Chapter 8: The Spotted Owl in Southern and Central Coastal California

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Introduction

Spotted owl populations found in southern and central coastal California have received much less attention than those inhabiting the Sierra Nevada because of economic (effect of habitat conservation measures on timber harvest) and social issues (community stability and desire for naturally functioning ecosystems). Yet there has been continued concern over the status of owl populations in this region since the first technical assessment of the California spotted owl "The California Spotted Owl: A Technical Assessment of Its Current Status" (CASPO) in 1992 (Eliason and Loe 2011,² LaHaye and Gutiérrez 2005, Verner et al. 1992c). In this chapter, we first summarize the areas of concern for southern California and central coastal California (hereafter we refer to this region as "southern California") portrayed in CASPO (Verner et al. 1992b). We then summarize new information gained since CASPO and revisit the status of threats to the owls. Finally, we provide some observations on the status of owls in southern California and potential management implications derived from new information.

Since the CASPO report, most new information on spotted owls stems from work on the San Bernardino population, which is the largest owl population in southern California (see below). This information has been reported in scientific journals and symposia or as part of targeted monitoring in a few mountain ranges. Whereas lack of funding within the U.S. Forest Service (USFS) has limited the acquisition of new information, the USFS has developed a California spotted owl strategy for southern California (see footnote 2; Loe and Beier 2004³). The original strategy was motivated by the extensive fires in southern California during 2003. This region-specific strategy was developed as a response to CASPO (Verner et al. 1992b).

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² Eliason, E.; Loe, S. 2011. Management indicator species account for California spotted owl in the southern California province. 61 p. Unpublished report. On file with: USDA Forest Service, San Bernardino National Forest, 602 S Tippecanoe Ave., San Bernardino, CA 92408.

³ Loe, S.; Beier, J.L. 2004. Conservation strategy for the California spotted owl (*Strix occidentalis occidentalis*) on the national forests of southern California. Unpublished report. On file with: USDA Forest Service, San Bernardino National Forest, 602 S Tippecanoe Ave., San Bernardino, CA 92408.

CASPO Assessment of Areas of Concern

In CASPO, four general areas of concern were identified for the California spotted owl (*Strix occidentalis occidentalis*) in southern and central coastal California (Verner et al. 1992b: 7):

- 1. The first was the potential loss of connectivity among mountain ranges in the region and between this region and the Sierra Nevada.
- 2. The second was the potential fragmentation of habitat within these insular areas that define the distribution of the owls in southern California (see below).
- 3. The third was the loss of habitat owing to water usage that leads to decline of riparian forest, high-severity fires that result in loss of habitat, and recreational use that results in either loss of habitat or disturbance to owls.
- The fourth concern was the lack of land use policies on private lands, adjacent to public lands, which could be used to mitigate the potential effects of development.

The CASPO also noted that if the owl metapopulation did not function sufficiently to facilitate demographic rescue, then populations would have to function independently (depend on their own population dynamic processes), which meant that these populations would have to depend solely on the amount and quality of habitat available to them to remain viable.

Distribution and Metapopulation

The spotted owl in southern California is distributed from Monterey County south to Mount Palomar near the Mexican border (fig. 8-1), and is found as far south as the Sierra San Pedro Martir in Baja California Norte (Gutiérrez et al. 1995). Both the Sierra San Pedro Martir and Sierra Juarez are southern extensions of the Peninsular Ranges that contain most of the populations in southern California. The subspecies of owl found on these two Mexican ranges is unknown but by its geographic location is thought to be the California spotted owl. Owls also occur in the Tehachapi Mountains that potentially link this population, by closest proximity, to the Sierra Nevada (Verner et al. 1992b). Notable is the apparent absence of owls from the Santa Cruz Mountains, which apparently have suitable forest types for spotted owls. Based on geographic proximity, the Carmel Valley should not have presented a substantial barrier to dispersal for birds inhabiting the south side of the



Figure 8-1—Approximate territory locations and distribution of the California spotted owl in southern California, 2014. The Sierra Nevada is also depicted on the map to show the proximity of the Sierra Nevada population with the southern California owl metapopulation.

Carmel Valley in the Santa Lucia Range. At the time of CASPO, there had been no systematic surveys for spotted owls in the Santa Cruz Mountains (Verner et al. 1992b). This was still the situation in 2016.

Within this large geographic distribution, the spotted owl in southern California is unique among west coast spotted owl populations because it occurs as a presumed metapopulation (LaHaye et al. 1994). Metapopulations are defined by distinct populations of individuals that function independently yet their dynamics are interrelated because of dispersal among populations (Hanski and Gilpin 1991). For the California spotted owl, the key issue is that the distance between populations is farther than owls typically disperse (Gutiérrez and Harrison 1996). The populations are generally distinct and isolated from each other because they exist within the high-elevation forests that are found above the unsuitable shrub and semiarid vegetation zones that serve as barriers to movement among populations. In metapopulations, all populations have an equal likelihood of extinction, which predicts that persistence of the regional spotted owl population is dependent on there being enough populations. However, this is not the case in southern California so, theoretically, some populations will have to serve as source populations to "rescue" populations that go extinct (Gutiérrez and Harrison 1996, LaHaye et al. 1994, Noon and McKelvey 1996, Noon et al. 1992). Hence, the spatial structure of populations and habitats within and among populations is critical to the functioning of this metapopulation (Gutiérrez and Harrison 1996, Noon and McKelvey 1996). Thus far, there is scant evidence that dispersal among populations is a central property of the metapopulation dynamics of owls in southern California because there have been no records of movement even between populations in relatively close proximity (i.e., adjacent mountain ranges) (LaHaye et al. 2001, 2004). The lack of documented owl movement among populations for this region is in stark contrast to that of Mexican spotted owls (S. o. lucida) in the American Southwest, where movement among mountain ranges (i.e., populations) is common and the population is generally considered to have a metapopulation structure (Gutiérrez et al. 1996, May et al. 1996). In addition, two habitat conditions affect spotted owls generally (habitat fragmentation and habitat heterogeneity); these conditions increase the complexity and also the risk of extinction for owls in the southern California metapopulation (LaHaye et al. 1994). In this regard, most of the detailed ecological studies of southern California have occurred in the San Bernardino Mountains, which harbors the largest population of owls in southern California, and consequently these results likely provide the most optimistic view of owls in southern California.

