

Chapter 4: Population Distribution and Trends of California Spotted Owls

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Distribution

Geographic Range

Following Verner et al.'s (1992) technical assessment of the California spotted owl (CASPO), we divided the range of the California spotted owl (*Strix occidentalis occidentalis*) into two major physiographic provinces: the Sierra Nevada and the mountains of southern California (Tehachapi Pass was the demarcation between the regions). Verner et al. (1992) noted that these provinces are geographically distinct and that movement of owls between them is probably rare, which remains true today (see "Population and Conservation Genetics of California Spotted Owls" section below). The California spotted owl is also found in the coastal mountains north to Monterey Bay, but much less is known about owl numbers and locations along the coast (see figs. 4-1 and 4-2). That portion of the southern Cascade Range that abuts the Sierra Nevada has been considered to encompass the range of the California spotted owl on the east side of California (see chapter 2). Where the ranges of the northern (*S. o. caurina*) and California spotted owls meet, a hybrid zone occurs in the area of contact near the Pit River (Barrowclough et al. 2011; see chapter 2). Hereafter, we refer to owls occurring south of the Pit River as belonging to the Sierra Nevada population of California spotted owls.

Within the Sierra Nevada population, the distribution of owls is relatively contiguous. The majority of owls occur within the mid-elevation, mixed-conifer forests on the west slope of the Sierra Nevada. Some owls also occur at lower elevations in the oak woodlands of the western foothills in the southern Sierra Nevada, at higher elevations in red-fir forests, and in conifer forests on the eastern slope of the mountains (Verner et al. 1992). In contrast, the owl population in central and southern California is more fragmented because owls inhabit major mountain ranges and mountain complexes that are isolated to varying degrees, which limits movement of individuals among these mountain ranges. In this chapter, we focus almost solely on the Sierra Nevada population of owls while deferring discussion of southern California to chapter 9. However, when discussing general properties of

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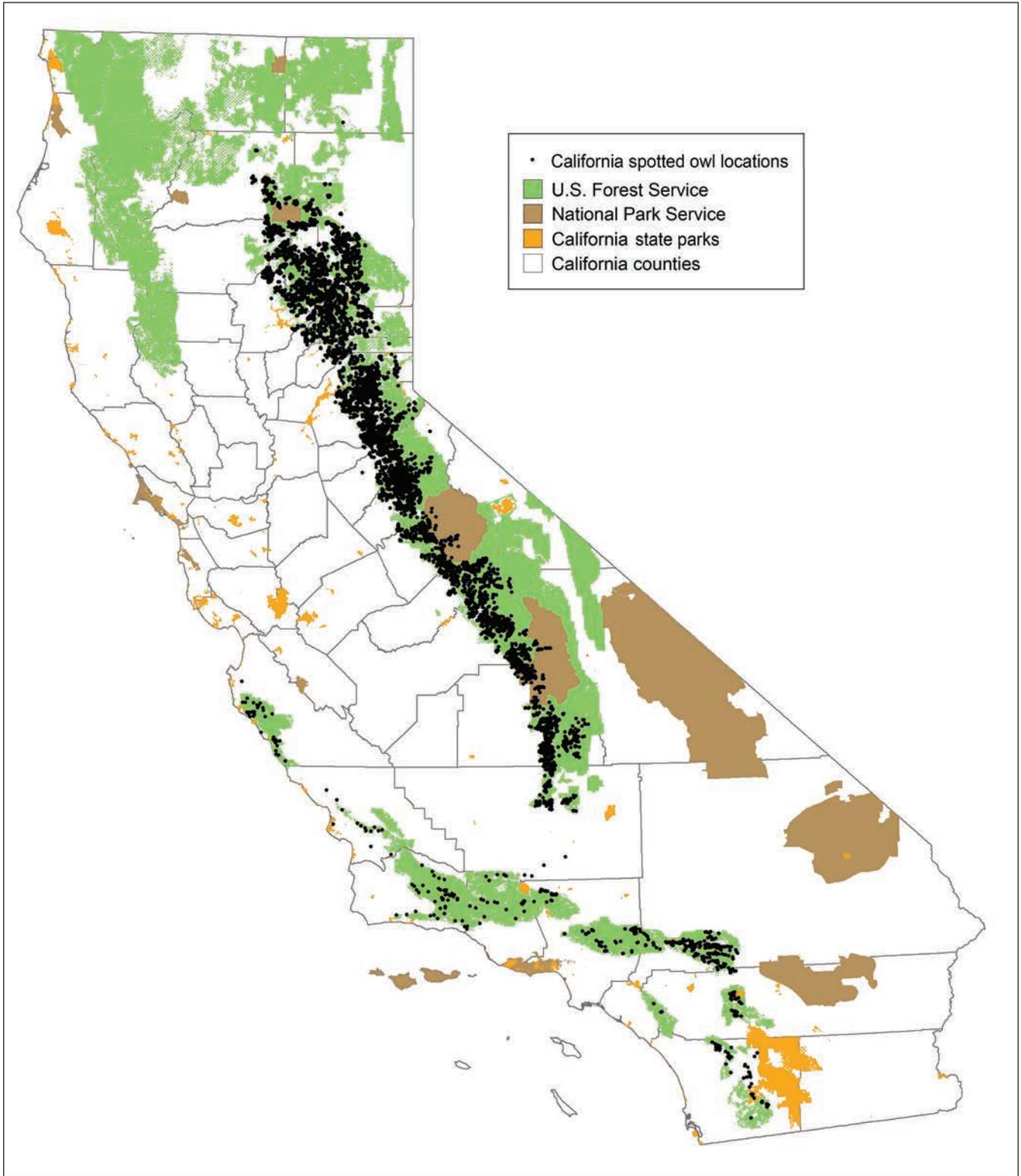


Figure 4-1—Unique detections of California spotted owls from 1900 through 1992 using databases provided by the California Department of Fish and Wildlife and Pacific Southwest Region of the U.S. Forest Service.

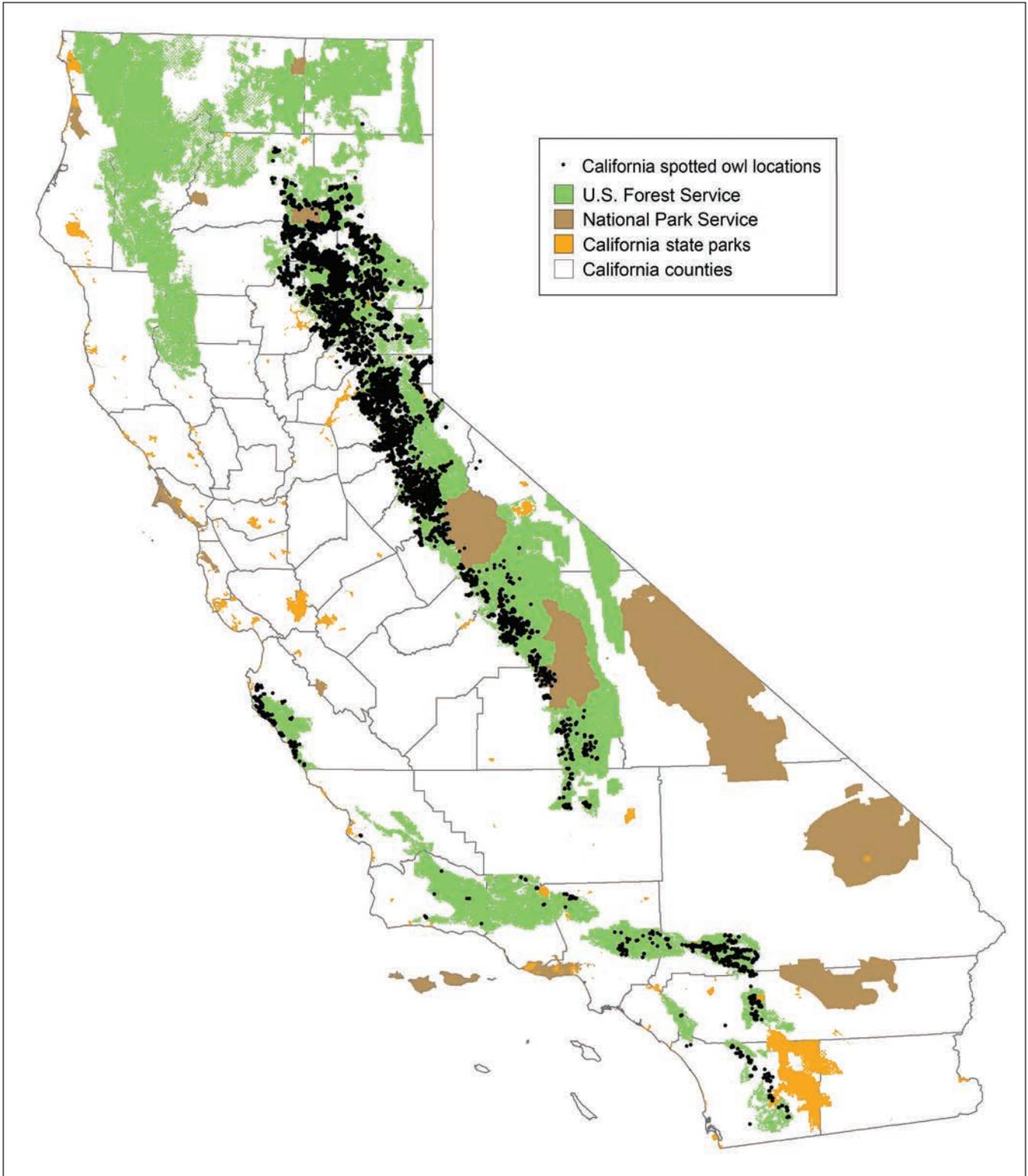


Figure 4-2—Unique detections of California spotted owls from 1993 through 2013 using databases provided by the California Department of Fish and Wildlife and Pacific Southwest Region of the U.S. Forest Service.

spotted owl population dynamics, we may also refer to other subspecies as well as southern California owl populations.

Distribution of Owls and Gaps in Distribution

Verner et al. (1992) noted that unlike the northern spotted owl, there were no obvious gaps in the distribution of the California spotted owl. This observation led them to recommend a conservation strategy based upon identification of habitat, protection of key habitat areas or activity centers around nests and roosts (i.e., protected activity centers PACs), and specific guidelines for timber harvest (restrictions on size of trees harvested, standards for tree basal area retention, and restrictions on canopy cover reductions; see chapter 1). To evaluate the CASPO premise of no gaps in the distribution, we obtained the California spotted owl databases from the California Department of Fish and Wildlife (CDFW) and the Pacific Southwest Region of the U.S. Forest Service (USFS). Both databases primarily included information for owl detections (i.e., mark-recapture or reproductive data were not consistently recorded), and many physical locations were represented by a large number of detections obtained over many years. Because we could not establish individual identities for most of the detections or, in many cases, even reliably assign detections to a specific owl territory, these databases cannot be used to infer trends in population size. However, they do provide a general, rangewide distribution of California spotted owls and some indication of the proportion of owls found on public versus private lands. Further examination of these databases showed that the CDFW database was missing many owl detections on USFS land, particularly after 1993. Therefore, we combined the databases and attempted to eliminate duplicate detections (i.e., detections in the same geographic location on the same date).

