

Chapter 2: The Biology of the California Spotted Owl

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Introduction

The spotted owl (*Strix occidentalis*) is one of the most studied raptors in the world (Lõmus 2004) because forest management throughout its range has the potential to negatively affect owl populations. Information on the California spotted owl (*S. o. occidentalis*) has been summarized in several literature reviews (e.g., Gutiérrez 1996; Gutiérrez and Carey 1985; Gutiérrez et al. 1995; Keane 2014; Roberts and North 2012; USFWS 1990, 1993, 2003, 2006; Verner et al. 1992a). However, the first comprehensive review of the biology of the California spotted owl was conducted by Verner et al. (1992a). Verner et al. (1992a) also served as a foundational chapter for the California spotted owl technical assessment “The California Spotted Owl: A technical Assessment of it’s current status” (CASPO) and its recommended owl management strategy (Verner et al. 1992b). Much has been learned about the biology of the California spotted owl since CASPO including new methods of data analysis to provide scientifically defensible results (Gutiérrez 2004, 2008). In this chapter, we summarize new information on the natural and life history of the California spotted owl that has been gathered primarily since CASPO (Verner et al. 1992b), but we also include new research about other owl subspecies (northern and Mexican spotted owls, *S. o. caurina* and *S. o. lucida*, respectively) when it is applicable to the California spotted owl. We cite the *Birds of North America* spotted owl account (Gutiérrez et al. 1995) for most information about northern and Mexican spotted owls published before 1995 rather than citing the original sources. Relatively more ecological knowledge is available for the northern spotted owl owing to its longer history of conservation concern and its commingling with old-growth forest protection issues (Gutiérrez et al. 1995, 2015; Redpath et al. 2013). Although this chapter is about the general biology of California spotted owls, most of the salient ecological information on habitat use and population dynamics is treated separately in chapters 3 and 4, respectively, of this assessment because those topics are particularly critical for understanding current population trends and developing

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future forest management plans. Indeed, we know more about spotted owl habitat and population dynamics than of most other species of conservation concern (Gutiérrez 2008, Löhms 2004). Finally, we occasionally include the theoretical underpinnings to support inferences we make about some new research findings.

Taxonomy

The three owl subspecies named above (northern, California, and Mexican) are the only subspecies recognized by the American Ornithologists' Union (AOU 1957). Whether the subspecies is a useful or valid taxonomic delineation is a much debated topic among ornithologists (e.g., Barrowclough 1982, Mayr 1982). This seemingly esoteric subject has been elevated as a topic of significance for the conservation of spotted owls because "subspecies" is a category recognized under the Endangered Species Act as a biological unit that can be considered for listing. This general subspecies controversy has led some to question the validity of some listing decisions using subspecies as a conservation unit because it has not always been clear that designated subspecies were phylogenetically distinct from other populations of a species (e.g., Zink 2004). In the case of the spotted owl, the subspecies boundaries are well defined so the subspecies as currently recognized are valid taxa (Zink 2004).

Typically, subspecies in birds have been recognized on the basis of plumage variation. For the spotted owl, the northern subspecies has the darkest brown plumage with the smallest white spots, and the Mexican subspecies has the lightest plumage with the largest white spots. California spotted owls are thought to be intermediate between them. However, these plumage characteristics exhibit clinal variation so they have not been useful for identification of subspecies in the field (Barrowclough 1990). Recent research using DNA analysis now shows a clear genetic differentiation among the subspecies (Barrowclough et al. 1999, 2005: chapter 4; Haig et al. 2004). Interestingly, California spotted owls are more closely related to Mexican than to northern spotted owls (Barrowclough et al. 1999, Haig et al. 2004). VanGelder (2003) also showed that vocal structures of the three subspecies supported the subspecies relationships that were defined by the mtDNA analysis of Barrowclough et al. (1999).

While the distributions of the two west coast subspecies and the Mexican subspecies are allopatric (separated in space), the distributions of northern and California spotted owl subspecies are parapatric (i.e., adjacent to each other in space; see fig. 2-1). This latter distribution pattern would enhance the likelihood of genetic introgression (exchange of genes between the subspecies). Indeed, introgression between northern and California spotted owls occurs and there is a cline of overlap