LaHaye et al. (1994) and Noon et al. (1992) modeled the dynamics of this metapopulation, while Beck and Gould (1992) provided verbal and visual descriptions of areas of potential concern for the southern California metapopulation. These studies clearly indicate that owl populations and habitat within populations are discontinuous. Noon et al.'s (1992: 189) simulation of the southern California metapopulation employed (and acknowledged) optimistic assumptions for owl survival rates in suitable habitat (i.e., they set survival rates high enough so that annual population growth rate $[\lambda] = 1$) and allowed for the possibility that λ increased by 2 percent per year. The reason for these assumptions was to examine how the habitat distributed over this large area might affect the metapopulation dynamics. At the time of their analysis (Noon et al 1992), there was only one owl demographic study in southern California, and its relatively short duration did not allow a meaningful estimation of the effect of environmental conditions on that population. They noted that it is critical to examine the effects of both demographic and stochastic (random variation owing to such things as drought and fires) variation on owl population dynamics. Some of the assumptions posed for metapopulation theory have been that dispersal capability of owls to move among independent populations (i.e., mountain ranges) must be sufficient, that the distances between mountain ranges affect system dynamics, that the risks to owls when moving between or among mountain ranges is not excessive, and that small populations with high turnover have to be augmented by immigration to persist. From these basic assumptions, they concluded that the San Bernardino population was critical to the persistence of the entire metapopulation because the many small populations benefited in the simulation by having a large source population (i.e., the San Bernardino/San Gabriel Mountains). Noon et al. (1992) also evaluated the effect of potential habitat configurations on owl demography and key properties of the metapopulation (e.g., how the spacing of habitat islands affected dispersal). Evidently, simulated populations were strongly affected by dispersal risks both within and among ranges, sizes of individual populations, and the distances among populations.

Noon et al. (1992) felt it was premature to assess extinction risk for the southern California owl metapopulation because there was insufficient data on several important variables (e.g., stochastic environmental variation, correlation in environmental conditions among populations), but LaHaye et al. (1994) had access to additional data and conducted such an analysis. They used a spatially structured metapopulation model that considered the number, size, and spatial location of each habitat patch and allowed for interaction among these patches (stochastic growth and dispersal among populations) and for correlation among environmental variation within the region (i.e., the degree to which environmental conditions were similar among areas supporting populations). Because they did not have information on all the populations, they relied on demographic information from the San Bernardino (i.e., the largest population in the metapopulation) and the San Jacinto Mountains (i.e., one of the smallest populations). They found that dispersal between these close populations was very low (no dispersal of color-marked owls was observed in 6 years of study), so they modeled a variety of dispersal rates and also modeled dispersal as a function of distance (i.e., dispersal rates declined with increasing distance between populations). Because they suspected that rainfall (a form of environmental variation) was correlated with spotted owl population dynamics (now demonstrated to be true; see LaHaye et al. [2004] and below), they modeled a range of environmental correlation even though rainfall was strongly correlated among the four mountain ranges examined. The correlations of rainfall

amounts among the San Bernardino, Santa Ynez, and Santa Ana Mountains and Mount Palomar ranged from 0.81 to 0.89. Their simulations suggested the metapopulation would likely either go extinct within the next 30 to 40 years or, under alternative hypotheses of deterministic decline and environmental fluctuations, would undergo a substantial decline but not go extinct, respectively. The effects of high environmental correlations and the vital rates were strong in influencing simulation results. They discussed a variety of alternative explanations for their results, most of which were not optimistic about the state of the metapopulation.

The insular nature of these populations also presented a unique opportunity to study particular facets of the owl's ecology (e.g., dispersal) that were more difficult to study in larger contiguous populations as shown by LaHaye et al. (1994). At the time of CASPO, only one long-term and several short-term studies were available for the technical assessment team (Verner et al. 1992c). One of these studies in the San Bernardino Mountains continued until 2000, while the others (San Jacinto Mountains and Mount Palomar) ended either before or shortly after CASPO was completed. Intensive study has been replaced by irregular monitoring sponsored by individual natinal forests (see footnote 2). Because of the very low numbers of birds in some populations and the apparent low dispersal, some of these populations appear to be in precarious conservation status, which makes this paucity of information an even greater concern (see footnote 2).

General Ecology

The ecology of spotted owls has been well described (e.g., chapter 2; Gutiérrez et al. 1995, Verner et al. 1992a), and the general ecology of spotted owls in this region does not appear to differ substantially from that of California spotted owls elsewhere (note: there is almost no information on spotted owls in Baja California Norte [Gutiérrez et al. 1995]). However, the details of environment, particularly climate, vegetation, and insularity, may affect the dynamics of the owl in southern California differently than they do in the Sierra Nevada (Gutiérrez and Pritchard 1990; Gutiérrez et al. 2011; LaHaye et al. 1992, 2001, 2004). The differences between owls in this region and the Sierra Nevada also have to be viewed not only within the context of the spatial fragmentation of populations (disjunct mountain ranges leading to metapopulation structure [i.e., insularity]), but also with respect to the spatial fragmentation of individuals (discontinuities of habitat owing to topography, elevation, soils, aspect, wildfire, and human impacts) and the natural heterogeneous makeup of cover types within owl territories. Very little is known about home range sizes of spotted owls in southern California but limited information suggests that home range size is variable (Zimmerman et al. 2001). Habitat fragmentation occurs

when habitat is discontinuous and that discontinuity affects population processes as a binary outcome (habitat or no habitat) (Franklin and Gutiérrez 2002). In contrast, habitat heterogeneity is the diversity of vegetation and successional stages within an area of interest (e.g., an owl territory), such that it reflects a multistate outcome (Franklin and Gutiérrez 2002).

Habitat

There are four major cover types used by spotted owls in southern California: riparian/hardwood forests and woodlands, live oak (*Quercus chrysolepis* Liebm.)/ bigcone Douglas-fir (*Pseudotsuga macrocarpa* (Vasey) Mayr) forest, mixed-conifer forest, and redwood (*Sequoia sempervirens* Lamb. ex D. Don Endl.)/California laurel (*Umbellularia californica* Hook. & Arn.) Nutt.) forest (Gutiérrez et al. 1992). Unlike the Sierra Nevada, most owls occur in cover types other than mixed-conifer forest (Gutiérrez et al. 1992) because mixed-conifer forest is only found at the highest elevations in most of these isolated mountain ranges.