We estimated that there were 15,322 spotted owl detections prior to 1992 (CASPO) and 34,365 detections from 1993 through 2013 (post-CASPO) (figs. 4-1 and 4-2). The increase in the number of detections after 1992 was largely due to increased survey effort on national forest lands. The overall distribution of owls was largely similar for the two time periods (pre-1993 and 1993–2013), but there were noticeably fewer detections after 1992 within the Transverse Range north of Santa Barbara on the Los Padres National Forest. As noted above, there appeared to be a significant gap in the owl's distribution between the Sierra Nevada and the mountains of southern and central California. In addition, there appeared to be gaps in the owl's distribution between the major mountain ranges of southern and central California, particularly along the central coast. Most spotted owl detections were on public lands (88 percent prior to 1993, 87 percent from 1993 through 2013), and for both time periods >90 percent of the detections on public lands were within U.S.

national forests. Although there were clearly more California spotted owls on public lands, we could not determine how much of the observed difference in detections on public versus private lands was due to greater survey effort on public lands, particularly around proposed timber sales within U.S. national forests. Private lands may constitute an important component of California spotted owl habitat throughout its range, and owl conservation would benefit from the effective management of habitat on private lands.

Demographic Rates

History of Demographic Research in the Sierra Nevada

Spotted owls exhibit high adult survival rates with low temporal variation, whereas their reproductive rates are low and vary greatly from year to year (Franklin et al. 2000, Seamans and Gutiérrez 2007). Franklin et al. (2000) invoked these patterns as a “bet-hedging” life history strategy (Stearns 1976) where natural selection has favored the evolution of long lifespans to increase the likelihood that individuals will experience years that are favorable for reproduction (see also chapter 2).

Data collected on five long-term California spotted owl study areas have provided substantial empirical data on demographic rates and population trends subsequent to CASPO (Verner et al. 1992). Of these five study areas, four were in the Sierra Nevada (see fig. 4-3)—three on national forests (Lassen, Eldorado, and Sierra) and one within Sequoia and Kings Canyon National Parks. Data collection began in 1986 on the Eldorado and in 1990 on the other three study areas; all of these studies continued through 2014. The fifth study area was located on the San Bernardino National Forest in southern California where data were collected from 1987 through 2000 (see fig. 4-3). Two meta-analysis workshops have been conducted to analyze demographic rates and population trends on the Sierra Nevada study areas (Blakesley et al. 2010, Franklin et al. 2004), but more recent studies have provided updated analyses that included additional data collected after the second meta-analysis (Conner et al. 2013, Tempel and Gutiérrez 2013, Tempel et al. 2014b).

Additionally, Sierra Pacific Industries (SPI) recently initiated systematic surveys on five study areas throughout the Sierra Nevada where the company owned significant amounts of land (proportion of land owned by SPI ranged from 34 to 69 percent).² Although Roberts et al. (see footnote 2) concluded that populations on

² **Roberts, K.; Hall, W.E.; Shufelberger, A.J.; Reno, M.A.; Schroeder, M.M. 2015.** The occurrence and occupancy status of the California spotted owl on Sierra Pacific Industries’ lands in the Sierra Nevada of California. 11 p. Unpublished document: On file with: Sierra Pacific Industries, 3950 Carson Rd., Camino, CA 95709.

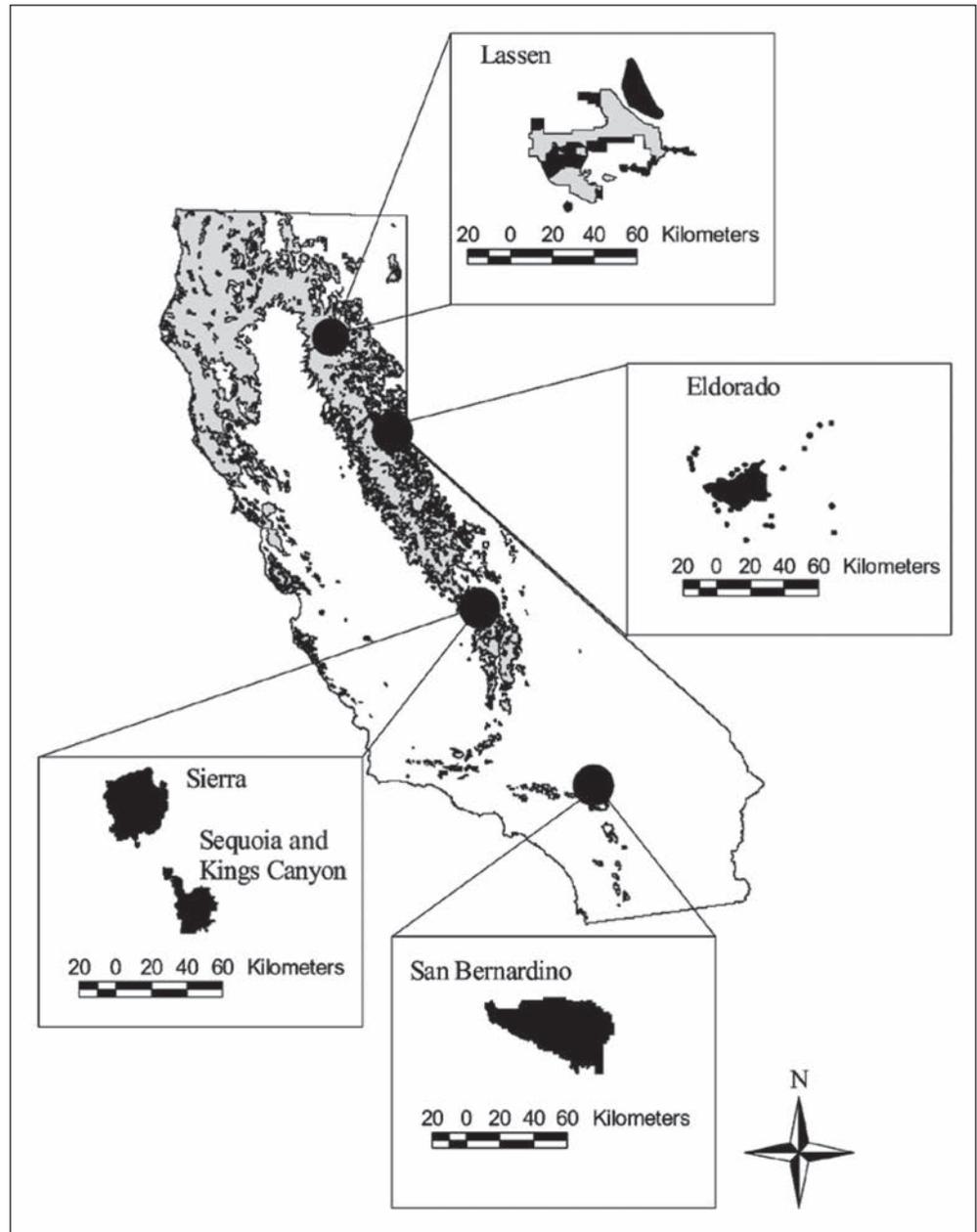


Figure 4-3—Locations of California spotted owl demography studies in relation to forested habitat (shaded gray) throughout California. (Franklin et al. 2004; reproduced with permission of © American Ornithological Union).

their study areas were stable or increasing, we contend that their survey data are currently insufficient to assess population trends for several reasons:

- Detection probabilities were not modeled.
- Surveys were conducted over a limited number of years (2012–2014), whereas trends on the study areas discussed above took more than 10 years to detect because spotted owls show high site fidelity and are long lived.
- Survey effort increased over time.
- There typically is a “learning curve” associated with initiation of occupancy studies that yields an increase of occupied sites solely related to accumulated knowledge of field technicians.
- Most of the owls were unmarked and thus could not be individually identified.

Roberts et al. (2015) also reported higher owl densities on their study areas than the Lassen and Eldorado National Forest study areas. However, we caution that density is not always a reliable indicator of habitat quality because large numbers of owls may be maintained in “sink” habitats (i.e., within-habitat reproduction is insufficient to balance local mortality) by continued immigration from more productive, nearby areas of “source” habitat (Pulliam 1988). Moreover, they sampled relatively small study areas, and there is often an “edge effect” associated with areas that are small relative to the home range size of the species being monitored. Although it is possible that the areas surveyed by Roberts et al. (see footnote 2) contain stable populations, additional years of data, including data on individual identification, reproduction, and survival, would be needed to make this determination.

Reproduction

Blakesley et al. (2010) reported substantial variation in reproductive rates (number of young fledged per territorial female for which reproduction was assessed) among the four Sierra Nevada study areas, ranging from 0.48 on the Sierra to 0.99 on the Eldorado. Because different studies sometimes use different units of measurement, we have used caution when comparing reproductive rates among studies. For example, Franklin et al. (2004) used the number of female young fledged per territorial female (assuming a 50:50 sex ratio among offspring), whereas Blakesley et al. (2010) used the total number of young fledged per territorial female. In addition, Seamans (2005) found that differences in field protocols used by researchers on different study areas affected estimates of annual reproductive rates, particularly whether one or two nonreproduction protocols were needed to infer nonreproduction. Therefore, in contrast to Franklin et al. (2004), Blakesley et al.

(2010) standardized field protocols among the four study areas such that the criteria for inferring nonreproduction had to be met on at least two surveys in a given year. However, this stricter requirement (i.e., two surveys vs. one) eliminated many data observations from the Eldorado because there were many instances when only one nonreproduction protocol was available; in most of these instances, it was likely that owls did not reproduce. This removal of observations where reproduction likely equaled zero could bias reproductive analyses that incorporate covariates for territories or individual owls. MacKenzie et al. (2009) recommended analyses using multistate occupancy models that distinguished between surveys where reproduction was detected or not detected to make more efficient use of reproductive data.

Blakesley et al. (2010) reported that reproduction declined over time on the Eldorado National Forest but was relatively constant on the other study areas. Furthermore, they found support for an even-odd (EO) year effect on reproductive rates for all four study areas (see chapter 2 for a discussion of this even-odd pattern) with the strongest pattern occurring for the Eldorado and Lassen National Forests; this pattern has also been reported for northern spotted owls (e.g., Forsman et al. 2011). Thus, spotted owl reproduction in much of the Sierra Nevada appeared to follow an alternating pattern where years of relatively high reproduction were followed by years of relatively low reproduction, although there remained much variation not explained by the even-odd pattern. In addition, Stoelting et al. (2015) could not simulate the even-odd cycle in California spotted owls using a cost of reproduction estimated for the Eldorado (see chapter 2).