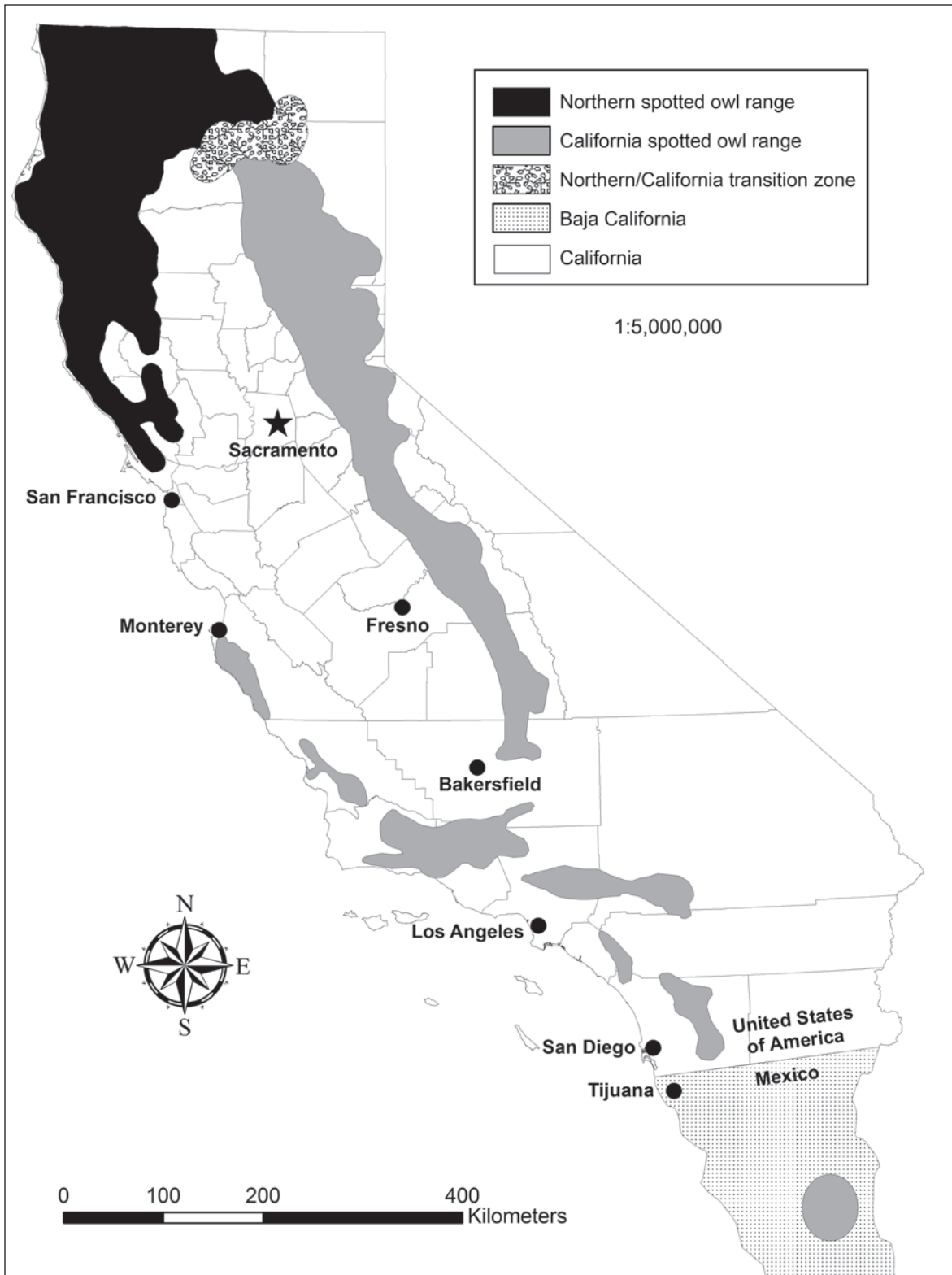


Figure 2-1—Range of the northern and California spotted owls (*Strix occidentalis caurina* and *S. o. occidentalis*, respectively) in the Sierra Nevada and their zone of overlap in northeastern California.

in northeastern California near the Pit River (Barrowclough et al. 2011; fig. 2-1). For purposes of owl management and conservation, the Pit River is recommended as the management dividing line between the northern and the California subspecies (Gutiérrez and Barrowclough 2005). Thus, the Hat Creek Ranger District of the Lassen National Forest is that unit of U.S. Forest Service managed land where the transition of the northern and California subspecies occurs (fig. 2-1).

Of relevance to this assessment is the systematic relationship of California spotted owls occupying various mountain ranges in southern and central coastal California. This relationship was unknown at the time of CASPO (Verner et al. 1992a). Although the “island” populations in southern California were traditionally classified as California spotted owls, those in central coastal California were thought to be either California or northern spotted owls owing to potential connectivity with populations in the south or proximity to birds in the north (i.e., northern spotted owls). Recent mtDNA analyses demonstrates that owls found in the Santa Lucia Mountains (i.e., the most northerly population of spotted owls on the central California coast) and birds from several southern California populations belong to the California spotted owl taxon (Barrowclough et al. 2005).

Genetic studies reveal that California spotted owls have low genetic variation. Barrowclough et al. (1999) proposed three hypotheses for this low genetic variation. The first was that there was a demographic population bottleneck (the population declined for unknown reasons, which led to loss of genetic variability). The second was that there was a selective sweep of a superior genotype. The third was that there was a founder event; a few founder owls immigrated to the Sierra and established a population, which provided a limited genepool for the population. At this time, these hypotheses have not been tested explicitly, but some could be tested using other genetic markers and tools (see chapter 9).

Ecology

The extensive research on spotted owls has allowed scientists to develop substantial insight about the life history strategy of the spotted owl. It is clear from this research that the spotted owl is a K-selected species, meaning that natural selection has favored the evolution of long lifespans and low reproductive rates as mechanisms to mediate the negative effects of unpredictable environmental conditions (in terms of weather variability, disturbance frequency, and other random events in nature). This life history strategy has led some scientists to suggest that they likely exhibit a “bet-hedging” life history strategy (Franklin et al. 2000, 2004). Understanding the spotted owl’s basic ecology is essential for developing predictions about the effects of disturbance. The effect of fire, logging, fuels treatments,

and drought stress on habitat (and perhaps individuals) related to climate change on different life history parameters (survival, reproduction, dispersal) and social structure and processes needs to be evaluated within the context of the owl's evolutionary history. For example, disturbance at the nest may cause nest desertion, and disturbance that lowers habitat quality may precipitate either territory abandonment or divorce (e.g., breaking of pair bonds) (Gutiérrez et al. 2011). The bet-hedging strategy predicts a species can overcome short-term negative factors but will have more difficulty overcoming the relatively longer term impact of reduction in habitat quality. Underpinning its evolutionary strategy is the nature of the animal itself—how it behaves, its social system, and how those relate to its reproductive ecology, survival, and dispersal.

Behavior

Vocalizations—

Spotted owls communicate using a variety of hoot, whistle, chitter, and “bark” vocalizations (Gutiérrez et al. 1995). They use a four-note hoot and a series (a long series of hoots based on a foundational four-note hoot) call when defending their territories. These two vocalizations are likely also used for pair bond maintenance and expressing excitement, respectively (Gutiérrez et al. 1995). VanGelder (2003) reported that the vocalizations of California spotted owls from the Sierra Nevada appeared to be adapted to forests having higher vegetation complexity than is found in forests occupied by Mexican spotted owls because vocalizations attenuated less when experimentally broadcast into foliage. Moreover, the structure of vegetation where spotted owls were found was a good predictor of song structure. These results indicated that vegetation structure exerted selection pressure on the structure of owl vocalizations.

Social system and territoriality—

Spotted owls have a monogamous mating system, with pairs forming relatively long-term pair bonds (Gutiérrez et al. 1995). However, spotted owls sometimes break pair bonds (i.e., “divorce”) after failing to produce young; birds that break pair bonds or whose mate has died will form new pair bonds with other birds (Blakesley et al. 2006; Gutiérrez et al. 1995, 2011). Coincident with their mating system and territoriality, California spotted owls show strong site fidelity (Berigan et al. 2012). Thus, frequent breeding dispersal (indicating lower site or mate fidelity) could be indicative of disruption of their social system.

Spotted owls are territorial, which means they defend an area by excluding other pairs or individuals from the core of their home range (Gutiérrez et al. 1995). For this reason, owls are dispersed rather than clumped within landscapes.

Moreover, core areas of California spotted owls tend to be spatially static over time (Berigan et al. 2012). For example, in the Sierra Nevada, spotted owl territories are more dispersed than expected by chance, and sites having similar occupancy rates are dispersed rather than being clumped (Seamans and Gutiérrez 2006). Unbiased estimates of adult survival derived from even very small sampling areas indicate that territorial owls generally do not shift territories or undergo breeding dispersal from an established territory (Blakesley et al. 2010, Gutiérrez et al. 2011, Zimmerman et al. 2007).

The risk of divorce or leaving a territory when a mate dies is significant. First, if a bird leaves its territory as a result of divorce or mate death, it will be unfamiliar with the landscape in a new territory, which places it at a disadvantage (e.g., no knowledge of locations of good foraging patches) (Hirons 1985). Second, divorce incurs other risks such as failing to find a new mate or finding a new mate that is not as high a quality as the one divorced. For example, Gutiérrez et al. (2011) reported that birds that lost mates because of a mate's presumed death (mate never detected again on the study area) tended to improve their reproductive success, whereas it was not clear that birds who divorced also improved their reproductive success. Thus, understanding the reasons why birds divorce may have important management implications if forest management activities that lead to disruption of pair bonds negatively affect demographic processes.