Smith et al. (2002) found owls distributed over a large altitudinal gradient (800 to 2600 m [2,625 to 8,530 ft]) in the San Bernardino Mountains, which was the limit of available habitats in this mountain range. Of the major cover types used by owls in this range, canyon live oak/bigcone Douglas-fir cover type had both the most territories and the highest density of territories (56 and $0.39/\text{km}^2$ [0.15 mi²], respectively; see also density comparisons with other areas in California below). The density of the 40 owl territories found in mixed-conifer/hardwood forest was 0.29 territories/km² (0.11 territories/mi²), and the density of the 48 territories found in mixed-conifer forest was 0.16 territories/km² (0.06 territories/mi²); Smith et al. (2002) partitioned the mixed-conifer type of Gutiérrez et al. (1992) into two categories based on the proportion of hardwoods found in the understory and subcanopy layer of the forest. LaHaye et al. (1997) speculated that the high density of owls in canyon live oak/bigcone Douglas-fir forests may be related to high densities of prey in the chaparral that typically surrounds this cover type because more young fledged in this forest type than other types in the San Bernardino Mountains. They reported that owl territories were clumped in space rather than being randomly distributed, which resulted in the mean nearest neighbor distance (1497 m [4,911 ft]) being significantly less than the distance between an equal number of random points (1787 m [5,862 ft]) (Smith et al. 1999).

Smith et al. (2002) also assessed vegetation patterns at three arbitrary scales and one biologically based scale (3, 20, 79, and 177 ha [7, 49, 195, and 437 ac]) within owl territories and compared these patterns to those found at same-sized plots at randomly chosen sites. These analysis areas were circular plots with radii of 100, 250, 500, and 750 m (328, 820, 1,640, and 2,460 ft), respectively. The 3-ha area represented the immediate area surrounding a nest or primary roost site, the 20-ha (49-ac) area was used to assess both natural and human-induced fragmentation, the 79-ha (195-ac) area represented a larger area around the nest but probably much less than a core area, and the 177-ha (437-ac) area represented half the nearest neighbor distance, which approximated the size of a territory (see chapters 2 and 3). Collectively, they classified 17 cover types that they collapsed to four cover types for ease of analysis and to focus on forested vegetation (Smith et al. 2002: 140). At all analysis scales, spotted owl sites contained more closed-canopy forest and less nonforest, open forest, and chaparral cover types than random areas. Moreover, these closed-canopy areas were in fewer but larger patches. Their analysis showed that as the amount of closed-canopy forest increased so did the probability that a site contained owls.

Although riparian/hardwood forests are used by owls in southern California, the owls in the San Bernardino Mountains that had riparian habitat in their home ranges had only minor portions of their home ranges in this cover type (Gutiérrez and Tempel, pers. obs.). These streamside forests and woodlands are also important owl habitats in other mountain ranges in southern California (Verner et al. 1992b).

Many studies of habitat structure have shown that spotted owls are habitat specialists (i.e., they use some cover types in greater proportion than their availability in the landscape), and this is also true for owls inhabiting the San Bernardino Mountains (Gutiérrez et al. 1995, LaHaye et al. 1997, Verner et al. 1992b). LaHaye et al. (1997) showed that owls in the San Bernardino Mountains used areas that had greater canopy cover and more complex vegetation structure than what was available to them (i.e., randomly selected areas; table 8-1) (LaHaye et al. 1997). Owls also selected nest sites that had greater canopy cover, larger trees, and greater basal areas of hardwoods and conifers than what was available to them.

Population Dynamics

There have been many analyses of owl population dynamics in southern California (Franklin et al. 2004; Gutiérrez and Pritchard 1990; Gutiérrez et al. 2011; LaHaye et al. 1992, 1994, 2001, 2004; Noon et al. 1992; Peery et al. 2012). Of these, five were comprehensive studies that provided estimates of finite rate of population change; all of these involved the same San Bernardino long-term demography study (Franklin et al. 2004; LaHaye et al. 1992, 1994, 2004; Noon et al. 1992). The others were focused more specifically on elements of population dynamics or climate change (Gutiérrez and Pritchard 1990, Gutiérrez et al. 2011, LaHaye et al. 2001, Peery et al. 2012).

Habitat variable	Nest points (N = 103)		Random points (N = 296)	
	Mean ^a	Percentage CV ^b	Mean	Percentage CV
Percentage canopy closure	79.3	22.3	52.4	49.9
Percentage slope	54.2	49.8	32.1	68.7
Broken-top tree basal area ^c	2.9	174.3	0.5	322.9
Snag basal area	4.8	116.7	1.8	217.8
Hardwood basal area (30.1 to 45 cm diameter at breast height [d.b.h.])	3.2	216.7	0.9	332.8
Hardwood basal area (>45 cm d.b.h)	4.9	144.7	0.8	380.4
Total conifer basal area	37.1	59.5	20.1	85.8
Conifer basal area (50.1 to 75 cm d.b.h.)	9.6	100.3	4.9	130.1
Conifer basal area (>75 cm d.b.h.)	19.1	77.4	6.7	124.2

Table 8-1—Structure characteristics of spotted owl habitat and random areas in the San Bernardino Mountains

^a Includes zero values for all variables.

^b Percentage coefficient of variation.

^c Square meters per hectare.

Source: Reproduced with permission from the Wilson Journal of Ornithology [formerly the Wilson Bulletin].

Density

Crude densities (the density irrespective of cover types present on the landscape) of owls in southern California are lower than densities in other areas of California (table 8-2), which reflects the spatial fragmentation of suitable habitat across the landscape. However, ecological density (the density of owls within all suitable cover types on the landscape) is similar to one population of northern spotted owls in northwest California before its decline (Franklin et al. 1990). This suggests that the habitat in southern California has a similar capacity for supporting spotted owls as the more mesic forests in northwestern California, the latter of which have been highly fragmented by logging during the last half of the 20th century. We note that almost all populations of spotted owls are declining throughout its range so current densities will be lower (e.g., see table 8-2 for northwestern California example).