Adult female California spotted owls (≥ 3 years old) have higher reproductive rates than subadult females (1 or 2 years old). For example, Blakesley et al. (2010) found that the annual proportion of subadult females among all territorial females had a strong negative correlation with reproductive rates on the Eldorado and Sierra National Forests. In addition, reproductive rates for adult females were much higher than those for subadult females on the Eldorado (Seamans and Gutiérrez 2007, Seamans et al. 2001, Tempel et al. 2014a) and Lassen National Forests (Blakesley et al. 2001) in analyses that were independent of the two California spotted owl meta-analyses (Blakesley et al. 2010, Franklin et al. 2004).

Reproductive rates have been correlated with climatic conditions, either during the previous winter or the early nesting period. Seamans and Gutiérrez (2007) reported that reproductive rates on the Eldorado were negatively correlated with El Niño events, which in California typically result in winters with greater precipitation and warmer temperatures than average. Additionally, they found that reproduction was negatively correlated with colder temperatures and greater precipitation

during incubation (April). Similarly, North et al. (2000) reported that colder temperatures and greater precipitation during the early breeding season (March to May) on the Sierra National Forest and Sequoia and Kings Canyon National Parks were negatively correlated with reproduction. Similar patterns have been observed for northern spotted owls (Franklin et al. 2000). These results have led to the hypothesis that colder temperatures and increased precipitation during the early nesting season negatively affect reproduction either by increasing the energetic requirements of owls, increasing the risk of egg exposure during incubation, or interfering with foraging (Franklin et al. 2000, Rockweit et al. 2012).

Finally, reproductive rates have been correlated with habitat characteristics, both within owl territories and at nest sites. When assessing the relationship between demographic rates (e.g., reproduction, survival, or occupancy) and habitat, scientists have considered various spatial scales as reference points. For example, at least four spatial scales have been used:

- The home range, which has been estimated from radiotelemetry locations
- The territory (the area actively defended by resident owls), which has typically been assumed to be approximately half the mean nearest neighbor distance between territory centers
- The core area of use within an animal's home range, which is an area that receives concentrated use and is thought to encompass critical components such as nest sites, refugia, and foraging areas (Samuel et al. 1985)
- The area immediately surrounding the nest site

On the Lassen National Forest, Blakesley et al. (2005) assessed the relationship between reproductive output and the surrounding habitat within owl territories (estimated as 203 ha [508 ac] using half the mean nearest neighbor distance, which they referred to as the “nest area”). They found that reproduction was negatively correlated with the amount of nonforest or forests dominated by small trees (<30 cm [12 in] diameter at breast height [d.b.h.]) and positively correlated with the amount of nesting habitat, which were forests dominated by medium (30 to 61 cm [12 to 24 in] d.b.h.) or large trees (>61 cm [24 in] d.b.h.) and having high canopy cover (>70 percent). Two different studies on the Eldorado National Forest found strong support for a negative correlation between reproduction and the amount of oak woodlands within owl territories (estimated as 150 ha [400 ac] using half the mean nearest neighbor distance) (Seamans 2005, Tempel et al. 2014a). On the Sierra National Forest, Hunsaker et al. (2002) reported a positive correlation between “productivity” and forests with >50 percent canopy cover at each of three different spatial scales (72 ha [178 ac], 168 ha [415 ac], and 430 ha [1,063 ac]) that roughly

corresponded to the home range, territory, and core area of use as defined above. The authors defined productivity as an index of reproductive output where productivity values at a territory ranged from zero to nine (0 = no owls present, 9 = nesting pair that produced three fledglings; see Hunsaker et al. [2002] for more details). At the spatial scale of the immediate nest area (0.05 ha [0.12 ac]), North et al. (2000) reported that reproduction was positively correlated with the foliage volume above the nest site.

Survival

Blakesley et al. (2010) reported high apparent survival of adult California spotted owls on the four Sierra Nevada study areas, ranging from 0.810 to 0.891. They also found that adults had higher annual survival rates than first- or second-year sub-adults and males have slightly higher survival rates than females. Higher survival rates for males (Seamans 2005, Seamans and Gutiérrez 2007, Tempel et al. 2014a) and adults (Tempel et al. 2014a) were also reported for the Eldorado National Forest in analyses independent from Blakesley et al. (2010). Data analyses for the Sierra Nevada studies have generally avoided estimation of juvenile survival rates because of potentially significant biases caused by undetected emigration of juveniles from the study areas (Burnham et al. 1996, Zimmerman et al. 2007). Estimates of nonjuvenile spotted owl survival have also been criticized as potentially biased because of undetected emigration of nonjuveniles (Boyce et al. 2005, Loehle et al. 2005), but this bias has been shown to be negligible because nonjuvenile owls (in contrast to juveniles) rarely disperse from study areas as large as those in the Sierra Nevada (Zimmerman et al. 2007). LaHaye et al. (2004) estimated that apparent juvenile survival rates in an insular population in the San Bernardino Mountains (i.e., juvenile emigration rates from this mountain range were negligible) was 0.368, which was similar to that reported on the Lassen National Forest (0.333) (Blakesley et al. 2001). Of note was that Blakesley et al. (2001) designed their study to improve estimation of juvenile survival.

Like reproduction, apparent survival has been correlated with habitat conditions within an owl territory. Blakesley et al. (2005) found that nonjuvenile survival was positively correlated with the amount of nesting habitat (see above) on the Lassen National Forest. In addition, Seamans (2005) and Tempel et al. (2014a) both reported that nonjuvenile survival rates on the Eldorado National Forest were positively correlated with the amount of forest dominated by medium (30 to 61 cm [12 to 24 in] d.b.h.) or large trees (>61 cm [24 in] d.b.h.) and having high canopy

cover (≥ 70 percent). Tempel et al. (2014a) also found a positive correlation between survival and the amount of edge between shrubs/saplings and forest, but the 95 percent confidence interval on the beta coefficient overlapped zero.

Seamans and Gutiérrez (2007) conducted the only study that assessed climate effects on survival of California spotted owls in the Sierra Nevada. They found that survival was positively correlated with snow depth, which was opposite of their a priori prediction. Their results further suggested a quadratic relationship between survival and the Southern Oscillation Index, such that survival was greatest in years that were not dominated by either El Niño or La Niña weather patterns. The Southern Oscillation Index is a measure of atmospheric pressure differences in the southern Pacific Ocean that provides an indication of the development and intensity of El Niño or La Niña events. In the Sierra Nevada, El Niño events typically result in warmer, wetter winters and La Niña events typically result in colder winters; thus the quadratic relationship suggested that survival was highest when winters were not too wet or too cold. Furthermore, their weather models explained less temporal variation in survival than they did in reproduction (60 vs. 84 percent); reproduction also exhibited much greater temporal variation than survival.

Population Size and Trends

Population Size

To our knowledge, there has never been a formal attempt to estimate rangewide population sizes of the California spotted owl. We have provided summaries of the number of known California spotted owl sites obtained from the CDFW and the USFS (see above; figs. 4-1 and 4-2), but these data were not collected as part of a scientifically rigorous sampling scheme throughout the owl's geographic range. Therefore, to assess whether the overall population is declining, we must rely upon population trends estimated from individual, long-term study populations. Fortunately, the four study areas in the Sierra Nevada from which estimates have been derived were large and spanned the extent of the mountain range, and thus likely provided a representative estimate of trends throughout the Sierra Nevada.

Population Trends

Population trends of spotted owls are typically reported as the annual rate of population change (λ_t) where λ_t indicates the population size in year $t + 1$ relative to the population size in year t . Thus, $\lambda = 1.0$ for a stationary population, $\lambda_t > 1.0$ for an increasing population, and $\lambda_t < 1.0$ for a declining population. Furthermore, the overall change in population size during a defined period of time is expressed as realized population change (Δ_t) where Δ_t indicates the population size in year t

relative to the population size at the beginning of the study period (Franklin et al. 2004). The realized population change is equivalent to the product of the annual rates of population change over the study period ($1 \times \lambda_1 \times \lambda_2 \times \lambda_3 \times \dots \lambda_{t-1}$). When assessing population trends, the processes affecting population change depend upon the scale of the population under consideration. Within the overall, rangewide population, changes in population size are due to a combination of reproduction and survival. However, within finite study areas, changes in population size are due to a combination of reproduction, survival, immigration, and emigration. Therefore, the estimates we report below for finite sampling areas will incorporate immigration and emigration of owls across study area boundaries, although the immigration and emigration rates are typically unknown.

Estimated population trends for spotted owls have benefitted from advances in analytical methods since the first northern spotted owl meta-analysis in 1993 (Gutiérrez 2008). Researchers first used stage-based population projection matrices and estimates of demographic rates to determine changes in abundance within specified age classes during annual time increments (Blakesley et al. 2001, LaHaye et al. 2004, Noon et al. 1992, Seamans et al. 2001). Using this approach, the annual rate of population change was obtained by finding the dominant eigenvalue for a defined population matrix. From the perspective of spotted owl studies, the “rate of population change” provided by projection matrices may be biased low because the estimated juvenile survival rates implicitly incorporate emigration (i.e., juvenile dispersal) from a study area, but the matrices do not account for immigration onto a study area. To accommodate this fact, Seamans and Gutiérrez (2007) and Seamans et al. (2001) used the estimated juvenile survival rate derived from an analysis of an insular spotted owl population in the San Bernardino Mountains as a surrogate for juvenile survival in the Eldorado National Forest under the assumption that the values would be similar between the Eldorado and southern California. From 1990 through 1999, population trends estimated using projection matrices suggested that both the Lassen ($= 0.910$, $SE = 0.025$; Blakesley et al. 2001) and Eldorado National Forests ($= 0.948$, $SE = 0.026$; Seamans et al. 2001) populations experienced significant declines.

However, Pradel (1996) developed a new method to estimate λ_t using mark-recapture data, which was motivated by a desire to obtain unbiased estimates of λ_t for northern spotted owl study areas (Gutiérrez 2008). This statistical method, referred to as a temporal symmetry model, estimated recruitment, nonjuvenile survival, and population change directly from the mark-recapture data. This approach implicitly incorporated both emigration and immigration because new recruits can be individuals that were either born on or immigrated onto a study area and apparent survival rates reflected either true mortality or emigration off a

study area. The first two and the last estimates of λ_t were not used in any analysis because the first and last estimates were confounded with recapture probability and the second estimate had a potential bias from “trap response” or a “learning curve” for field crews at the beginning of studies (Hines and Nichols 2002). “Trap responses” have occurred when observers preferentially sampled known owl sites or when owls either avoided or preferentially responded to human presence by virtue of behavioral conditioning. “Learning curves” have been a function of personnel becoming familiar with a new study area and accomplishing work objectives more efficiently as they gained experience (i.e., if the same number of observers detected more owls because of greater experience, the population could falsely be assumed to be growing when it is not). The Pradel method was used in the two California spotted owl meta-analyses (Blakesley et al. 2010, Franklin et al. 2004). Franklin et al. (2004) reported that the Pradel estimates of mean λ_t from 1992 through 1999 for the Sierra Nevada studies (except the Eldorado) were < 1.0 , but all of the 95 percent confidence intervals overlapped 1.0, which meant that it was uncertain if declines had actually occurred. Subsequently, Blakesley et al. 2010 reported that the Pradel estimates of mean λ_t from 1992 through 2002 were < 1.0 for the Sierra and Lassen National Forest and slightly > 1.0 for the Eldorado National Forest and Sequoia and Kings Canyon National Parks, but again all of the 95 percent confidence intervals overlapped 1.0. However, the estimate of Δ_t for the Lassen National Forest suggested that this population declined over the study period.