Not all spotted owls are territorial, and these nonterritorial individuals are called "floaters" (Franklin 1992). Some floaters are younger birds in search of their first territory, but others seem to be birds that have left a territory and become nonterritorial for unknown reasons. These floaters can occur within or outside the home ranges of territorial birds, but it is unknown whether they are tolerated by resident birds or simply not detected by resident pairs because they do not attempt to defend an area using vocalizations. Although floaters do not contribute to the reproductive output of a population, they can influence population dynamics because they provide a pool of birds that could colonize vacant territories or pair with single birds (Franklin 1992).

The territory (the area that is actively defended by birds) of a pair is likely smaller than their home range although no one has precisely estimated the size of the areas they will actively defend (i.e., their true territories). Rather, from a management perspective, the concept of territory has been "approximated" by various derivations of a "core area" such as a protected activity center or PAC (an area of about 121 ha [300 ac]) that was created to anticipate the likely essential areas used for nesting and roosting, but not for foraging or even territorial defense (Verner

et al. 1992b). Other researchers have attempted to estimate the core area (the area of concentrated use) of both northern and California spotted owls (Bingham and Noon 1997) and to examine how well PACs accommodate long-term use by spotted owls for nesting and roosting (Berigan et al. 2012). Based on their assessment of the Lassen demographic study population, Bingham and Noon (1997) suggested that the core area for California spotted owls was about 813 ha (2,009 ac), which was substantially larger than the designated size of a PAC (about 121 ha [300 ac]). One reason for this disparity was that Bingham and Noon (1997) estimated the core area based on analysis of radiotelemetry data, whereas PACs were designated by contiguous association of preferred habitats at and around nests and primary roosts (Verner et al. 1992b).

Intraspecific interactions—

Members of a pair of spotted owls divide roles when nesting. Females incubate eggs and brood young, while males provision females with food so they can maintain incubation with little interruption (Gutiérrez et al. 1995). Males defend the territory at this time more predictably than females. Thus, males are often detected first in occupancy surveys, while females that are actually present at the same sites may go undetected until later surveys. When eggs hatch, the owlets are guarded and fed by both parents, but the female tends to continue brooding (Gutiérrez et al. 1995).

Because spotted owl home ranges are relatively large, it is likely impossible for territorial pairs to defend their entire home range from other spotted owls, so home ranges of adjacent owls often overlap (Gutiérrez et al. 1995). Because spotted owls are central-place foragers, they expand their activities outward from their nests or roosts to forage on prey that is patchily distributed and that can be depleted through predation within those foraging patches (Carey et al. 1992, Carey and Peeler 1995, Ward et al. 1998). Thus, their activity declines within far patches relative to close patches as distance from the territory center increases owing to travel time. They engage in conspecific interactions with “neighbors” (i.e., adjacent territorial owls) and “strangers” (non-neighbors and dispersing owls) through hooting vocalizations, and these hooting bouts intensify as foreign owls encroach on areas near the territory center. Spotted owls apparently recognize their neighbors because Waldo (2002) experimentally demonstrated the “dear enemy hypothesis” for spotted owls, where territorial spotted owls responded more strongly to broadcasts of the vocalizations of a stranger than a known neighbor. The adaptive advantage of such a conspecific response is that territorial owls do not have to expend energy defending a territory from an individual with whom they have already established a territory boundary.

Inbreeding is a conspecific interaction that is generally considered maladaptive because of the potential for the expression of deleterious alleles. Inbreeding can occur between distant and close relatives (siblings, half-siblings, and parents with offspring). A comprehensive analysis of inbreeding has not been done for spotted owls, but “incest” (inbreeding of close relatives) has been reported for both northern and California spotted owls (Carlson et al. 1998).

Interspecific interactions—

Spotted owls in California are not apex predators in their food chain. Great horned owls (*Bubo virginianus*) are sympatric, larger, and can prey on spotted owls (Gutiérrez et al. 1995). However, spotted and great horned owls do not usually use the same habitats; great horned owls typically occupy more open habitats than spotted owls (Johnson 1992). Moreover, the simulated presence of great horned owls in the territories of spotted owls does not suppress calling behavior in spotted owls (Crozier et al. 2005), which suggests that great horned owls either are not generally a threat to spotted owls or they are not likely to be in the same habitats. Finally, spotted owls will sometimes nest in the same stand as great horned owls even though great horned owls are known to prey on spotted owls (Gutiérrez et al. 1995).

The invasion of the barred owl (*Strix varia*) in western North America has raised concern over the potential for this species to negatively affect spotted owls (Gutiérrez et al. 2007, USFWS 1990). Barred owls were first documented in California in 1981, and by 2004, one barred owl has been detected as far south as Kings Canyon National Park in the southern Sierra Nevada (Dark et al. 1998, Steger et al. 2006). The barred owl invasion has been of substantial concern for spotted owl conservation and will be covered in detail in chapters 7 and 9. Spotted owls also interact with other species on a daily basis. For example, they are routinely mobbed by other bird species (Gutiérrez et al. 1995), and they are victims of kleptoparasitism, when other species steal prey the owls have cached (Hunter et al. 1993).

Activity patterns—

Spotted owls are primarily active at night. They hunt, defend, socialize, and conduct exploratory movements at night (Gutiérrez et al. 1995). However, they also can be active at dusk when they often socialize and begin to hunt, but they will opportunistically prey on species that are active during the day (Gutiérrez et al. 1995, Laymon 1991). During the day, however, they primarily sleep, conduct self-maintenance, and guard young while roosting in complex-structured forests (Gutiérrez et al. 1995). Roost stands are often areas used consistently by owls over many years (Berigan et al. 2012). The areas around nest sites, together with roost sites, serve as the center of

activity for spotted owls (i.e., a prediction of central-place foraging theory) (Carey and Peeler 1995). Their night time foraging locations can be anywhere within the home range, both within the core area and well beyond it (Williams et al. 2011).

Although spotted owls are most active at night, there are periods during the night when they are more active than others. For example, activity is highest during the periods 1 to 3 hours after sunset to 1 to 3 hours before sunrise (Gutiérrez et al. 1995). These general activity periods have been quantified by Delaney et al. (1999), where the highest prey delivery rates occurred at these times. Owls progressively increase prey delivery rates to the nest as young mature, while females spend less time in attendance of young as the brood-rearing period progresses (Delaney et al. 1999).