Reproduction

Franklin et al. (2004) estimated fecundity (number of female young produced per territorial female) for the San Bernardino Mountain population and found uncertainty among the models which represented hypothesized relationships. Their top model specified an even-odd pattern for reproduction, but this model was only slightly better than the "null" (intercept-only) model. Moreover, the parameter coef-

	Crude density				
Time period 1980–early 1990s	Time period most recent	Location	Source		
	Owls/km ²				
0.015	No recent estimate	San Bernardino Mountains	LaHaye et al. 2004, Smith et al. 2002		
0.059^{a}	0.051^{b}	Lassen National Forest	Keane 2016 ^c		
0.18^{a}	0.16^{b}	Eldorado National Forest	Keane2016 ^c		
0.151 ^{<i>a</i>}	0.151^{b}	Southern Sierra Nevada	Keane 2016 ^c		
0.184 ^{<i>a</i>}	0.184^{b}	Sequoia and Kings Canyon	Franklin et al. 2004,. Keane 2016 ^c		
1.21	No recent estimate	San Jacinto Mountains	Noon et al. 1992		
0.64	No recent estimate	Mount Palomar	Gutiérrez and Pritchard 1990		
0.235	0.123	Northwest California	Franklin et al. 1990, Franklin 2016 ^d		
	Ecological density				
0.58	No recent estimate	San Bernardino	Smith et al. 2002		
0.544	No recent estimate	Northwestern California	Franklin et al. 1990		

Table 8-2—Crude (density over an entire study area) and ecological (density within cover types that are preferentially selected relative to available cover types) densities of spotted owls in California

^{*a*} Year of lowest density within span of years (1990–2000) studied by Franklin et al. 2004; density calculated from raw data because density was not estimated by Franklin et al 2004.

^b Year of lowest density within span of years (1990–2005) studied by Blakesley et al. 2010; density calculated from raw data because density was not estimated by Blakesley et al.

^c Keane, J. K. 2016. Personal communication. Research wildlife ecologist, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, 1731 Research Park Dr., Davis, CA 95618.

^d Franklin, A. F. 2016. Personal communication. Supervisory research biologist and project leader, Wildlife Pathogens and Food Security & Safety Project, USDA/APHIS/WS National Wildlife Research Center, 4101 Laporte Avenue, Fort Collins, CO 80521-2154.

ficient for the even-odd relationship was not significantly different than zero. The estimate of fecundity derived using the top model was 0.362 female young produced per female, which was similar to the Lassen (0.336), slightly lower than the Eldorado (0.409), and slightly higher than the Sierra and Sequoia and Kings Canyon (0.284 and 0.289, respectively) long-term demography studies (Franklin et al. 2004).

LaHaye et al. (2004) used several more years of data than did Franklin et al. (2004) and derived different analyses from those of Franklin et al. (2004) in two significant ways. First, they created models that hypothesized relationships between weather and owl reproduction and other vital rates (see below). Second, they estimated rates of population change using a different approach than Franklin et al. (2004; see also chapter 4). Many studies of spotted owls have used weather variables to examine patterns in owl vital rates (e.g., Franklin et al. 2000, Seamans et al. 2002, Seamans 2007). Weather has been shown to affect animals directly (e.g., by affecting energy needs) and indirectly (e.g., by affecting plants, which produce food for the prey upon which the owl depends). Thus, analyses that assess weather effects have provided insight into environmental processes and conditions that have the potential to affect owls.

In the San Bernardino Mountains, LaHaye et al. (2004) showed that fecundity varied annually from 0.00 to 0.47 for subadult owls to 0.18 to 0.51 for adult owls. The top model suggested that the data were best explained by the additive effects of age and weather covariates. Owls experienced reduced fecundity during wet springs but increased fecundity when the previous weather year was wetter. Thus, owls reproduced best during a dry spring that followed a wet winter. Interestingly, this weather relationship (model) explained 100 percent of the temporal process variation in the data where 62 percent of the variation in the data was process variation and 38 percent was sampling variation. Process variation is the variation in the data that is attributable to the underlying processes that affect fecundity, whereas sampling variation is the variation attributable to sampling error.

Owls use old forest for nesting sites (Gutiérrez 1985). However, as has been shown for other California spotted owl populations (Gutiérrez et al. 1992), owls in the San Bernardino Mountains will use other nest structures besides old trees (LaHaye et al. 1997). Spotted owls used nine tree species for nesting, and the majority of nest types were platform nests (59 percent). Cavity (24 percent) and broken top (17 percent) nests were used less frequently (LaHaye et al. 1997). However, they found no difference in nesting success among owls using different nest structures (LaHaye et al. 1997). Moreover, they found no difference between successful and unsuccessful nests with respect to habitat at the spatial scale of either the nest or nest stand (LaHaye et al. 1997). However, owls nesting in canyon live oak/bigcone Douglas-fir forests had higher reproduction than those nesting in other forest types, and the authors speculated that this may have been due to higher prey densities in chaparral surrounding this forest type.

Survival

We restrict our comments to the most recent population analyses for the San Bernardino Mountains because earlier studies used smaller datasets from this population (Franklin et al. 2004, LaHaye et al. 2004). Apparently, survival probabilities of adult spotted owls were estimated to be 0.815 (Franklin et al. 2004) or 0.796 (LaHaye et al. 2004), which were similar to estimates for most Sierra Nevada populations of owls. In addition, LaHaye et al. (2004) also estimated separate survival probabilities for first- and second-year subadults as 0.692 and 0.88, respectively. The slight difference between these estimates is related to the use of several additional years of data by LaHaye et al. (2004). LaHaye et al. (2004) also found that estimates of survival were most correlated with the age of owls and precipitation in the preceding winter, but there was uncertainty among weather variables in competing models. However, second-year subadult survival was higher than adult survival (0.88 and 0.80, respectively), which was different than other spotted owls populations. They also estimated juvenile survival to be 0.37. Analyses of the population have yielded the only unbiased estimates of juvenile spotted owls based on mark-recapture data (Zimmerman et al. 2003). LaHaye et al. (2004) also reported finding no temporal process variation in nonjuvenile survival, suggesting it was nearly constant over time.