Population trends have been recently reanalyzed for all four study areas using new statistical techniques and incorporating additional data collected after the second meta-analysis (Conner et al. 2013, Tempel and Gutiérrez 2013, Tempel et al. 2014b). Conner et al. (2013) used the Pradel model within both maximum-likelihood and Bayesian frameworks to conclude that the Lassen and Sierra study populations had median λ_t less than 1.0. In addition, their Bayesian analysis showed that the Lassen and Sierra study areas had 0.69 and 0.40 probabilities, respectively, of declining by ≥ 15 percent over the study period. In contrast, the Sequoia and Kings Canyon National Parks study population had a median $\lambda_t > 1.0$ and only a 0.04 probability of a ≥ 15 -percent decline. The authors recently updated their analyses to include additional data collected in 2012 and 2013, which suggests it is even more likely that the Lassen and Sierra National Forests study populations have declined (fig. 4). Bayesian methods will allow generation of a posterior distribution for Δ_t , which allows the estimation of probabilities of specified declines of interest rather than the classic statistical approach of rejecting or accepting the null hypothesis that $\hat{\Delta} = 1.0$ at a specified probability level (typically $p = 0.05$). Thus, Conner et al. (2013) suggested that Bayesian methods were more informative for managing species of conservation interest than traditional statistical methods.

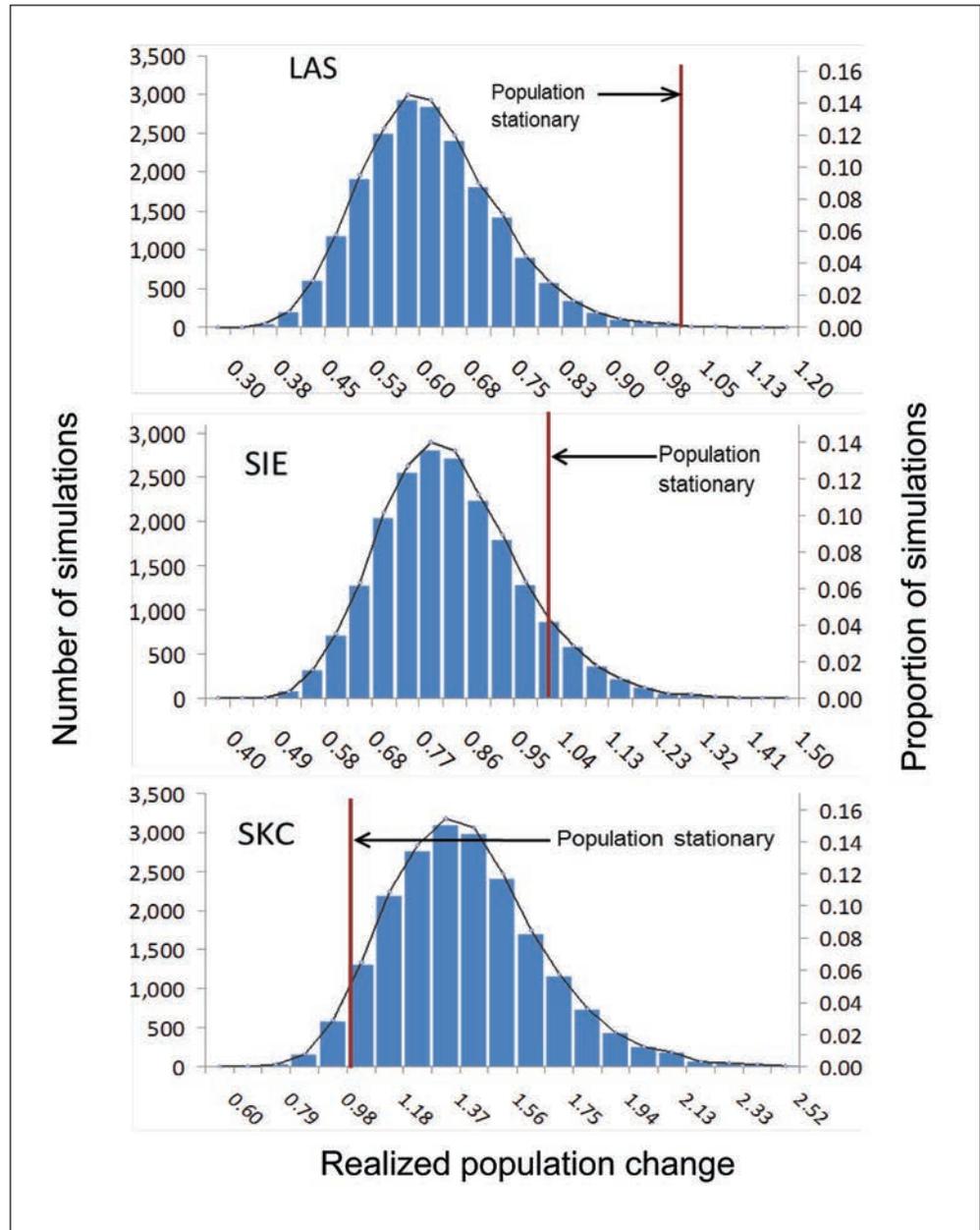


Figure 4-4—Estimated posterior distributions of overall realized population change (Δ_t) of California spotted owls based on posterior distributions of λ_t from 10,000 Markov chain Monte Carlo simulations. Data are from three Sierra Nevada study areas (Lassen [LAS], Sierra [SIE], and Sequoia and Kings Canyon [SKC]), 1990–2013 (used with permission of John Keane).

Tempel and Gutiérrez (2013) used the Pradel model to estimate $\hat{\Delta} = 0.725$ (95 percent confidence interval = 0.445 to 1.004) for the Eldorado study population from 1993 through 2010; this result closely matched the estimated trends in territory occupancy. They also noted that the Eldorado “density” study area was not surveyed entirely prior to 1993 because of funding constraints, which resulted in a gradual expansion of their study area size from 1990 through 1993 until funding

was adequate to survey the entire study area, and that the initial λ_t estimates would have been biased had they included mark-recapture data collected prior to 1993.

Tempel et al. (2014b) then developed an integrated population model (IPM) for the Eldorado National Forest study population that used all data collected on the Eldorado (occupancy, reproductive, and mark-recapture histories for juveniles and nonjuveniles) in a unified analysis. They first used a multistate occupancy model that accounted for imperfect detection to obtain annual counts of the number of young produced and the number of nonjuvenile territorial birds. These counts were then used as input data to the IPM, along with the mark-recapture histories. The IPMs offer several advantages over the traditional analysis of individual datasets, including greater precision in parameter estimates and the ability to estimate demographic parameters (e.g., immigration rates) for which no explicit data are available. They found that mean λ was <1.0 ($\hat{\Delta} = 0.969$, 95 percent credible interval = 0.957 to 0.980), which resulted in a 50 percent decline in population size from 1990 through 2012 ($\hat{\Delta} = 0.501$, 95 percent CRI 0.383 to 0.641; see fig. 4-5). Tempel et al. (2014b) were able to use data from 1990 through 1992 because the multistate occupancy model imputed the count values at territories that were not surveyed in a given year and the mark-recapture data were used solely to estimate apparent survival rates.

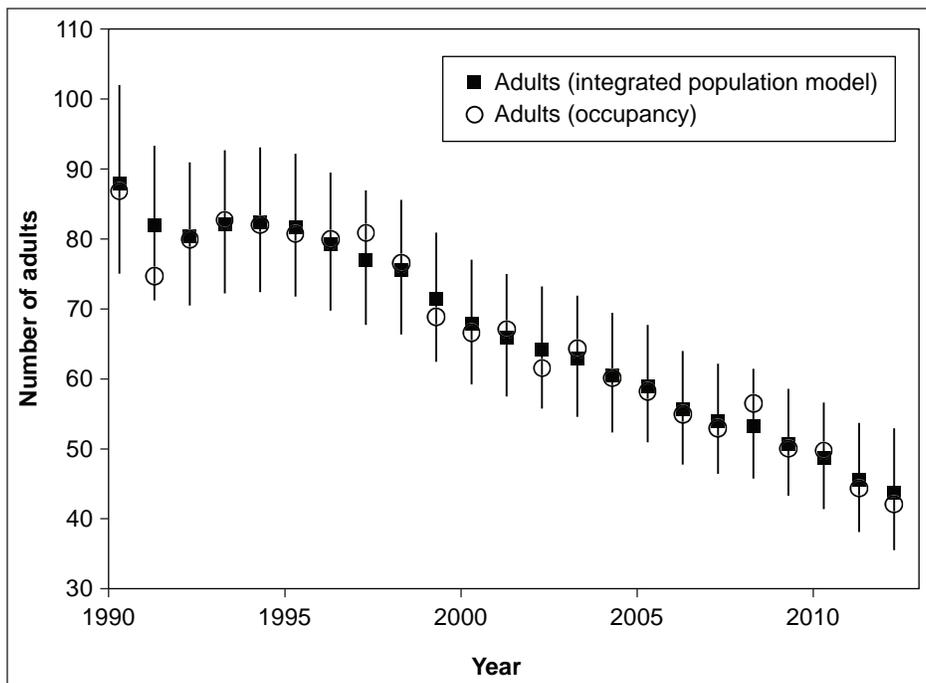


Figure 4-5—Posterior means (95 percent CRI [credible interval]) of realized population change from a Bayesian integrated population model for California spotted owls in the central Sierra Nevada, 1990–2012 (Tempel et al. 2014a; reproduced with permission of Elsevier Inc.®).

They attributed the larger observed decline (cf. Tempel and Gutiérrez [2013]) to the use of additional data and an increase in the number of territories occupied by single owls during the study. They also found that changes in λ were more highly correlated with immigration rate than any other demographic rate (reproductive rate, juvenile survival, and nonjuvenile survival), which suggested that changes in population size were also influenced by processes occurring outside of the study area.

Blakesley et al. (2001) and Seamans and Gutiérrez (2007) performed sensitivity analyses to assess which demographic rates had the most influence on changes in λ . Blakesley et al. (2001) reported that λ was most sensitive to changes in adult female survival on the Lassen National Forest, but fecundity contributed more to observed variation in λ because fecundity varied more than survival. Similarly, Seamans and Gutiérrez (2007) found that λ was most sensitive to changes in survival of nonjuvenile owls on the Eldorado National Forest, but that reproductive output and survival made similar contributions to changes in λ because reproductive output varied more than survival. The authors of both of these studies, as well as Tempel et al. (2014b), observed that juvenile survival made the least contribution of any demographic rate to changes in λ .