Response to human activities—

The spotted owl has long been recognized for its tame behavior because it often tolerates close approach by humans (Gutiérrez et al. 1995). Tameness has often been mistaken for adaptability or lack of disturbance effects in animals. However, many studies have shown that animals may exhibit no outward signs of stress when they are actually having a physiological stress response (Beale 2007). Indeed, a study of northern spotted owls suggested that birds had elevated levels of corticosterone, a stress hormone whose metabolites can be detected in feces, when living near roads or areas that had been logged (Wasser et al. 1997). In contrast, Tempel and Gutiérrez (2004) analyzed corticosterone metabolites in feces of spotted owls from the central Sierra Nevada and found that corticosterone levels were best explained by the breeding state of individuals and how samples were stored in the field, rather than by the presence of roads or habitat type.

In another assessment of spotted owl response to humans, Swarthout and Steidl (2003) conducted an experimental study of the behavioral response of Mexican spotted owls to recreational hikers and showed that Mexican spotted owls changed certain activity patterns in response to both high levels of recreation use and to the presence of observers. They suggested that spotted owls were tolerant to moderate levels of disturbance (i.e., noise not within 100 m [328 ft] of roosting birds, <50 hikers per day), but high levels of recreational activity could cause disturbance (Swarthout and Steidl 2003). Swarthout and Steidl (2003) results also suggested that researchers should minimize their time and activities when working near spotted owls.

Reproductive Ecology

Reproduction is a vital rate that contributes to population growth and will be covered in chapter 4. However, it is important to set the context of the spotted owl's reproductive ecology in both relative and evolutionary contexts. Spotted owls exhibit the lowest reproductive rate among North American owls (Johnsgard 1988).

Mean reproductive output (number of young produced per female) across years has varied among the five long-term demography monitoring areas in the Sierra Nevada and southern California (0.555 to 0.988 young/female) (Blakesley et al. 2010, Franklin et al. 2004; see also chapter 4 for details). Moreover, the range in annual reproduction by California spotted owls is extremely variable, ranging from no young produced within a demographic study area in a given year to nearly all birds nesting (Blakesley et al. 2010, Franklin et al. 2004, Seamans and Gutiérrez 2007b, Tempel et al. 2014). As previously noted, this highly variable rate of reproduction coupled with a high survival rate has given rise to the hypothesis that California spotted owls, like northern spotted owls, exhibit a bet-hedging life history strategy (Franklin et al. 2000, Stearns 1976). In the case of the California spotted owl, natural selection has favored the evolution of high survival rates that allow the owls to forgo breeding in “bad” years so they can breed in “good” years. Bad and good are relative terms here and can mean the difference between years of high and low prey or years of inclement or mild weather during the critical nesting period. The significance of this bet-hedging strategy is that lack of reproduction at a site for a few years does not necessarily mean the site is of low quality, but rather it could be related to overall poor environmental conditions leading to absence of reproduction (Stoelting et al. 2014).

There are several environmental or ecological factors that have been examined to explain patterns of reproduction in California spotted owls. Reproductive success is often correlated with annual variation in weather (LaHaye et al. 1997, MacKenzie et al. 2012, North 2002, North et al. 2000, Seamans and Gutiérrez 2007b, Stoelting et al. 2014). The focus on the relationship with weather and vital rates is common because weather is easily measured and can be used to infer both indirect and direct potential effects on owls (e.g., it influences plant growth and thus prey populations, which affects energy budgets of owls). The influence of weather on reproduction is, however, confounded by the substantial variation in the distribution and abundance of the owl’s prey (Ward et al. 1998). Weather can potentially affect spotted owls directly either by increasing energy demands of owls, increasing the risk of exposure of eggs when females have to leave the nest, and interfering with hunting and indirectly by influencing plant growth, which affects population dynamics of owl prey (Franklin et al. 2000, Rockweit et al. 2012, Seamans and Gutiérrez 2007b, Weathers et al. 2001).

A peculiar element of reproductive variability in spotted owls, including California spotted owls, is an alternating pattern of high and low years of reproductive

output (Blakesley et al. 2010, Franklin et al. 2004). This pattern has been labeled the even-odd effect of reproductive output in owl population studies (Franklin et al. 1999, 2004). North (2002: 118) also reports “distinct annual fluctuations” of good and bad years of reproduction. Why this pattern occurs is unknown, but a logical hypothesis is that there is a “cost of reproduction” borne by owl pairs successfully raising young (Forsman et al. 2011, MacKenzie et al. 2009). That is, birds that reproduce successfully in one year are less likely to breed in the subsequent year because there is an energetic cost to reproduction that presumably reduces the condition of females (MacKenzie et al. 2009, Stoelting et al. 2014). However, Stoelting et al. (2014) simulated the even-odd cycle in California spotted owls and found that the observed cost of reproduction was insufficient either to generate or to maintain this even-odd pattern. Stoelting et al. (2014) hypothesized that some external, widespread environmental factor was likely responsible for generating and maintaining this cycle (see also North 2002). Interestingly, the even-odd effect in northern spotted owls appears to be waning with time (Dugger et al. 2016).

Other observations about individual costs of reproduction have been linked to California spotted owls. California spotted owls typically fledge one to three young (Gutiérrez et al. 1995), with three young in a brood being uncommon (Tempel et al. 2014). There are records of four-egg clutches or broods, but these are extremely rare, having been recorded only twice in southern California (Dunn 1901, LaHaye 1997). Thus, a question arises about the optimal clutch (brood) size for owls. Peery and Gutiérrez (2013) showed that when juveniles fledge from broods of two they have a greater survival probability than if they fledge either from a single or triplet brood. More importantly, this effect carried over to subadult and adult age classes. This occurs even though it should be more difficult for parents to provision two chicks than one chick. Finally, Peery and Gutiérrez (2013) reported that indices of territory quality, based on chick survival, were positively correlated with indices of territory quality based on parental reproductive output.

Whether owls successfully breed at sites also seemed to influence whether they will remain on those sites. For example, Gutiérrez et al. (2011) showed that owls having higher reproductive output compared to the entire population were less likely to disperse. While their result was confounded by mate quality (i.e., a bird might be more likely to stay at a site if they have a “high-quality” mate), they also found that owls were less likely to leave sites where owl reproduction was higher than the population average, which partially controlled for the effect of mate quality because these long-term effects accounted for multiple owls occupying the same sites.

The distribution and abundance of owl prey is another key factor that influences spotted owl reproductive success. Yet, studies of owl prey have lagged behind the study of other aspects of owl ecology even though prey are central to understanding the ecology of a predator (Newton 1979). The reason for this lack of study is simply that prey studies are costly, rather than failure by scientists to recognize this obvious connection (Gutiérrez 1985b). Much of our knowledge about spotted owl prey comes either from studies of northern spotted owls or the small mammal literature, although there are exceptions (Waters and Zabel 1995, Waters et al. 2000, Zabel and Waters 1997). However, there have been several studies relating spotted owl habitat to owl reproduction and others enumerating prey in the diet (see below).