Dispersal

The demographically closed nature of the San Bernardino study area has provided insight on dispersal for both juvenile and adult owls (Gutiérrez et al. 2011, LaHaye et al. 2001). Spotted owls exhibit obligate juvenile dispersal (i.e., they always disperse from the natal areas in their year of hatching) (Gutiérrez et al. 1995). In the San Bernardino population, of 478 juveniles banded between 1987 and 1998, 67 males and 62 females successfully dispersed (i.e., they were relocated as a territorial bird elsewhere on the study area) from their natal areas. Males dispersed slightly less distance than females, but the difference was not statistically significant (mean for males = 10.1 km [6.3 mi], $SD = \pm 7.6$ km [4.7 mi]; mean for females = 11.7 km [7.3 mi], $SD = \pm 8.1$ km [5.0 mi]). In general, female birds disperse farther than male birds, but there are many exceptions to this generality (Greenwood 1980). By age 4, almost all birds had settled on territories, but about 40 percent of them took 2 to 4 years to settle, which indicated they were floaters during that time. Floater owls, as described in chapter 2, will usually not exhibit territorial behavior (i.e., hoot in response to vocal lures or other owls hooting). The rather short dispersal distances reported by these authors were likely a reflection of a "reflective boundary" of unsuitable habitat at the edge of the study area (LaHaye et al. 2001). No spotted owls have been found successfully dispersing between or among the San Bernardino, San Gabriel, and San Jacinto Mountains, which are adjacent ranges, despite surveys and banding of owls within all three ranges (LaHaye et al. 2001, 2004). This suggests that interpopulation dispersal, the key to maintenance of a metapopulation structure, is rare, which seems to support the more pessimistic projections of LaHaye et al.'s (1994) metapopulation modeling.

LaHaye et al. (2001) evaluated the dispersal distances between and among juveniles fledged in pairs and triplets, respectively. They found no correlation in

the distances that related birds dispersed. In addition, they also found evidence for conspecific attraction because most owls settled at or near sites that were occupied the prior year (LaHaye et al. 2001).

Peery and Gutiérrez (2013) used the same dataset as LaHaye et al. (2001) to assess whether juvenile survival was influenced by parental reproductive output under the hypothesis that the offspring of parents producing large broods would have relatively low survival probabilities, as expected under classic life-history theory (i.e., there is a cost to the owls because of the effort required to reproduce). They found that individuals that fledged in pairs had a greater probability of surviving their first year than individuals that fledged as singletons or in triplets. Moreover, improved survival for individuals that fledged in pairs carried over to subadult and adult stages. These authors also showed that indices of territory quality based purely on reproductive output were strongly correlated with indices based on offspring fitness that accounted for heterogeneity in survival rates. Thus, if reproductive output of owls within territories is known, the information could be used in conjunction with occupancy and survival information to rank territories for conservation planning.

Almost a third (29 percent) of all territorial females and nearly a fifth (19 percent) of males on the San Bernardino study area dispersed at least once during that 12-year study (Gutiérrez et al. 2011). Spotted owls may disperse following either the breaking of a pair bond or when a mate dies. Gutiérrez et al. (2011) found that birds that had higher reproductive output than the population average were less likely to disperse, which suggests that birds based their choices on the perceived quality of either particular territories or particular mates. The former hypothesis was supported by a post-hoc analysis that birds occupying territories of higher quality (i.e., territories whose occupants over time had higher than average reproductive output) were less likely to disperse. Of course, the territory and the individuals occupying a territory were confounded in their analyses, which was reflected in the relatively low variation explained by their models. Birds that dispersed following the death of their mate tended to improve their reproductive output. However, this latter result was likely related to paucity of data.

Occupancy

The most complete data on territory occupancy in southern California exists for the San Bernardino and San Jacinto Mountains within the San Bernardino National Forest (SBNF). In addition to surveys conducted under the demographic study from 1987 through 1998 on the SBNF, extensive monitoring of known owl territories was resumed from 2003 through 2011 within the two mountain ranges. This monitoring revealed (see footnote 2) a significant decline (about 50 percent) in territory occupancy from 1989 through 2010 on the SBNF. Although Eliason and Loe only reported naïve estimates of territory occupancy (i.e., conducted no statistical modeling to account for imperfect detection), their naïve occupancy estimates likely were unbiased because a large number of surveys (up to six) were typically conducted at each territory during a given year. Surveys were also conducted within other national forests in southern California from 2003 through 2011, but we can make no inferences about trends in occupancy within other mountain ranges because only a small number of locations were sporadically surveyed. As discussed in chapter 4, Lee et al. (2013) found no statistically significant effects of fire or salvage logging on spotted owl territory occupancy in the San Bernardino Mountains from 2003 to 2011. However, they recognized that fire and salvage logging may have had negative effects on occupancy that were biologically meaningful. For example, territories that experienced fire had a 0.062 less probability of being occupied by an owl pair the following year than unburned sites; postfire salvage logging reduced this probability by an additional 0.046. In particular, local extinction markedly increased when >50 ha (124 ac) burned at high severity within a 203-ha (502-ac) region around territory centers.

Population Trends

The most comprehensive studies of the San Bernardino owl population by Franklin et al. (2004) and LaHaye et al. (2004) differed in their approaches and intent. Franklin et al. (2004) conducted a meta-analysis of all extant California spotted owl demographic studies so they were intent on keeping methodologies and data structures similar. In the former case, they used Pradel's temporal symmetry model to estimate population rate of change because the Sierra Nevada study areas were demographically open and thus had biased data with respect to juvenile survival. However, as also noted above, the San Bernardino population was closed so they used a Leslie projection matrix to estimate population rate of change because estimates of juvenile survival were not biased by undetected emigration (LaHaye et al. 2004, Zimmerman et al. 2007). The Pradel model answers the question: "Are the owls on the study area being replaced?" The Leslie projection matrix answers the question "Are the owls on the study area replacing themselves?" Thus, both estimators are valid; they simply confer different inferences.

Franklin et al. (2004) found a linear decline in population over the time considered ($\lambda = 0.98$), but the confidence interval overlapped 1.0 so there was uncertainty

about an actual decline. In contrast, LaHaye et al. (2004) estimated $\lambda = 0.91$ and the confidence limit did not overlap 1.0, which indicated that the population in the San Bernardino Mountains declined approximately 9 percent/year over the period of study (1987–1998). LaHaye et al. (2004) also analyzed their data using the same time period as Franklin et al. (2004) and estimated that $\lambda = 0.92$, which was still a significant decline but much lower than Franklin et al.'s (2004) estimate. This difference relates to the closed San Bernardino population, which allowed LaHaye et al. (2004) to use a Leslie projection matrix to estimate lambda. Finally, Franklin et al. (2004) developed a metric called "realized population change" that depicted the change in population size over time relative to the initial population size. Consistent with their estimate of lambda, realized change for the San Bernardino population was not significantly different than 1. This metric was developed because it is difficult to detect trends in populations when they are small (Franklin et al. 2004, Tempel and Gutiérrez 2013). Thus, estimates of the decline of owls in the San Bernardino Mountains were supported by an estimator that was able to take advantage of the internal dynamic processes (stage-specific survival and reproduction) exhibited by this owl population.