Thus far, despite its obvious relevance, researchers have attempted only one comprehensive assessment of how changes in habitat conditions within California spotted owl territories are correlated with changes in λ . Tempel et al. (2014a) created annual vegetation maps for owl territories on the Eldorado National Forest that differed over time because of timber harvest, wildfire, and forest succession. They found that reproduction was negatively correlated with medium-intensity timber harvests and the amount of hardwood forest within territories, where “medium-intensity harvests” encompassed a range of harvest types (group selection, single-tree selection, thinning for hazardous fuels reduction, fuel break, commercial thin). In addition, they found that nonjuvenile survival was positively correlated with the amount of high canopy cover (≥ 70 percent) forest dominated by medium or large trees (see above). However, life-stage simulations showed that changes in λ at the territory scale were more correlated with changes in the amount of high canopy cover forest than with the other variables they measured ($R^2 = 0.74$ for a logarithmic regression; see fig. 4-6).

Site Occupancy

A growing number of studies have assessed site occupancy for California spotted owls, where the site has typically been defined as a unique owl territory based on the presence of roosting or nesting owls. Occupancy studies can be one or more years in length, but only multiseason studies provide information on changes in

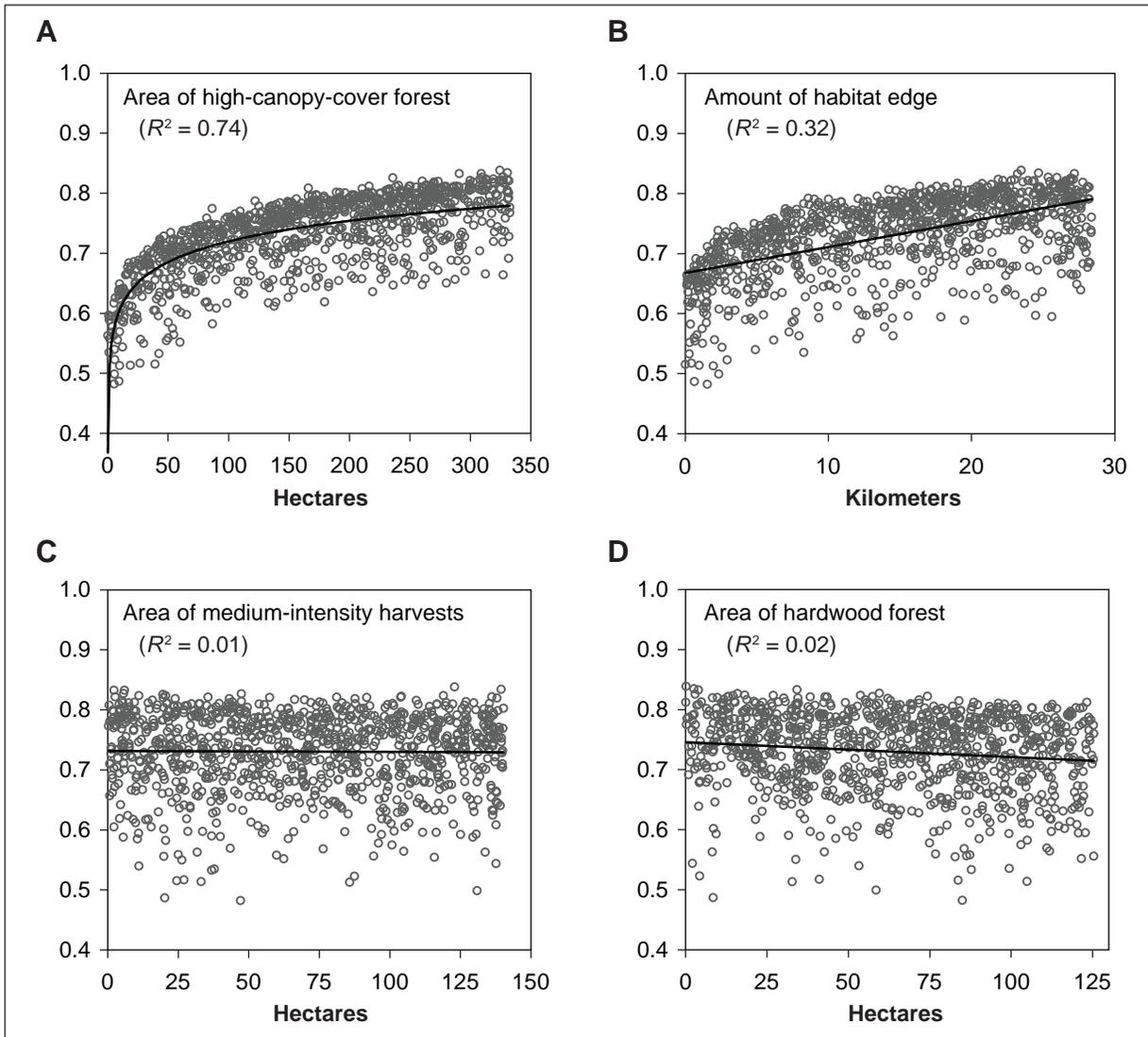


Figure 4-6—Results of a life-stage simulation analysis to assess the sensitivity of annual population growth rate (λ) of California spotted owls to changes in forest vegetation conditions within owl territories. One thousand values of λ were generated by drawing the following habitat variables from a uniform distribution: (a) area (ha) of high canopy cover (≥ 70 percent) forest dominated by trees ≥ 30.5 cm (≥ 12 in) diameter at breast height; (b) amount (km) of habitat edge; (c) area (ha) of medium-intensity timber harvests; and (d) area (ha) of hardwood forest (Tempel et al. 2014b; reproduced with permission of 2014 Ecological Society of America [©]).

occupancy status over time and what factors (e.g., habitat conditions, timber harvest, wildfire) are correlated with these changes. Changes in occupancy status are the combined effect of two processes:

- Local colonization, which is the probability that a previously unoccupied site becomes occupied.
- Local extinction, which is the probability that a previously occupied site becomes unoccupied (MacKenzie et al. 2003).

Refer to chapter 3 for a review of how habitat and habitat disturbances such as wildfire and logging affect spotted owl territory occupancy dynamics.

Because spotted owl territories can only be occupied by one or two individuals, occupancy-based studies may be a cost-effective alternative to mark-recapture studies for assessing owl population trends. Indeed, as we previously noted, Tempel and Gutiérrez (2013) found that trends in territory occupancy on the Eldorado National Forest from 1993 through 2010 closely matched population trends estimated from mark-recapture data using the Pradel model. However, Tempel et al. (2014a) analyzed data on the Eldorado from 1990 through 2012 using an integrated population model and found a larger population decline than Tempel and Gutiérrez (2013), partly owing to an increase over time in the number of territories occupied by single owls. Thus, multistate occupancy models that distinguish between territories occupied by single owls from those occupied by owl pairs may be preferable when inferring demographic trends from spotted owl occupancy data. Furthermore, occupancy studies are ideally suited to assess owl responses to management activities (e.g., timber harvest or prescribed burns), wildfire, climate, and other factors.

Population and Conservation Genetics of California Spotted Owls

Genetic methods and principles can provide valuable insights into the population status and management of species of conservation concern in many ways (Allendorf and Luikart 2007). These include (1) identifying conservation units, (2) estimating connectivity (i.e., gene flow and dispersal) among fragmented populations, (3) quantifying the level of genetic variation present within populations, and (4) characterizing demographic history. Genetic information can be applied to several other aspects of species conservation, but we limit our review to the four topics listed above, which in our opinion are the most relevant to the conservation of California spotted owls. We also note that issues associated with spotted owl-barred owl (*Strix varia*) hybridization are discussed in detail in chapter 6. For each of the conservation genetic issues we discuss, we first provide a brief overview of relevant population genetics principles to help interpret previous genetic studies on spotted owls and inform future management and research directions.

Conservation Units

A conservation unit is typically defined as a group of individuals that merits conservation attention independent of other such groups (Ryder 1986). Conservation units have been defined in several ways and applied to species with a variety of objectives. Typically, “evolutionary significant units” (ESUs) refer to populations

that are reproductively isolated from other populations and, as a result, have evolved unique adaptations through natural selection (Moritz 1994, Ryder 1986). The ESUs are conserved because the adaptations that differentiate them from other groups of conspecifics may be important for the persistence of the entire species in light of rapid environmental change. In contrast, a “management unit” (MU) generally represents a demographically independent population that receives little immigration from other populations (Moritz 1994, Palsbøll et al. 2007). The MUs are managed independently of other units because they are not expected to be “rescued” via immigration. From a legal perspective, two roughly parallel types of conservation units can be listed as “threatened” or “endangered” under the Endangered Species Act (ESA 1973): a taxon (species or subspecies) and a distinct population segment (DPS). The subspecies concept was defined in chapter 2, and as described therein can be listed under the ESA with the objective of preserving the evolutionary potential of the species, similar to the rationale behind delineating ESUs. The DPS status can be assigned to a population based on its evolutionary, ecological, or geopolitical discreteness, significance to the entire range of the species, and conservation status. In practice, the delineation of all types of conservation units is frequently informed using genetic data given the genetic underpinnings of adaptive traits (Crandall et al. 2000, Moritz 1994, Palsbøll et al. 2007).

As described in chapter 2, spotted owls are clearly divided into three well-delineated subspecies based on phylogeographic patterns in the mitochondrial DNA (Barrowclough et al. 1999, 2005; Haig et al. 2004) as well as differences in microsatellite allele frequencies among populations (Funk et al. 2008a). With the exception of a small number of California spotted owl haplotypes detected within the geographic range of northern spotted owls, the three subspecies appear to be “reciprocally monophyletic” based on the control region of the mitochondrial genome (i.e., all sampled haplotypes were more closely related to other haplotypes in the same subspecies than to those of the other subspecies) (Haig et al. 2004). Thus, these three groups could be also be considered as discrete ESUs, each of which is important to conserve in order to maintain the evolutionary potential of the species, at least according to one commonly used definition for ESUs (Moritz 1994).

Within the range of the California subspecies, genetic data appears to support the designation of multiple MUs. Owls in the Sierra Nevada are clearly genetically distinct from owls in the mountains of southern California (Barrowclough et al 1999, 2005; Funk et al. 2008a; Haig 2004). Large areas of unsuitable lowland habitat between the Sierra Nevada and southern California mountains certainly impede dispersal to the point that owls in these two regions are demographically independent. Indeed, Barrowclough et al. (2005) estimated that approximately zero

to one female migrant was exchanged between these two regions per generation. Some mountain ranges within southern California may also be demographically independent, and thus could be treated as discrete MUs, given limited gene flow (Barrowclough et al. 2005; see also below) and that little dispersal by marked individuals has been observed as part of mark-recapture studies (LaHaye et al. 2001). However, additional genetic analyses that include nuclear DNA would be needed to define MUs within southern California.