Barrows (1985, 1987) first showed that California spotted owls took relatively larger prey when they were nesting, and they shifted their diet from larger to smaller prey when they failed in their breeding attempt. Thrailkill and Bias (1989) also found that diets of breeding owls contained more large prey by both frequency and biomass than nonbreeding owls. These early diet studies were both relatively limited either in terms of sample size (number of territories sampled in breeding and nonbreeding categories) or pellets collected per territory. These sample size limitations were overcome by Smith et al. (1999) who collected over 8,000 pellets from 109 territories in the San Bernardino Mountains over several years. They found that successful nesting owls had a greater percentage of biomass of large prey than small prey in diets relative to nonnesting owls. However, there was no difference in size of prey eaten between successful nesters and those pairs that attempted to nest but failed, suggesting that nests failed for reasons other than prey dynamics. However, the relationship between large prey in the diet and propensity for breeding was not clearly established for owls inhabiting the Sierra National Forest (Munton et al. 2002). Although it seems logical that spotted owl prey may be affected by abundance of pine seed production and thus affect owls, North (2002) found no such relationship in the southern Sierra Nevada.

Evaluating habitat quality is challenging because owls and sites are confounded (see “Management Implications” below). That is, it is difficult to partition the effect of “high-quality” individuals from the quality of the habitat (when there are two or more potentially explanatory factors whose effects are difficult to distinguish, they are said to be confounding). Recognizing these confounding effects, LaHaye et al. (1997) found in the San Bernardino Mountains that owls nesting in lower elevation oak (*Quercus chrysolepis* Liebm.)/big cone fir (*Pseudotsuga macrocarpa* (Vasey) Mayr) cover types had higher reproductive output than those nesting in other higher elevation cover types (LaHaye et al. 1997). Hunsaker et al. (2002) showed that owls occupying sites having canopy cover greater than 50 percent had greater

productivity, and these sites also had higher occupancy rates than sites with lower canopy cover. North (2002) reported that owls in certain territories almost always produced young, even in bad years. North's finding could be related either to variation in territory quality, variation in owl quality, or an interaction between the two, but North did not have sufficient data to examine these possibilities. However, he reported that owls which occupied higher quality territories (weighted by reproduction output) used the same nests repeatedly, whereas owls occupying lower quality territories used a nest only once, which suggested local site factors were important in addition to broad regional influences.

Habitat Associations

California spotted owl habitat associations are provided in detail in chapter 3. However, we here provide some generalities and hypotheses about habitat use and their relevant ecological context. Spotted owls are primarily forest inhabitants. Their habitat selection and habitat requirements are among the most controversial issues related to spotted owl conservation because of the economic implications of habitat conservation and the design of forest management plans. However, we present some general concepts related to owl habitat and the evolution of habitat selection in California spotted owls.

Theoretically, habitat quality of a species should be reflected in individual home range size and, therefore, the spacing and density of individual territories in a population. For spotted owls, a specific hypothesis about this theory could be that home range sizes should be smaller in areas of higher habitat quality. Yet, because of territorial interactions (see next paragraph), there will be a threshold of population density, regardless of relative habitat quality. However, the relationship between density thresholds relative to habitat quality in different landscapes is unknown.

One avenue to assess habitat quality is to observe patterns of animal space use as a function of the predictions derived from ecological theory because predictions of theory can be tested with empirical data. This has been done as two general theories of habitat selection have been investigated in spotted owls—the ideal free and ideal despotic theories (Fretwell 1972, Fretwell and Lucas 1969). The ideal free theory predicts that if animals have perfect knowledge of their environment (i.e., are “ideal”), they will select the best habitat first and sequentially select lower quality habitats when higher quality ones are occupied. The ideal despotic theory predicts that territorial animals will exclude (i.e., are “despots”) other individuals of the same species from occupying the same habitats (i.e., territorial behavior prevents simultaneous space use regardless of habitat quality because of intraspecific competitive exclusion). Recent evidence suggests California spotted owls follow an

ideal despotic distribution of habitat selection because occupancy is correlated with “territory fitness” (“territory fitness” is a measure of territory quality based on the survival and reproduction of all owls that occupy that territory over time) (Zimmerman et al. 2003). In a seemingly counterintuitive observation, territorial behavior also seems to influence habitat selection by owls native to an area because owls immigrating into a population settle closer to territorial pairs than do owls from that population who are switching territories within the population (i.e., immigrant owls may be using presence of conspecifics as cues to settle in suitable habitat) (Seamans and Gutiérrez 2006). This suggests that both behavioral factors and intrinsic habitat quality influence habitat selection by spotted owls. Territorial behavior can constrain the allocation of space (habitat) among individuals of a population (there is an upper limit for density) and serve as a cue to naïve owls about territorial quality.

Much has been discussed about the use of private lands by California spotted owls in the Sierra Nevada because in some places, public and private lands occur in near-alternating parcels and commercial timberland is abundant (Bias and Gutiérrez 1992, Gutiérrez 1994, Moen and Gutiérrez 1997). Private and public lands often have been managed differently, which may result in different dominant forest types and forest structure. Irwin et al. (2007) studied foraging owls on primarily private land in the northern Sierra Nevada and found that owls tended to forage near nests, small streams, and areas with a diversity of conifer species and hardwoods versus areas dominated by ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson). In an area of alternating public-private ownership parcels (i.e., “checkerboard” ownership pattern) in the central Sierra Nevada, spotted owls rarely used private land for nesting and roosting (Bias and Gutiérrez 1992, Gutiérrez 1994, Moen and Gutiérrez 1997). This result has been enigmatic because spotted owls occur elsewhere on private land in the Sierra Nevada (Irwin et al. 2007, Roberts 2015²). The findings from the central Sierra Nevada have also prompted work to determine if this pattern is related to placement of nest sites relative to hard edges (spotted owls placed their nests farther from edges than predicted by chance [Phillips et al. 2010]) and their use of private land for foraging (Williams et al. 2014). In the latter study, the researchers found that owls used private land proportionately less than its availability when foraging, even when controlling for central-place foraging tendencies.

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Habitat structure—

The structure of spotted owl habitat has long been of interest because original research suggested that spotted owls were old-growth dependent (e.g., Carey 1985, Forsman et al. 1983). Subsequently, the nature of owl-habitat relationships has been expanded to include the concept of forest structure (Solis and Gutiérrez 1990). This concept suggests that California spotted owls are habitat specialists because they select an array of forests and forest structures that are different than what is generally available on the landscape (Gutiérrez et al. 1992, Verner et al. 1992a). For example, they select sites that have larger trees, higher canopy cover, and more coarse woody debris than occurs on sites available to them (chapter 3). Research on the structure of spotted owl vocalizations also supports this forest-structure relationship because it appears California spotted owl vocal structure evolved in response to “complex” forest structure (VanGelder 2003). Song is the fundamental way by which most birds communicate (defend territories, attract mates, maintain pair bonds), and thus there is a large body of research on the adaptive nature of vocalizations relative to habitat that a species occupies.