Threats

Here we return to the factors noted by CASPO as threats to the long-term viability of the southern California owl metapopulation (Verner et al. 1992b: 7). In addition, we address the concerns raised by LaHaye and Gutiérrez (2005) and provide new potential concerns that have surfaced since CASPO (see footnote 2) (Peery et al. 2012).

Natural Connectivity Among Populations

Successful dispersal among populations is the only way that this metapopulation can continue to function naturally (LaHaye et al. 2004, Verner et al. 1992b). Connectivity among populations is influenced by barriers and by dispersal habitat. In 1992, the threat of barriers was urban and suburban development, while the threat to habitat was the elimination of riparian areas that might serve as corridors. The current situation is worse because development continues unabated within both the Los Angeles Basin and the surrounding deserts. Moreover, many wind turbines have been erected in several areas that could serve as potential dispersal corridors between mountain ranges and between the southern California region and the Sierra Nevada. Wind turbines pose a potential threat of unknown magnitude to owls. There are no intact riparian forests that could act as corridors to assist owls dispersing among mountain ranges. At the time of CASPO, reservoirs were not specifically considered a barrier to dispersal, but at least one owl drowned in its apparent attempt to cross one in the area between the San Bernardino and San Gabriel Mountains.⁴ Thus, we add two types of infrastructure development as potential threats to dispersal—wind farms and large reservoirs. Finally, the link between the Sierra Nevada population and southern California through the Transverse Ranges has also not improved and likely has deteriorated owing to continued human development.

Integrity of Habitat Supporting Each Population

With dispersal reduced among populations, rescue effects will not be a factor in the functioning of the metapopulation. Rather, each population will persist or go extinct, in part, as a function of its own habitat conditions. Habitat loss could result from fires and salvage logging (see above). There are as yet, no restrictions on logging on private forest land within the range of the owl other than those imposed by the California Forest Practices Act. Habitat is also being lost or fragmented as a result of primary and secondary home building (LaHaye and Gutiérrez 2005). However, there is no longer any commercial timber harvest on national forests within the owl's range in southern California (see footnote 2). Yet we still do not know if key habitat elements are declining (e.g., large residual trees).

Water Diversion and Stream Channelization

LaHaye and Gutiérrez (2005) provided no evidence for current loss of riparian habitat owing to the water diversion threat noted by Verner et al. (1992b). Yet this threat remains as well as the threat of channelization to control waterflow (i.e., flood protection). Some owls, particularly those at low elevations, have parts of their territories within riparian habitats and these activities either degrade or eliminate these riparian areas. Riparian areas have high species diversity so they likely represent suitable owl foraging sites if they contain tree cover. The U.S. Forest Service has made some progress by requiring that water be hauled into some vacation homes and camps instead of being diverted from streams (see footnote 2). This should reduce some negative impact to riparian areas, but the effect of these new regulations has not been quantified (see footnote 2).

Wildfire

Wildfire has long been a concern for its potential impact on owls and their habitat, but its overall effect on owl populations is not clear (see chapters 3 and 4 as well as

⁴ LaHaye, W.S. 1996. Personal communication. Wildlife biologist, 10156 Pine Place, Morongo Valley, CA 92256.

above discussion). Given the loss of habitat owing to other factors (e.g., urbanization and drought, see below), fires are likely a contributing factor in this loss.

Human Recreation

Southern California has a very large and dense human population and the surrounding mountain ranges are used heavily for recreation. LaHaye and Gutiérrez (2005) and others (see footnote 2) voiced concern that recreational activities could negatively affect owls indirectly through disturbance and degradation or loss of habitat to accommodate this recreational activity.

Drought

LaHaye et al. (2004) showed that precipitation was correlated with reproductive patterns. Thus, the general drought pattern that has been affecting southern California for the past two decades will probably have some negative impact on owl demography, primarily by reducing reproductive output. The recent and future droughts will only exacerbate this concern.

Air Pollution

Air pollution is a well-known phenomenon in southern California. It can potentially affect vegetation dynamics, which in term could affect the habitat of owls and their prey (LaHaye and Gutiérrez 2005). Although air pollution is an issue that is being addressed at many levels through policies and law, it still is affecting some of these owl habitat islands. It also poses a direct threat to owls because birds do not possess a DNA repair mechanism for lung tissue (Rombout et al. 1991).

Mining

Several owl territories in the San Bernardino Mountains are possibly being affected by carbonate mining operations (see footnote 2). The two impacts stemming from these mining operations are side-casting of rock from roads and tailings and water diversion that affects riparian habitat.

Marijuana Cultivation

We are unaware of the extent of marijuana (*Cannabis* sp.) cultivation in southern California, but it is prevalent throughout the rest of rural and mountainous California. Recent evidence indicates widespread use of rodenticides to control rodents that eat these plants has led to secondary poisoning of Pacific fishers (*Pekania pennanti*) in the southern Sierra Nevada (Gabriel et al. 2012). These rodenticides are now being found in a high percentage of barred owls (*Strix varia*) in northwestern California.⁵ If barred owls are being poisoned, then spotted owls are probably also being affected because these species often use the same habitats where they co-occur (Gutiérrez et al. 2007). Thus, we feel it prudent to list this activity as a potential threat to spotted owls in southern California.

Cumulative Effect of Small-Scale Management Actions

Many small-scale activities are conducted by land managers within the range of the owl in southern California, which by themselves may not significantly affect owls but could do so collectively. Some examples of these are hazard tree removals for roads, powerlines, building camps, building vacation homes, diverting water for special uses, and developing ski areas (see footnote 2).

Invasive Species and Disease

The barred owl potentially was first observed in southern California in January 2016 in Los Angeles County but has not yet been verified.⁶ In addition, West Nile virus occurs in southern California, but there is no evidence it is affecting owls (chapter 7). However, invasive plants may be a threat to owl habitat (see footnote 2). Plant species such as cheatgrass (*Bromus tectorum* L.), Chinese tree of heaven (*Ailanthus altissima* (Mill.) Swingle), and tamarisk (*Tamarix ramosissima* Ledeb.) can potentially affect owl habitat either through competition and displacement or providing fuel for fires. Sudden oak death syndrome has also affected owl habitat in some parts of the Los Padres National Forest (see footnote 2).