Connectivity in Fragmented Populations

Understanding the level of connectivity among populations that are isolated to some degree by habitat fragmentation or physiographic barriers (e.g., nonforested habitat between mountain ranges) has several important implications for the conservation of species, where connectivity can refer to gene flow (the movement of genes) or dispersal (movement of individuals). The isolation of formerly contiguously distributed populations into remnant habitat patches can impede gene flow and dispersal, thereby hastening extinction through a variety of genetic and demographic processes symptomatic of small populations (Keller and Waller 2002). As a result, a daunting array of genetic approaches has been developed to quantify gene flow and dispersal and assess whether habitat fragmentation has affected these processes to the point where management intervention is required (Lowe and Allendorf 2010). It is important to recognize that different genetic methods often yield inferences about gene flow and dispersal that apply to different time scales (i.e., a single generation to thousands of generations) and have a range of limitations, including the assumption of genetic drift-migration equilibrium (stable gene flow and effective population size) and difficulty at estimating dispersal when it is high enough to affect local population dynamics (Paetkau et al. 2004, Palsbøll et al. 2007, Peery et al. 2008). Moreover, maintaining the distinction between gene flow and individual dispersal is important because the dispersal of individuals does not necessarily translate to gene flow (Nosil et al. 2005, Peery et al. 2010).

Although spotted owl habitat within the Sierra Nevada has been extensively modified over the past approximately 150 years, we expect relatively little effect of historical habitat fragmentation on gene flow or dispersal in California spotted owls in this region. Spotted owls and their habitat remain reasonably well-distributed across the Sierra Nevada and the species is a strong disperser (Forsman et al. 2002). In the only genetic-based study of connectivity within the Sierra Nevada, Barrowclough et al. (2005) estimated gene flow among spotted owl populations sampled in the northern, central, and southern Sierra Nevada using coalescent approaches applied to patterns of mitochondrial sequence variation. Their estimates of the

effective number of female migrants ranged from zero (northern to central) to 25 (central to northern) per generation. An estimate of 25 migrants per generation is considered reasonably high from a population genetics perspective, whereas zero is clearly low. Gene flow estimates using this method, however, represent long-term averages (i.e., over evolutionary time scales) and do not necessarily reflect current rates of gene flow (or dispersal). Further study using nuclear genetic markers (e.g., microsatellites) and landscape-scale sampling could provide additional insights into current rates of gene flow and dispersal within the Sierra Nevada, as well as the environmental factors that influence these processes. Funk et al. (2008b) conducted such a “landscape genetics” study for northern spotted owls using 10 microsatellites to understand how landscape-scale topographic features such as major mountain ranges, valleys, and rivers impeded gene flow. In this study, gene flow was impeded by natural barriers such as mountain ranges without suitable owl habitat at higher elevations and, paradoxically, smaller and relatively undeveloped valleys, but not the large and extensively modified Willamette Valley.

As described above, Barrowclough et al. (2005) estimated low levels of gene flow among California spotted owl populations occurring in the mountains of southern California. Clearly, the natural isolation of these mountain ranges by unsuitable habitats such as deserts has acted as a barrier to gene flow over long time scales. However, urbanization and habitat development over the past century could have increased the isolation of these populations and further reduced gene flow and dispersal (LaHaye and Gutiérrez 2005, Verner et al. 1992). Additional genetic-based studies of connectivity using nuclear genetic markers could provide insight into the extent to which habitat fragmentation currently threatens southern California populations.

Genetic Variation Within Populations

Conserving adaptive genetic variation within populations is important for maintaining the evolutionary potential of species (Frankel and Soulé 1981). Loss of alleles occurs at a relatively rapid rate in small (e.g., bottlenecked) populations because of the enhanced effects of genetic drift, and the resultant loss of alleles with adaptive significance can compromise the ability of the species to adapt to future environmental change (Frankham et al. 1999, Lande and Shannon 1996, O’Brien and Evermann 1988). Inbreeding, the mating of close kin, is also more likely to occur in bottlenecked populations because remaining individuals tend to be related. Rare deleterious alleles are more likely to be expressed in inbred populations owing to high levels of homozygosity, which can result in declines in individual fitness (i.e., inbreeding depression) and increase the likelihood of extinction (Keller and Waller

2002). Thresholds for effective population sizes below which species will become vulnerable to the loss of adaptive genetic variation and inbreeding have been the subjective debate among scientists and are likely species-specific traits. Nevertheless, consensus exists that preventing the loss of adaptive genetic variation and inbreeding depression is best accomplished by maintaining large, well-connected populations.

California spotted owls exhibit relatively little sequence variation in the mitochondrial DNA control region compared to northern and Mexican (*S. o. lucida*) spotted owls (Barrowclough et al. 1999, 2005; Haig et al. 2004). Because the control region is a nonprotein coding sequence, it likely reflects the evolutionary history of mitochondrial genes given that the mitochondrial DNA represents a single nonrecombining genome. Indeed, nucleotide diversity, which represents the average number of nucleotide differences per site across pairs of randomly selected DNA sequences, is several times lower in California spotted owls sampled in the Sierra Nevada than in populations of the other two subspecies (Barrowclough et al. 1999, 2005). Moreover, no sequence variation was detected in the mitochondrial control region of owls sampled in southern California, either in an initial screening of 10 individuals in the San Bernardino and San Jacinto Mountains (Barrowclough et al. 1999), or in an expanded sample of 38 individuals that included owls from Mount Palomar (Barrowclough et al. 2005). Barrowclough et al. (1999, 2005) offered three possible explanations for relatively low observed mitochondrial diversity in California spotted owls:

- Small historical and current effective population sizes
- Historical population expansion (i.e., a colonization event or in situ recovery from a historical bottleneck)
- A beneficial mutation followed by a “selective sweep.”

Of these possibilities, clearly a population bottleneck would have the most detrimental impacts on the evolutionary potential of California spotted owls.

Genetic variation has also been assessed in a rangewide study of spotted owls using a panel of 10 microsatellite loci (tandemly repeating nuclear DNA sequences; Funk et al. 2008a). Although Funk et al. (2008a) did not directly report heterozygosity or allelic diversity for each sampled population, they stated that minimum expected heterozygosity across sampling sites was 0.685, which included two localities in the Sierra Nevada. This level of heterozygosity is typical of wild populations and, at face value, does not seem symptomatic of a severe population bottleneck. Caution, however, should be exercised when interpreting levels of genetic variation present in microsatellite markers because of “ascertainment bias,” which results

from researchers selecting the most polymorphic loci from a larger panel of candidate loci for use in population genetic studies. Highly polymorphic loci are useful for characterizing population genetic structure, understanding introgression, and estimating dispersal, but may be subject to high mutation rates and, therefore, yield an optimistic perspective of effective population size. Clearly, additional work is needed to fully characterize understanding of the demographic and microevolutionary factors that have shaped present-day genetic variation in spotted owls (see “Characterizing Demographic History” section below).

To date, tests of inbreeding or inbreeding depression have not been conducted for California spotted owls. However, several lines of evidence suggest that inbreeding does not currently threaten California spotted owls in the Sierra Nevada. First, Funk et al. (2008a) reported that observed heterozygosity did not deviate from expected heterozygosity for any of their sampled populations (inbred populations are expected to have lower observed than expected heterozygosity) across their panel of microsatellite loci. Second, natal dispersal is strong in spotted owls (Forsman et al. 2002) and, as a result, incestuous matings are rarely observed in this species (Carlson et al. 1998, Forsman et al. 2002). Third, in the Sierra Nevada, California spotted owls remain well-distributed and occur at higher abundances than typically observed in populations experiencing noticeable impacts of inbreeding depression. By contrast, spotted owls in the mountains of southern California are distributed among relatively small and insular populations that are likely connected by low levels of gene flow and are likely to be more susceptible to inbreeding. Nevertheless, even in the Sierra Nevada, future reductions in owl habitat from timber harvesting, fire, and climate change could result in smaller, more isolated owl populations that are more susceptible to the detrimental effects of inbreeding.

Characterizing Demographic History

Changes in effective population size, such as bottlenecks, often register signals in the DNA of the individuals that make up the population. Thus, the demographic history of a population of interest can be studied by examining relevant aspects of genetic variability in present-day populations. Genetic methods provide an appealing means for understanding changes in effective population because they only require a population sample taken at a single point in time, as opposed to long-term population monitoring (although historical samples can strengthen inferences). Consequently, many population genetic methods have been developed that can be used to characterize the demographic history of species of conservation concern such as California spotted owls (e.g., Beaumont 1999, 2003; Cornuet and Luikart

1996; Garza and Williamson 2001). However, as with genetic estimators of connectivity, caution must be exercised when interpreting the results of genetic-based assessments of demographic history as they often require making assumptions (e.g., about the way genes mutate) that are difficult to test, and results can be sensitive to violations of assumptions (Peery et al. 2012).

Applications of genetic data to questions of demographic history in California spotted owls are few, but as discussed above, this subspecies has depauperate mitochondrial DNA variation compared to northern and Mexican spotted owls (Barrowclough 1999, 2005; Haig 2004). Demographic explanations for relatively low genetic variation in California spotted owls, both in the Sierra Nevada and southern California, are uncertain but include persistently small populations, population bottlenecks, and recent colonization followed by population expansion (Barrowclough et al. 1999, 2005). These three competing hypotheses could be tested using coalescent methods applied to a panel of nuclear markers (e.g., microsatellites) or mitochondrial DNA (Beaumont 1999, 2003; Drummond and Rambaut 2007; Wu and Drummond 2011), as well as based on differences in microsatellite diversity statistics (Cornuet and Luikart 1996, Garza and Williamson 2001, Luikart and Cornuet 1998). Indeed, Funk et al. (2010) used genetic bottleneck tests based on microsatellite diversity statistics to test for declines in effective population size in northern spotted owls and demonstrated that bottlenecks were generally apparent in populations that demographic studies indicated were declining. Again, although such methods are sensitive to several potentially important assumptions, careful application of bottleneck tests and associated methods could provide important and novel insights into the demographic history of California spotted owls. Moreover, these genetic methods have the potential for reconstructing demographic history on longer time scales than spanned by California spotted owl demography studies (about 25 years), which could provide insights into how historical changes in forest extent and structure and climate have affected this subspecies. Finally, emerging genomic methods now provide increasing opportunities for more detailed reconstructions of the demographic history of California spotted owls (Hung et al. 2014).