Several hypotheses have been generated to explain why owls select old/mature forests (e.g., nest site selection, ambient temperature moderation, availability of prey), and these hypotheses are relevant under the habitat structure selection hypothesis (Carey 1985, Forsman et al. 1983, Gutiérrez 1985a). To these, we add an additional hypothesis that the owls themselves have evolved in fire-adapted forest ecosystems because all landscapes spotted owls now inhabit experience some type of historical fire regime. In addition, their resilience to fire of low and moderate severity is consistent with this fire-adapted hypothesis. Under either a predominantly accepted hypothesis that a frequent, low- to moderate-severity fire regime was the historical norm in the Sierra Nevada (chapter 5) and an alternative that posits a mixed-severity fire regime prevailed in the West historically (e.g., DellaSala and Hanson 2015 and references therein; SNEP 1996), there is uncertainty about the precise distribution and abundance of various forest types and structures under historical fire regimes. This uncertainty is underscored by the fact that the current sites spotted owls use for nesting and roosting in the Sierra Nevada indicate that there was a relatively high density of large trees on the landscape in many places. That is, the large, old trees at current owl sites were present in presettlement times (Gutiérrez et al. 1992). The importance of this uncertainty is that it can lead to different predictions for desired future conditions of forests. To this end, we propose that neither of these hypotheses about historical fire regimes

is inconsistent with creating and maintaining suitable spotted owl habitat (e.g., under the predominant fire paradigm, the structure of old-growth forests that were under a suppression regime returned to a condition likely to be suitable for owls, at least in terms of diameter distribution of trees and size of trees, after two cycles of return fire) (Lydersen and North 2012). Hence, the forest structure hypothesis is important to consider when thinking about appropriate management actions. In addition, because fire suppression has led to unnaturally high densities of trees in most places and owls often inhabit these areas, we think that describing suitable owl sites as “dense” may obfuscate the discussion about spotted owls. For one, the word “dense” is a normative term and, therefore, conjures different visualizations among people about both tree density and vegetation structure, which then leads to concerns about such things as spotted owl habitat being a fire hazard, susceptibility of trees to insects and diseases, and effects of climate change on forests. For another, there are many forests that do not have spotted owls because either they have such a high density of trees or high foliage volume that it may impede hunting by owls, or they have low prey densities (these were among the original hypotheses linking owls to old-growth forests). Consequently, as qualitative expressions to aid discussion, the terms “multistoried structure” or “complex-structured forest” seem more appropriate terms to describe owl habitat than does the term “dense” because most dense forest stands without tree age or size structure do not harbor owls. In this context, complex-structured forests do not necessarily have to have the density of trees that often occurs in stands following long periods of fire suppression. Moreover, achieving this type of forest structure does not seem incompatible with reintroduction of fire as a natural process (Lydersen and North 2012).

Disturbance—

The effect of disturbance on owls and their habitat has been a concern, particularly the effect of large, high-severity fires and associated salvage of fire-killed trees. These can potentially affect owls negatively (Clark et al. 2011, 2013; Lee et al. 2013, 2015b; see also chapters 3 and 4). Moreover, climate change will likely increase the frequency of these types of fires. Research has shown that low- and moderate-severity fires have little or no effect (acute or chronic) on spotted owls (Bond et al. 2002, Roberts 2008, Roberts et al. 2011). This result has not been surprising given that spotted owls evolved in forests that experienced fire frequently. One study of radio-marked owls showed that owls will forage in areas that have been burned (Bond et al. 2009) while another study showed that owls foraged at the edge of burns (Eyes 2014). Studies of territory occupancy showed that mixed-severity fires had no effect on owls (Lee et al. 2012, Roberts 2011) while high-severity fires had negative

effects (Clark et al. 2013, Lee et al. 2013). However, the owl territories in studies by Clark et al. (2013) and Lee et al. (2013, 2015b) were also affected by salvage logging. Lee and Bond (2015a) reported a high occupancy rate of owl territories in the first year following the very large Rim Fire in the southern Sierra Nevada. Recently, however, Jones et al. (2016) demonstrated a strong first-year impact of the King Fire in the central Sierra Nevada on California spotted owls. Almost all territories that were occupied prior to the fire, but experienced >50 percent high-severity fire, became unoccupied following the fire—with several owls moving to the less severely burned territories. Moreover, GPS-tagged owls exhibited strong avoidance of high-severity fire burned patches, particularly those in the main, high-severity patch. Currently, additional research has been undertaken to examine the longer term impacts of the Rim Fire on the owl population studied by Lee and Bond (2015a; Keane 2015³). Differences in the inferred effects of the Rim and King Fire studies could be the result of more patchily distributed high-severity-fire burned patches in the Rim Fire, or differences in methodology between the two studies (e.g., the King Fire study used marked birds, whereas the Rim Fire study did not). Ongoing work at both sites will provide more perspective on the relative and longer term impacts of these fires and whether there are different outcomes to fire effects, as these early studies indicate.

Similarly, logging, especially when used as a treatment to reduce fire hazard, is of particular concern (Verner et al. 1992b) because logging treatments will be a mechanism to reduce fuel loading in forests. Logging has long been presumed to negatively affect spotted owls through loss of habitat (Gutiérrez et al. 1995). Effects of logging have been demonstrated recently both indirectly and directly. Seamans and Gutiérrez (2007a) showed that occupancy declined when at least 20 ha of high-canopy, mature forest was lost from a territory, but they did not partition losses attributable either to logging or fire. Tempel et al. (2014) showed that the proportion of high-canopy, mature forest was the best predictor of occupancy by owls. In their study, the owl population had declined by 50 percent over the sampling period, so the assumption was that disturbance by various kinds of logging was partially responsible for the decline. Finally, Stephens et al. (2014) demonstrated experimentally that logging treatments designed to reduce fire risk resulted in a loss of owls. As noted above, there appears to be a compounding effect on occupancy of salvage logging following fire in owl territories (Clark et al. 2013; Lee et al. 2013, 2015b).

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Diet

The general diet of spotted owls has been well described in the literature (Gutiérrez et al. 1995). Spotted owls prey primarily, by biomass, on medium-sized small mammals, particularly dusky-footed woodrats (*Neotoma* spp.) and flying squirrels (*Glaucomys sabrinus*) (Gutiérrez et al. 1995). However, they eat a wide array of other small mammals, such as mice and voles, as well as birds, lizards, and insects. Flying squirrels are found in closed-canopy forests, usually at higher elevations than woodrats. Woodrats also use closed-canopy forests and oak woodlands, early-seral-stage forests (e.g., clearcuts and fire-disturbed landscapes), and shrub cover types. Recent studies have generally confirmed past observations of owl diet, but there have been some notable differences recorded (see below).