Climate Change

Intuitively, California spotted owls in southern California would seem to be vulnerable to the warmer and drier conditions expected under climate change scenarios given the xeric nature of this region (relative to other areas occupied by this subspecies). Peery et al. (2012) assessed the potential impacts of climate change on California spotted owls in the San Bernardino Mountains by first correlating annual demographic rates (survival and reproduction) to weather conditions, and then using demographic-weather relationships to project the population forward in time under

⁵ Higley, J.M. 2015. Personal communication. Wildlife biologist, Hoopa Valley Tribe, 80 Willow Ln, Hoopa, CA 95546.

⁶ **Garrett, K.L. 2016.** Personal communication. Ornithology collections manager, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007.

alternative climate change scenarios. According to their model, viability at the end of the 21st century was relatively insensitive to climate change under all scenarios considered, whereas the viability of two Mexican spotted owl populations was projected to decline substantially as a function of climate change. Viability in the San Bernardino Mountains did not decline largely because reproduction is lower in cold, wet nesting seasons, and such conditions are expected to attenuate under climate change. At least two important caveats need to be mentioned regarding the findings of this study. First, neither changes in wildfires, which may increase in frequency and severity, nor other agents of disturbance (e.g., insects and diseases) were modeled. Second, expected changes in temperature under climate change exceeded the variability that occurred during the period used to develop demography-weather relationships. Thus, the authors assumed that relationships between weather and owl demography will hold under a novel climate space, an assumption that may not be valid.

Although milder nesting conditions may improve reproductive success (Peery et al. 2012), the owl's bioclimatic niche will almost certainly move to higher elevations in southern California. It is unclear whether suitable owl habitat will be able to track elevational changes in the owl's bioclimatic niche within the timeframe needed to avoid mismatches between needed forest conditions and suitable climate. Moreover, the spotted owl's bioclimatic niche will likely occur over more narrow elevational gradients in southern California as the climate warms, which could cause a contraction in the distribution (and reduction in abundance) of owls in the region. Finally, low intermountain dispersal rates in southern California suggest that spotted owls may not be able to track latitudinal shifts in their bioclimatic niche (LaHaye et al. 2001).

Chapter Summary

The status of the spotted owl in southern California is, if not dire, significantly more deteriorated than when it was evaluated as part of CASPO (Verner et al. 1992c). Most information stems from the largest population of owls in southern California, which should have the highest potential for self-sustaining viability. If this population is undergoing substantial decline (50 percent; see footnote 2) (LaHaye et al. 2004), we can assume other populations in southern California are declining as well. The large number of threats, concomitant with no apparent remedies to them, suggests that every effort be made to maintain the integrity of existing suitable forests. Minnich (1980) indicates that canyon live oak/bigcone Douglas-fir forests may have declined in the past century as a result of fire. Canyon live oak/bigcone Douglas-fir forests are often surrounded by highly flammable chaparral and scrub cover types and

therefore could be a priority for fire treatments. However, the tenuous nature of the metapopulation makes active management to reduce fire risk arguably a more risky activity than in other regions. Regardless, maintaining all habitat elements known to be used by owls, especially large trees (both conifers and hardwoods), diverse forest structure, snags, and high canopy cover in mature forests, appears to be a key factor in conserving owls. Areas at higher elevations are also likely to be of greater importance in the future given predictions of climate change and potential use of refugia at higher elevations (Jones et al. 2016, Peery et al. 2012). As noted by CASPO (Verner et al. 1992c), efforts to improve connectivity among mountain ranges and facilitate northerly movements to areas that may be resilient to climate change are important. A spatial population modeling exercise that incorporates climate change and evaluates functional connectivity could greatly facilitate such planning. Finally, assuming the San Bernardino population could first be stabilized and then increased, it may well be time to consider reintroducing owls from this population to other areas where populations have become extinct to provide artificial "rescue effects" in this metapopulation. However, if extinction of populations is from loss or fragmentation of habitat, translocations would not be beneficial.

Literature Cited

- Beck, T.W.; Gould, G.I., Jr. 1992. Background and the current management situation for the California spotted owl. 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: 37–53.
- Blakesley, J.A.; Seamans, M.E.; Conner, M.M.; Franklin, A.B.; White, G.C.; Gutiérrez, R.J.; Hines, J.E.; Nichols, J.D.; Munton, T.E.; Shaw, D.W.H.; Keane, J.J.; Steger, G.N.; McDonald, T.L. 2010. Population dynamics of spotted owls in the Sierra Nevada, California. Wildlife Monographs. 174: 1–36.
- 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: 539–590.
- Franklin, A.B.; Gutiérrez, R.J. 2002. Spotted owls, forest fragmentation, and forest heterogeneity. Studies in Avian Biology. 25: 203–220.

- 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.R.;
 Britting, S. 2004. Population dynamics of the California spotted owl (*Strix* occidentalis occidentalis): a meta-analysis. Ornithological Monographs. 54: 1–54.
- Franklin, A.B.; Ward, J.P.; Gutiérrez, R.J.; Gould, G.I., Jr. 1990. Density of northern spotted owls in northern California. Journal of Wildlife Management. 54: 1–10.
- Gabriel, M.W.; Woods, L.W.; Poppenga, R.; Sweitzer, R.A.; Thompson, C.; Matthews, S.M.; Higley, J.M.; Keller, S.M.; Purcell, K.; Barrett, R.H.; Wengert, G.M.; Sacks, B.N.; Clifford, D.L. 2012. Anticoagulant rodenticides on our public and community lands: spatial distribution of exposure and poisoning of a rare forest carnivore. PLoS ONE. 7 e40163. doi:10.1371/journal. pone.0040163.
- **Greenwood, P.J. 1980.** Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour. 28: 1140–1162.
- Gutiérrez, R.J. 1985. An overview of recent research on the spotted owl. In:
 Gutiérrez, R.J.; Carey, A.B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-GTR-185. Portland, OR:
 U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 39–49.
- Gutiérrez, R.J.; Cody, M.; Courtney, S.; Franklin, A.B. 2007. The invasion of barred owls and its potential effect on the spotted owl: a conservation conundrum. Biological Invasions. 9: 181–196.
- Gutiérrez, R.J.; Franklin, A.B.; LaHaye, W.S. 1995. Spotted owl (*Strix occidentalis*). In: Poole, A.; Gill, F., eds. The birds of North America No. 179: life histories for the twenty-first century. Washington, DC: The Philadelphia Academy of Sciences and The American Ornithologists' Union. 28 p.
- Gutiérrez, R.J.; Harrison, S. 1996. Applying metapopulation theory to spotted owl management: a history and critique. In: McCullough, D., ed. Metapopulations and wildlife conservation. Covelo, CA: Island Press: 167–185.
- **Gutiérrez, R.J.; LaHaye, W.S.; Zimmerman, G.S. 2011.** Breeding dispersal in an isolated population of spotted owls (*Strix occidentalis*): evidence for improved reproductive output. Ibis. 153: 592–600.