Chapter Summary

Population data gathered subsequent to CASPO demonstrates that owl populations have declined over the past 20 years on three of the four long-term demographic study areas in the Sierra Nevada, which removes one of the key uncertainties of CASPO. Because these study areas were not selected at random, it cannot be inferred unequivocally that they represent the status of spotted owls in the entire Sierra Nevada. However, these study areas are large, span the entire length of the

Sierra Nevada, occur primarily in the mid-elevation forests that have the highest densities of owls, and exhibit no obvious special selection criteria that would likely result in the bias of derived information. Therefore, we infer that spotted owl populations in the Sierra Nevada are declining on most landscapes. We note that the populations that have declined are all located on national forests, and the only stationary population is located within Sequoia and Kings Canyon National Parks. The differences among study areas may have been related to differences in forest management, the presence of giant sequoia (*Sequoiadendron giganteum* (Lindl.) J. Buchholz) groves in Sequoia and Kings Canyon National Parks, differences in the proportion of oak woodlands, or some combination of these factors (Blakesley et al. 2010). We further note that whereas barred owls have negatively affected northern spotted owl populations, barred owls have appeared on the study areas in the Sierra Nevada only within the past 10 years and are either uncommon (Lassen) or extremely rare (Eldorado and Sierra National Forests, Sequoia and Kings Canyon National Parks). Thus, the observed population declines on the Eldorado and Sierra cannot be attributed to barred owls, and these declines may intensify if barred owls continue their southern range expansion in the future. Finally, these studies highlight the importance of long-term monitoring studies of long-lived species where small annual population declines are difficult to detect but result in large cumulative declines over long time periods.

Reproductive output and nonjuvenile survival contribute more to variation in spotted owl population size than juvenile survival. It is now well established that California spotted owl survival (and reproduction, to a lesser degree) is dependent upon having a sufficient amount of high canopy cover forest containing larger trees within breeding territories. This forest cover type has been positively correlated with survival rates at all four of the long-term demographic study areas and with reproductive rates at two of the study areas (Lassen and Sierra). Furthermore, Tempel et al. (2014a) noted that population growth rate (λ , which is determined by reproduction and survival) at the territory scale was strongly dependent upon the amount of high canopy cover (≥ 70 percent) forest within owl territories. Their results also suggested that maintaining between 100 and 150 ha (247 and 370 ac) of high canopy cover forest within owl territories would be sound conservation practice because small changes in annual population growth rate can translate into large changes in realized population size over extended periods of time, and populations in the Sierra Nevada have already declined by as much as 50 percent over the past two decades. In addition, 100 to 150 ha is a more realistic target than managing for amounts of high canopy cover forest (e.g., 200 ha) that maximized population growth in Tempel et al. (2014a). This amount of habitat also coincides with the size

of spotted owl PACs, which have been consistently used for nesting and roosting over a 24-year period on the Eldorado (Berigan et al. 2012). Finally, some evidence exists that northern and California spotted owls may benefit from some habitat heterogeneity and edge between forest types (Franklin et al. 2000, Tempel et al. 2014a), but the best available data indicate that sufficient high canopy cover forest is needed within owl territories.

A key remaining uncertainty is the degree to which changes in demographic rates and population abundance are related to various types of habitat disturbance such as high-severity wildfire and timber harvest. Thus far, the evidence for how disturbance may affect spotted owls has been mixed. Tempel et al. (2014a) reported that local colonization was negatively correlated with wildfire, but that timber harvest had relatively minor effects on reproduction, nonjuvenile survival, and territory occupancy. However, they found that territory fitness and occupancy were highly correlated with the amount of high canopy cover forest within owl territories, so disturbances that reduce this cover type could negatively affect spotted owl populations. Other studies that focused specifically on site occupancy and wildfire suggested that owls were resilient to low- and moderate-severity fire, but vacated territories when large areas were burned at high severity. Because of the remaining uncertainty on how timber harvest and wildfire affect spotted owls, the apparent benefits that closed-canopy forests provide owls, and the substantial recent population declines in some regions, landscape-scale fuel treatments implemented to reduce fire risk within owl habitat cannot be adequately assessed for their efficacy without an accompanying rigorous monitoring program.

Ideally, future research would be conducted within an experimental context, but experimental studies are likely to be impractical because of logistical difficulties and the large home ranges of spotted owls. Therefore, researchers and managers will likely need to continue to rely on correlative, quasi-experimental approaches that account for logging and wildfire effects in a rigorous manner. In addition, simulation modeling of owl populations at larger spatial scales where the model parameter values are based on empirical results from smaller study areas may provide insights into regional population dynamics. For example, recent modeling for the northern spotted owl suggested that the demographic performances of regional metapopulations were more affected by complex source-sink dynamics among the metapopulations than by metapopulation specific habitat values (Schumaker et al 2014).

Genetic investigations support treating California spotted owls in the Sierra Nevada and southern California, collectively, as a discrete ESU in light of their genetic divergence from the northern and Mexican subspecies. Further, genetic exchange and dispersal between southern California and Sierra Nevada owl populations appears to be very low, suggesting that owls in these two regions should be treated as independent management units. Genetic variation is low and may constrain the ability of California spotted owls to adapt to inevitable future environmental change, and further population declines could result in even lower levels of genetic variation and greater constraints on evolutionary potential. Evidence for historical (long-term) population declines from genetic data is equivocal but could be tested with additional analyses. In general, rapidly emerging technologies and analytical frameworks within the field of “conservation genomics” provide exciting new opportunities for characterizing the population structure and demographic history of California spotted owls.

Literature Cited

- Allendorf, F.W.; Luikart, G. 2007.** Conservation and the genetics of populations. Malden, MA: Blackwell Publishing. 642 p.
- Barrowclough, G.F.; Groth, J.G.; Mertz, L.A.; Gutiérrez, R.J. 2005.** Genetic structure, introgression, and a narrow hybrid zone between northern and California spotted owls (*Strix occidentalis*). *Molecular Ecology*. 14(4): 1109–1120.
- Barrowclough, G.F.; Gutiérrez, R.J.; Groth, J.G. 1999.** Phylogeography of spotted owl (*Strix occidentalis*) populations based on mitochondrial DNA sequences: gene flow, genetic structure, and a novel biogeographic pattern. *Evolution*. 53(3): 919–931.
- Barrowclough, G.F.; Gutiérrez, R.J.; Groth, J.G.; Lai, J.E.; Rock, D.F. 2011.** The hybrid zone between northern and California spotted owls in the Cascade-Sierran suture zone. *Condor*. 113(3): 1–9.
- Beaumont, M.A. 1999.** Detecting population expansion and decline using microsatellites. *Genetics*. 153(4): 2013–2029.
- Beaumont, M.A. 2003.** Estimation of population growth or decline in genetically monitored populations. *Genetics*. 164(3): 1139–1160.

- Berigan, W.J.; Gutiérrez, R.J.; Tempel, D.J. 2012.** Evaluating the efficacy of protected habitat areas for the California spotted owl using long-term monitoring data. *Journal of Forestry*. 110(6): 299–303.
- Blakesley, J.A.; Noon, B.R.; Anderson, D.R. 2005.** Site occupancy, apparent survival, and reproduction of California spotted owls in relation to forest stand characteristics. *Journal of Wildlife Management*. 69(4): 1554–1564.
- Blakesley, J.A.; Noon, B.R.; Shaw, D.W.H. 2001.** Demography of the California spotted owl in northeastern California. *Condor*. 103(4): 667–677.
- Blakesley, J.A.; Seamans, M.E.; Conner, M.M.; Franklin, A.B.; White, G.C.; Gutiérrez, R.J.; Hines, J.E.; Nichols, J.D.; Shaw, D.W.H.; Munton, T.E.; Keane, J.J.; Steger, G.N.; Noon, B.R.; McDonald, T.L.; Britting, S. 2010.** Population dynamics of spotted owls in the Sierra Nevada, California. *Wildlife Monographs*. 174: 1–36.
- Boyce, M.S.; Irwin, L.L.; Barker, R. 2005.** Demographic meta-analysis: synthesizing vital rates for spotted owls. *Journal of Applied Ecology*. 42(1): 38–49.
- Burnham, K.P.; Anderson, D.R.; White, G.C. 1996.** Meta-analysis of vital rates of the northern spotted owl. In: Forsman, E.D.; DeStefano, S.; Raphael, M.G.; Gutiérrez, R.J., eds. *Demography of the northern spotted owl: studies in avian biology* No. 17. Lawrence, KS: Allen Press: 92–101.
- Carlson, P.C.; LaHaye, W.S.; Franklin, A.B. 1998.** Incestuous behavior in spotted owls. *Wilson Bulletin*. 110(4): 562–564.
- Conner, M.M.; Keane, J.J.; Gallagher, C.V.; Jehle, G.; Munton, T.E.; Shaklee, P.A.; Gerrard, R.A. 2013.** Realized population change for long-term monitoring: California spotted owl case study. *Journal of Wildlife Management*. 77(7): 1449–1458.
- Cornuet, J.M.; Luikart, G. 1996.** Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. *Genetics*. 144(4): 2001–2014.
- Crandall, K.A.; Bininda-Emonds, O.R.P.; Mace, G.M.; Wayne, R.K. 2000.** Considering evolutionary processes in conservation biology. *Trends in Ecology and Evolution*. 15(7): 290–295.
- Drummond, A.J.; Rambaut, A. 2007.** BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*. 7: 214.

Endangered Species Act of 1973 [ESA]; 16 U.S.C. 1531–1536, 1538–1540.

Forsman, E.D.; Anthony, R.G.; Dugger, K.M.; Glenn, E.M.; Franklin, A.B.; White, G.C.; Schwarz, C.J.; Burnham, K.P.; Anderson, D.R.; Nichols, J.D.; Hines, J.E.; Lint, J.B.; Davis, R.J.; Ackers, S.H.; Andrews, L.S.; Biswell, B.L.; Carlson, P.C.; Diller, L.V.; Gremel, S.A.; Herter, D.R.; Higley, J.M.; Horn, R.B.; Reid, J.A.; Rockweit, J.; Schaberl, J.P.; Snetsinger, T.J.; Sovern, S.G. 2011. Population demography of northern spotted owls: studies in avian biology no. 40. Berkeley, CA: University of California Press. 106 p.

Forsman, E.D.; Anthony, R.G.; Reid, J.A.; Loschl, P.J.; Sovern, S.G.; Taylor, M.; Biswell, B.L.; Ellingson, A.; Melsow, E.C.; Miller, G.S.; Swindle, K.A.; Thraillkill, J.A.; Wagner, F.F.; Seaman, D.E. 2002. Natal and breeding dispersal of northern spotted owls. *Wildlife Monographs*. 149: 1–35.

Frankel, O.H.; Soulé, M.E. 1981. Conservation and evolution. Cambridge, United Kingdom: Cambridge University Press. 327 p.

Frankham, R.; Lees, K.; Montgomery, M.E.; England, M.E.; Lowe, P.R.; Briscoe, D.A. 1999. Do population size bottlenecks reduce evolutionary potential? *Animal Conservation*. 2(4): 255–260.

Franklin, A.B.; Anderson, D.R.; Gutiérrez, R.J.; Burnham, K.P. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs*. 70(4): 539–590.