Diet analysis has been a mainstay of owl studies because owls regurgitate indigestible parts of their prey as consolidated “pellets,” which can be found at roost and nest sites (Marti 1987). These pellets contain bones, hair, nails, beaks, feathers, scales, and exoskeletons. So it is somewhat surprising that only three reports on diet composition based on pellet analyses have been published since CASPO (Munton et al. 1997, Munton 2002, Smith et al. 1999). Owls generally swallow small prey whole and dismember larger animals to swallow smaller chunks. However, they often decapitate prey and when they do this, they swallow the head first and then the body, or cache the body to eat later (Gutiérrez et al. 1995). They will also swallow the head of a prey item and give the rest of the prey to young. For these reasons, strict protocols have been observed when enumerating prey items to avoid double counting individuals in a sample (Marti 1987).

Munton et al. (1997) identified 664 prey remains from 520 pellets found at 11 territories in low-elevation (300 to 586 m [984 to 1,923 ft]) oak and riparian deciduous cover types in the Sierra and Sequoia National Forests of the southern Sierra Nevada. They identified 20 species of prey of which mammals comprised 96 percent, by biomass, of the diet. Woodrats and pocket gophers (*Thomomys* spp.) comprised 80 and 11 percent of the biomass, respectively. Interestingly, the contribution of woodrats, mice, and birds to the diet was lower during the breeding season than nonbreeding season, and the contribution of voles and pocket gophers to the diet showed the opposite pattern. This could mean either that the diversity of prey in the diet increased during the breeding season, the results were a function of sampling limitations, or the results were a function of annual variation in diet among pairs (Munton et al. 1997).

Munton et al. (2002) expanded their earlier study of lower elevation cover types by examining 1,140 pellets collected at territories between 305 and 2316 m (1,000 and 7,600 ft) on the Sierra National Forest. In addition, they added 1 year of data (1998) to their original 6-year study. Their sampled sites in this 2002 study included all those sites from the 1997 study except for the low-elevation sites on the Sequoia National Forest. They identified 2,038 individual prey items from 1,140 pellets. As before, woodrats dominated (74 and 82 percent biomass in diet in nonbreeding and breeding seasons, respectively) the diet in oak woodlands and riparian-deciduous forests (i.e., low elevation), whereas in conifer forests at higher elevations, northern flying squirrels comprised 77 percent of the prey biomass in the diet. Pocket gophers comprised the second most important food by biomass at both low and higher elevations. These results were different from earlier studies reported for the mid- to high-elevation owl habitats in the central Sierra Nevada (Laymon 1988, Thraillkill and Bias 1989) where woodrats tended to dominate in the mid-elevation forest types, suggesting that there were differences in the prey community between the central and southern Sierra Nevada.

Smith et al. (1999) reported on a large study of owl diet in the San Bernardino Mountains of southern California. They sampled the entire population of territorial owls, 109 territories, between 1987 and 1991, and identified 8,441 individual prey in pellets. Dusky-footed woodrats (*N. fuscipes*) were the most important prey by both percentage frequency (42) and biomass (74). They also found that the proportion of biomass attributed to woodrats increased as elevation increased, which was opposite to other owl diet studies where the proportion of the diet attributable to woodrats decreased with increasing elevation (e.g., Verner et al. 1992a). They found that their large sample size resulted in reasonably precise estimates of woodrats on a territory-by-territory basis but not pocket gophers, which might explain why Munton et al. (2002) found a preponderance of pocket gophers in the diet (i.e., a few sites with large samples of pocket gophers might have skewed the results). In the San Bernardino study, flying squirrels were uncommon in the mountain range and constituted only 3 percent of the biomass of the diet. This latter result was likely related to flying squirrels being at the southern edge of their range, and their low abundance did not provide owls an alternative prey source at high elevations as they did in the Sierra Nevada. Diet studies of Mexican spotted owls have revealed that

both medium-sized small mammals like woodrats and smaller mammals like mice and voles (e.g., *Peromyscus* spp. and *Microtus* spp.) can be important for reproduction in owls (Ward 2001). Thus, reproduction can occur when there are high populations of various prey species, and these prey populations can differ among years, habitats, and regions.

Cause-Specific Mortality

Predation—

Spotted owls are subject to predation by great horned owls, northern goshawks (*Accipiter gentilis*), and red-tailed hawks (*Buteo jamaicensis*) (Gutiérrez et al. 1995). Great horned owls can potentially prey on adults or young, and goshawks will take juvenile owls (Gutiérrez et al. 1995). In addition, one likely case of predation of an adult spotted owl by a barred owl has been reported (Leskiw and Gutiérrez 1998).

Accidents—

Accidents are an additional source of mortality in spotted owls. There are records of spotted owls dying from collisions with automobiles and tree branches (Gutiérrez et al. 1985, Williams et al. 2011). In addition, there is one record of an owl being electrocuted when perching on a power line or transformer (Gutiérrez et al. 1996).

Disease and infection—

The appearance and rapid spread of West Nile virus has been a concern because spotted owls, like other owls, are quite susceptible to the disease (Gancz et al. 2004). Louse flies (family *Hippoboscidae*), which are common external parasites of spotted owls (Hunter et al. 1994), were implicated in a West Nile outbreak among North American owls, including a spotted owl, in a captive holding facility in Ontario, Canada, so an existing vector for the virus is present in most spotted owl populations (Gancz et al. 2004). Hull et al. (2010) conducted a survey of antibody titers of California spotted owls and found no evidence of West Nile infection. However, because of the virus' apparent virulence to owls, it is doubtful that one could detect it through surveillance monitoring. Bacteria can also cause disease in spotted owls. Thomas et al. (2002) reported a fatal spirochetosis (an acute, septicemic disease) in a northern spotted owl, which was caused by a bacterium, *Borrellia* sp. It was unknown whether this disease regularly occurs in spotted owl populations.

