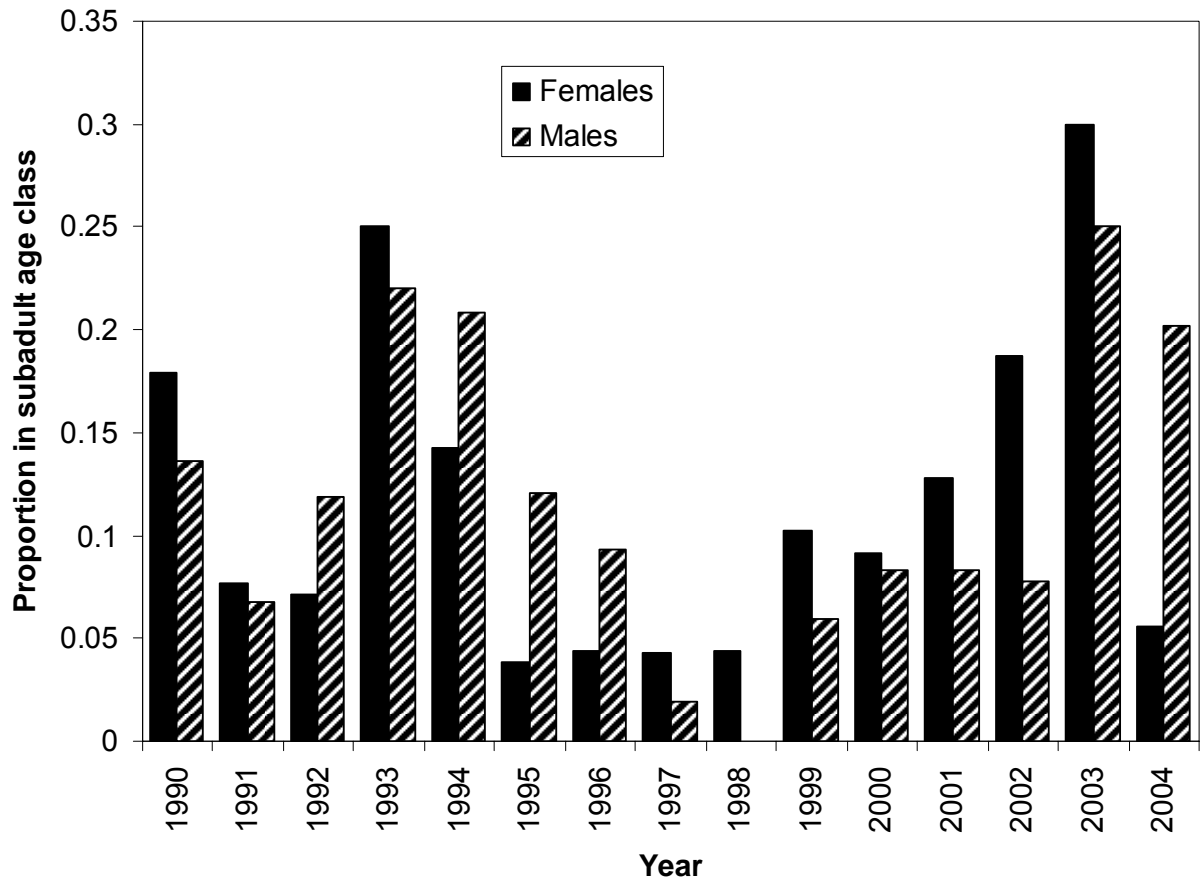


Figure 2. Proportion of California spotted owl population in the subadult age class (age < 3 years).