Franklin, A.B.; Gutiérrez, R.J.; Nichols, J.D.; Seamans, M.E.; White, G.C.; Zimmerman, G.S.; Hines, J.E.; Munton, T.E.; LaHaye, W.S.; Blakesley, J.A.; Steger, G.N.; Noon, B.R.; Shaw, D.W.H.; Keane, J.J.; McDonald, T.L.; Britting, S. 2004. Population dynamics of the California spotted owl (*Strix occidentalis occidentalis*): a meta-analysis. *Ornithological Monographs*. 54: 1–54.

Funk, W.C.; Forsman, E.D.; Johnson, M.; Mullins, T.D.; Haig, S.M. 2010. Evidence for recent population bottlenecks in northern spotted owls (*Strix occidentalis caurina*). *Conservation Genetics*. 11(3): 1013–1021.

Funk, W.C.; Forsman, E.D.; Mullins, T.D.; Haig, S.M. 2008a. Introgression and dispersal among spotted owl (*Strix occidentalis*) subspecies. *Evolutionary Applications*. 1(1): 161–171.

- Funk, W.C.; Forsman, E.D.; Mullins, T.D.; Haig, S.M. 2008b.** Landscape features shape genetic structure in threatened northern spotted owls. Open-File Report 2008-1240. Reston, VI: U.S. Department of the Interior, Geological Survey. 12 p.
- Garza, J.C.; Williamson, E.G. 2001.** Detection of reduction in population size using data from microsatellite loci. *Molecular Ecology*. 10(2): 305–318.
- Gutiérrez, R.J. 2008.** Spotted owl research: a quarter century of contributions to education, ornithology, ecology, and wildlife management. *Condor*. 110(4): 792–798.
- Haig, S.M.; Mullins, T.D.; Forsman, E.D. 2004.** Subspecific relationships and genetic structure in the spotted owl. *Conservation Genetics*. 5(5): 683–705.
- Hines, J.E.; Nichols, J.D. 2002.** Investigations of potential bias in the estimation of λ using Pradel's (1996) model for capture-recapture data. *Journal of Applied Statistics*. 29(1–4): 573–587.
- Hung, C.M.; Shaner, P.J.L.; Zink, R.M.; Liu, W.C.; Chu, T.C.; Huang, W.S.; Li, S.H. 2014.** Drastic population fluctuations explain the rapid extinction of the passenger pigeon. *Proceedings of the National Academy of Sciences of the United States of America*. 111(29): 10636–10641.
- Hunsaker, C.T.; Boroski, B.B.; Steger, G.N. 2002.** Relations between canopy cover and the occurrence and productivity of California spotted owls. In: Scott, J.M.; Hegland, P.J.; Morrison, M.L., eds. *Predicting species occurrences: issues of accuracy and scale*. Washington, DC: Island Press: 687–700.
- Keller, L.F.; Waller, D.M. 2002.** Inbreeding effects in wild populations. *Trends in Ecology and Evolution*. 17(5): 230–241.
- LaHaye, W.S.; Gutiérrez, R.J. 2005.** The spotted owl in southern California: ecology and special concerns for maintaining a forest-dwelling species in a human-dominated desert landscape. In: Kus, B.E.; Beyers, J.L., eds. *Planning for biodiversity: bringing research and management together. Proceedings of a symposium for the south coast ecoregion*. Gen. Tech. Rep. PSW-GTR-195. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 199–209.
- LaHaye, W.S.; Gutiérrez, R.J.; Dunk, J.R. 2001.** Natal dispersal of the spotted owl in southern California: dispersal profile of an insular population. *Condor*. 103(4): 691–700.

- LaHaye, W.S.; Zimmerman, G.S.; Gutiérrez, R.J. 2004.** Temporal variation in the vital rates of an insular population of spotted owls (*Strix occidentalis occidentalis*): contrasting effects of weather. *Auk*. 121(4): 1056–1069.
- Lande, R.; Shannon, S. 1996.** The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution*. 50(1): 434–437.
- Loehle, C.; Irwin, L.; Rock, D.; Rock, S. 2005.** Are survival rates for northern spotted owls biased? *Canadian Journal of Zoology*. 83(10): 1386–1390.
- Lowe, W.H.; Allendorf, F.W. 2010.** What can genetics tell us about population connectivity? *Molecular Ecology*. 19(15): 3038–3051.
- Luikart, G.; Cornuet, J.M. 1998.** Empirical evaluation of a test for identifying recently bottlenecked populations from allele frequency data. *Conservation Biology*. 12(1): 228–237.
- MacKenzie, D.I.; Nichols, J.D.; Hines, J.E.; Knutson, M.G.; Franklin, A.B. 2003.** Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*. 84(8): 2200–2207.
- MacKenzie, D.I.; Nichols, J.D.; Seamans, M.E.; Gutiérrez, R.J. 2009.** Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology*. 90(3): 823–835.
- Moritz, C. 1994.** Defining ‘evolutionarily significant units’ for conservation. *Trends in Ecology and Evolution*. 9(10): 373–375.
- Noon, B.R.; McKelvey, K.S.; Lutz, D.W.; LaHaye, W.S.; Gutierrez, R.J.; Moen, C.A. 1992.** Estimates of demographic parameters and rates of population change. In: Verner, J.; McKelvey, K.S.; Noon, B.R.; Gutiérrez, R.J.; Gould, G.I., Jr.; Beck, T.W., eds. *The California spotted owl: a technical assessment of its current status*. Gen. Tech. Rep. PSW-GTR-133. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 175–186.
- North, M.; Steger, G.; Denton, R.; Eberlein, G.; Munton, T.; Johnson, K. 2000.** Association of weather and nest-site structure with reproductive success in California spotted owls. *Journal of Wildlife Management*. 64(3): 797–807.
- Nosil, P.; Vines, T.H.; Funk, D.J. 2005.** Reproductive isolation caused by natural selection against immigrants from divergent habitats. *Evolution*. 59(4): 705–719.
- O’Brien S.J.; Evermann, J.F. 1988.** Interactive influence of infectious disease and genetic diversity in natural populations. *Trends in Ecology and Evolution*. 3(10): 254–259.

- Paetkau, D.; Slade, R.; Burden, M.; Estoup, A. 2004.** Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. *Molecular Ecology*. 13(1): 55–65.
- Palsbøll, P.J.; Bérubé, M.; Allendorf, F.W. 2007.** Identification of management units using population genetic data. *Trends in Ecology and Evolution*. 22(1): 11–16.
- Peery, M.Z.; Beissinger, S.R.; House, R.F.; Bérubé, M.; Hall, L.A.; Sellas, A.; Palsbøll, P.J. 2008.** Characterizing source-sink dynamics with genetic parentage assignments. *Ecology*. 89(10): 2746–2759.
- Peery, M.Z.; Hall, L.A.; Sellas, A.; Beissinger, S.R.; Moritz, C.; Bérubé, M.; Raphael, M.G.; Nelson, S.K.; Golightly, R.T.; McFarlane-Tranquilla, L.; Newman, S.; Palsbøll, P.J. 2010.** Genetic analyses of historic and modern marbled murrelets suggest decoupling of migration and gene flow after habitat fragmentation. *Proceedings of the Royal Society B-Biological Series*. 277(1682): 697–706.
- Peery, M.Z.; Kirby, R.; Reid, B.N.; Stoelting, R.; Doucet-Béer, E.; Robinson, S.J.; Vasquez-Carrillo, J.N.; Palsbøll, P.J. 2012.** Reliability of genetic bottleneck tests for detecting recent population declines. *Molecular Ecology*. 21(14): 3403–3418.
- Pradel, R. 1996.** Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics*. 52(2): 703–709.
- Pulliam, H.R. 1988.** Sources, sinks, and population regulation. *American Naturalist*. 132(5): 652–661.
- Rockweit, J.T.; Franklin, A.B.; Bakken, G.S.; Gutiérrez, R.J. 2012.** Potential influences of climate and nest structure on spotted owl reproductive success: a biophysical approach. *PLoS ONE*. 7(7): e41498. doi:10.1371/journal.pone.0041498.
- Ryder, O.A. 1986.** Species conservation and systematics: The dilemma of subspecies. *Trends in Ecology and Evolution*. 1(1): 9–10.
- Samuel, M.D.; Pierce, D.J.; Garton, E.O. 1985.** Identifying areas of concentrated use within the home range. *Journal of Animal Ecology*. 54(3): 711–719.
- Schumaker, N.H.; Brookes, A.; Dunk, J.R.; Woodbridge, B.; Heinrichs, J.A.; Lawler, J.J.; Carroll, C.; LaPlante, D. 2014.** Mapping sources, sinks, and connectivity using a simulation model of northern spotted owls. *Landscape Ecology*. 29(4): 579–592.

- Seamans, M.E. 2005.** Population biology of the California spotted owl in the central Sierra Nevada. Saint Paul, MN: University of Minnesota. 141 p. Ph.D. dissertation.
- Seamans, M.E.; Gutiérrez, R.J. 2007.** Sources of variability in spotted owl population growth rate: testing predictions using long-term mark-recapture data. *Oecologia* 152(1): 57–70.
- Seamans, M.E.; Gutiérrez, R.J.; Moen, C.A.; Peery, M.Z. 2001.** Spotted owl demography in the central Sierra Nevada. *Journal of Wildlife Management*. 65(3): 425–431.
- Stearns, S.C. 1976.** Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51(1): 3–47.
- Stoelting, R.E.; Gutiérrez, R.J.; Kendall, W.L.; Peery, M.Z. 2015.** Life history trade-offs and reproductive cycles in spotted owls. *Auk*. 132(1): 46–64.
- Tempel, D.J.; Gutiérrez, R.J. 2013.** Relation between occupancy and abundance for a territorial species, the California spotted owl. *Conservation Biology*. 27(5): 1087–1095.
- Tempel, D.J.; Gutiérrez, R.J.; Whitmore, S.A.; Reetz, M.J.; Stoelting, R.E.; Berigan, W.J.; Seamans, M.E.; Peery, M.Z. 2014a.** Effects of forest management on California spotted owls: implications for reducing wildfire risk in fire-prone forests. *Ecological Applications*. 24(8): 2089–2106.
- Tempel, D.J.; Peery, M.Z.; Gutiérrez, R.J. 2014b.** Using integrated population models to improve conservation monitoring: California spotted owls as a case study. *Ecological Modelling*. 289: 86–95.
- Verner, J.; McKelvey, K.S.; Noon, B.R.; Gutiérrez, R.J.; Gould, G.I., Jr.; Beck, T.W., eds. 1992.** The California spotted owl: a technical assessment of its current status. Gen. Tech. Rep. PSW-GTR-133. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 285 p.
- Wu, C.H.; Drummond, A.J. 2011.** Joint inference of microsatellite mutation models, population history and genealogies using transdimensional Markov Chain Monte Carlo. *Genetics*. 188(1): 151–164.
- Zimmerman, G.S.; Gutiérrez, R.J.; LaHaye, W.S. 2007.** Finite study areas and vital rates: sampling effects on estimates of spotted owl survival and population trends. *Journal of Applied Ecology*. 44(5): 963–971.