Parasites—

Several survey screenings for hematozoa (blood parasites) have revealed that spotted owls harbor a variety of hematozoa such as *Plasmodium* sp., *Leucocytozoon* sp., *Haemoproteus* sp., *Trypanosoma*, *Atoxoplasma* sp., and microfilariae (Gutiérrez 1989, Ishak et al. 2008, Lewicki et al. 2015, Wood and Herman 1943). California

spotted owl populations were found to have the highest rates of infection when compared to northern spotted owls, barred owls, and 387 other species of owls (Gutiérrez 1989, Ishak et al. 2008). Therefore, if the hematozoa that infect spotted owls has deleterious health consequences (e.g., compromising its immune system), then it could be an advantage to invading barred owls because barred owls have lower rates of hematozoa infection and hematozoa diversity (Ishak et al. 2008, Lewicki et al. 2015). Further, given the high rates of infection of California spotted owls, such an effect might be more pronounced in competitive interactions between this subspecies and the invading barred owl. Lewicki et al. (2015) tested several hypotheses relative to the consequences of the invasion of barred owls into the spotted owl's range and found support for two hypotheses about the relationship between invasive species and their parasites—the Enemy Release Hypothesis (ERH) and the Parasite Spillover Hypothesis (PSH). The ERH postulates that host populations of invasive species will harbor lower parasite species richness in their invaded ranges relative to their original ranges, while PSH postulates that invasive species will serve as reservoirs for native parasites, which will increase exposure of native species to native parasites, resulting in higher proportions of infective native species within populations (Lewicki et al. 2015: 1714). The ERH was supported by the finding that barred owls from the east coast had higher infection rates than barred owls from the west coast, but the PSH was supported by the finding that spotted owls had higher probabilities of infection than west coast barred owls (Lewicki et al. 2015).

Hunter et al. (1994) found seven species of ectoparasites belonging to five arthropod families either on live spotted owls or museum skins. The authors considered three species (a mite, a tick, and a flea) to be accidental on spotted owls because they typically are found on rodents, the normal prey of spotted owls. The remaining parasites were chewing lice (*Strigiphilus syrnii* and *Kurodaia magna*) and louse flies (*Icosta americana* and *Ornithoica vicina*). Of these parasites infecting owls as true hosts, *I. americana* was found on live California spotted owls, and an unidentified *Strigiphilus* sp. was found on a museum skin of an owl from Mariposa County in the Sierra Nevada. However, Bequaert (1952) found *O. vicina* on a California spotted owl. No helminth or other endoparasites have been reported from the California spotted owl but likely exist because they are found in northern spotted owl populations (Gutiérrez et al. 1995).

Chapter Summary

While most of the information gathered on spotted owls subsequent to CASPO has been devoted to monitoring population trends and spatial distributions (see chapter 4), much new biological information about California spotted owls has also been

collected (see also chapters 3, 4, and 7). This new knowledge about spotted owl natural and life history has application to the management of the owl because it illuminates spotted owl requirements and responses of owls to disturbance (particularly logging and fire).

Studies of physiological stress in spotted owls suggest that many routine forest operations (e.g., trail maintenance, brush removal, timber cruising and marking) are not likely to affect owls if they occur beyond 100 m from the nest or primary roost site (Tempel and Gutiérrez. 2003). However, more intrusive activities like road building and timber harvest have greater potential to disturb owls and their seasonal restriction near owl nests should be maintained.

Because spotted owls defend their territory using vocalizations described above, they can be detected with high probability during surveys, given sufficient survey effort. Moreover, the site fidelity exhibited by a territorial pair and the consistency of their spatial location among years (Berigan et al. 2012) suggest that monitoring of spotted owls over large areas can be accomplished using call-based surveys (Tempel and Gutiérrez 2013). Indeed such call-based surveys have been the foundation of long-term demographic monitoring in the Sierra Nevada and southern California (Blakesley et al. 2010, Connor et al. 2013, Franklin et al. 2004, LaHaye et al. 2004, Tempel et al. 2014). However, the keys to unbiased call-based surveys are adequate survey effort (Tempel and Gutiérrez 2013), recognition of owl vocalizations by observers, year-to-year consistency within survey areas, and meeting the closure assumption of occupancy estimation (i.e., birds do not move in and out of surveyed areas; this is difficult to discern with unmarked birds). These studies have shown that spotted owls exhibit strong site fidelity, which has management implications. For example, Berigan et al. (2012) showed that owls used the same core areas, which contained a large proportion of the PACs established for their conservation for nesting and roosting over long time periods (>20 years). A PAC is designated whenever an owl is located on public land. However, the majority of PACs were delineated shortly after CASPO designed this concept in 1992. They now constitute essentially the only places where owls are currently found, suggesting that PACs are an essential management application. They could also represent the only remaining relatively large patches of nearly contiguous nesting/roosting habitat in the Sierra Nevada on public land. The PACs are also consistent management constructs relative to the hypothesis that spotted owls are central-place foragers. Thus, modifying PACs runs the risk of losing the owls within those PACs (see also chapter 8). The strong site fidelity of owls has several implications for management because birds may persist at sites even when site quality has been lowered because

of disturbance(s), which makes it difficult to assess the effect of disturbance on spotted owls. Moreover, Seamans and Gutiérrez (2007a) showed a correlation with habitat change and territory occupancy, which suggests that maintaining key habitat areas is important to these birds.

Research on reproductive ecology provides numerous potential management implications, but there remains uncertainty about these implications. The relationship between brood size and territory quality suggests that territories can be ranked in terms of their contribution to the population, but presumed low-quality territories might actually be indicative of “low-quality” individuals inhabiting those sites. Moreover, territories with high turnover or low occupancy rates (which are currently presumed to be low quality) might actually improve as a result of forest succession and tree growth. The relationship between habitat and owl nesting success and reproductive output is important to managers because knowing which habitats might contribute to greater reproduction can inform management actions. Nevertheless, like other relationships involving reproductive output, habitat and individual quality are confounded. That is, are owls at a given site consistently successful because of the habitat conditions, the owls themselves (quality or experience), or both? This suggests, in addition to predictions from population viability theory, that “decommissioning” unoccupied PACs limits future options because PACs might be recolonized if they improve in quality with time (see Seamans and Gutiérrez 2007a). As another example, if owls exhibit low reproduction and PACs are removed for such reason, it will likely negatively affect the population because the bet-hedging life history strategy predicts that these owls will breed sometime and therefore may actually be important contributors to population demographic processes over the long term.

Franklin et al. (2000) suggested that good habitat may buffer owls against the effects of bad weather. That is, while managers cannot control weather, they can manage habitat and conserve existing high-quality habitat because such habitat confers survival or reproductive advantages to owls when bad weather occurs relative to lower quality habitat (Franklin et al. 2000). These research findings suggest that it is prudent, if not necessary, to maintain sufficient amounts of high-quality habitat (high canopy, large trees, complex-structured habitat) rather than low-quality habitat (i.e., habitats with forest condition metrics on the low end of the observed distribution used by owls).

Studies of diet analysis suggest that different management techniques could enhance prey habitat in low- and higher elevation habitats and among habitats within similar elevation zones. For example, at higher elevations in the Sierra Nevada, closed-canopy forests should be promoted to benefit the primary prey species (flying

squirrel), but some amount of chaparral and early-seral stage forest can be maintained to benefit the primary prey species at lower elevations (woodrats).

In summary, substantial new information on California spotted owls has emerged since CASPO. This new information has the potential to inform management. Yet, there continues to be uncertainty about important aspects of the owl's biology, specifically how the owl is affected by disturbance (see also chapter 8).

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