- **Gutiérrez, R.J.; Pritchard, J. 1990.** Distribution, density, and age structure of spotted owls on two southern California habitat islands. Condor. 92: 491–495.
- Gutiérrez, R.J.; Seamans, M.E.; Peery, M.Z. 1996. Intermountain movement by Mexican spotted owls (*Strix occidentalis lucida*). Great Basin Naturalist. 56: 87–89.
- Gutiérrez, R.J.; Verner, J.; McKelvey, K.S.; Noon, B.R.; Steger, G.S.; Call,
 D.R.; LaHaye, W.S.; Bingham, B.B.; Senser, J.S. 1992. Habitat relations of the California spotted owl. 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: 79–147.
- Hanski, I.; Gilpin, M. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society. 42: 3–16.
- Jones, G.; Gutiérrez, R.J.; Tempel, D.J.; Zuckerberg, B.; Peery, M.Z. 2016. Using dynamic occupancy models to inform climate change adaptation strategies for California spotted owls. Journal of Applied Ecology. 53. 895–905.
- LaHaye, W.S.; Gutiérrez, R.J. 2005. The spotted owl in southern California: ecology and special concerns for the maintenance of a forest-dwelling species in a human-dominated desert landscape. In: Kus, B.E.; Beyers, J.L., tech. coords. Planning for biodiversity: bringing research and management together. 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.; Akcakaya, H.R. 1994. Spotted owl metapopulation dynamics in southern California. Journal of Animal Ecology. 63: 775–785.
- LaHaye, W.S.; Gutiérrez, R.J.; Call, D.R. 1992. Demography of an insular population of spotted owls (*Strix occidentalis occidentalis*). In: McCullough, D.R.; Barrett, R.H., eds. Wildlife 2001: populations. New York: Elsevier Press: 803–814.
- LaHaye, W.S.; Gutiérrez, R.J.; Call, D.R. 1997. Nest-site selection and reproductive success of California spotted owls. Wilson Bulletin. 109: 42–51.
- 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: 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: 1056–1069.
- May, C.A.; Peery, M.Z.; Gutiérrez R.J.; Seamans, M.E.; Olson, D.R. 1996. Feasibility of a random quadrat study design to estimate changes in density of Mexican spotted owls. Res. Pap. RMRS-RP-322. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 12 p.
- Minnich, R.A. 1980. Wildfire and geographic relationships between canyon live oak, Coulter pine, and big-cone Douglas-fir forests. In: Plumb, T.R., tech. coord. Ecology, management, and utilization of California oaks. Gen. Tech. Rep. PSW-GTR-44. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 55–61.
- Noon, B.R.; McKelvey, K.S. 1992. Stability properties of the spotted owl metapopulation in southern California. 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: 187–206.
- Noon, B.R.; McKelvey, K.S. 1996. A common framework for conservation planning: linking individual and metapopulation models. In: McCullough, D., ed. Metapopulations and wildlife conservation. Covelo, CA: Island Press: 139–165.
- **Peery, M.Z.; Gutiérrez, R.J. 2013.** Life-history tradeoffs in spotted owls (*Strix occidentalis*): implications for assessment of territory quality. Auk. 130: 132–140.
- Peery, M.Z.; Gutiérrez, R.J.; Kirby, R.; LeDee, O.E.; LaHaye, W. 2012. Climate change and spotted owls: potentially contrasting responses in the Southwestern United States. Global Change Biology. 18: 865–880.
- Rombout, P.J.A.; Donans, J.A.M.A.; vanBree, L.; Marra, M. 1991. Structural and biochemical effects in lungs of Japanese quail following a 1-week exposure to ozone. Environmental Research. 54: 39–51.
- Smith, R.B.; LaHaye, W.S.; Gutiérrez, R.J.; Zimmerman, G.S. 2002. Spatial habitat characteristics of an insular spotted owl (*Strix occidentalis*) population in southern California. In: Newton, I.; Kavanagh, R.; Olson, J.; Taylor, I., eds. Ecology and conservation of owls. Collingwood, Victoria, Australia: CSIRO Publishing: 137–147.

- Smith, R.B.; Peery, M.Z.; Gutiérrez, R.J.; LaHaye, W.S. 1999. The relationship between spotted owl diet and reproductive success in the San Bernardino Mountains, California. Wilson Bulletin. 111: 22–29.
- Tempel, D.J.; Gutiérrez, R.J. 2013. Relation between occupancy and abundance for a territorial species, the California spotted owl. Conservation Biology. 27: 1087–1095.
- Verner, J.; Gutiérrez, R.J.; Gould, G.I., Jr. 1992a. The California spotted owl: general biology and ecological relations. 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: 55–77.
- Verner, J.; McKelvey, K.S.; Noon, B.R.; Gutiérrez, R.J.; Gould, G.I., Jr.; Beck, T.W. 1992b. Assessment of the current status of the California spotted owl, with recommendations for management. 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: 3–26.
- Verner, J.; McKelvey, K.S.; Noon, B.R.; Gutiérrez, R.J.; Gould, G.I., Jr.; Beck, T.W. 1992c. 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.
- 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: 963–971.
- Zimmerman, G.S.; LaHaye, W.S.; Gutiérrez, R.J. 2001. Breeding-season home ranges of spotted owls in the San Bernardino Mountains, California. Western Birds. 32: 83–87.
- Zimmerman, G.S.; LaHaye, W.S.; Gutiérrez, R.J. 2003. Empirical support for a despotic distribution in a California spotted owl population. Behavioral Ecology. 14: 433–437.