The Heat Is On: Spotted Owls and Wildfire

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Severe Forest Fire and Wildlife Response

Wildfires are the primary natural disturbance in western forests of the United States, and native plants and animals have been living with fire for thousands of years of their evolutionary history. Forest fires typically burn in a mosaic of different severities. "High-severity" fire kills most or all of the dominant vegetation in a stand and creates what scientists have termed "complex early seral forests," where standing dead trees, fallen logs, resprouting shrubs, tree seedlings, and herbaceous plants comprise the structure (Swanson et al., 2011; DellaSala et al., 2014). Complex early seral forests differ from postfire harvested forests in that dead trees remain on-site, providing food sources and shelter for numerous wildlife species (Hutto, 2006; Swanson et al., 2011; DellaSala et al., 2014).

Wildlife responses to wildfire are complex, because fire itself burns in complex patterns. Responses are influenced by such factors as time since fire, fire severity, size of burned patches, previous disturbance history, amount and configuration of different prefire habitat types, and postfire management activities like harvesting timber and spraying herbicides. Studies that incorporate these covariates can better elucidate the complexity of wildlife responses to high-severity fire and generate results that are informative for wildlife management and conservation.

In this article, I explore the relationship between high-severity wildfire and a species associated with late-successional forests of the Western United States, the spotted owl (*Strix occidentalis*). Current recovery efforts for this threatened species assume wildfire is a primary threat, and therefore, widespread timber harvest for "fuel reduction" (ie, thinning) is needed to reduce fire severity in dry forests occupied by the spotted owl. However, such recommendations are misguided, as explained in the succeeding text.

The Spotted Owl: An Old-Forest Icon

The spotted owl (**Fig. 1**) is one of the rarest birds to breed in the mainland of the United States and an excellent example of a species whose response to wildfire is more complex than scientists once believed. The spotted owl is a medium-sized forest-dwelling nocturnal raptor, with mottled brown and white barring on its feathers and large, dark brown eyes (Gutiérrez et al., 1995). The species is strongly associated with mature and old-growth (ie, late-successional) conifer and mixed-conifer–hardwood forests with thick overhead canopy and many dense, old, live, and dead trees and fallen logs (Gutiérrez et al., 1995). These owls feed primarily upon small mammals (Gutiérrez et al., 1995). All three subspecies of spotted owls are in decline throughout their range (Seamans et al., 2002; Forsman et al., 2011; Conner et al., 2013; Tempel and Gutiérrez, 2013). It is widely believed that severe wildfire is a cause of recent declines (USFWS, 2011, 2012), but there is growing scientific evidence that this threat is overblown.

Why is it so widely believed that severe fire is harmful to spotted owl populations? Spotted owls have been intensively studied since the 1970s, but research on these owls in fire-affected landscapes did not begin until the early 2000s. Thus, much of what scientists previously understood about habitat associations of spotted owls was derived from studies in forests that had not experienced recent fire.

The scientific literature has established that the optimal habitat for spotted owl nesting, roosting, and foraging in long-unburned forests is provided by conifer and mixed-conifer–hardwood forests dominated by large (30–61 cm but typically >61 cm) trees with medium (50–70) but typically high (>70) percent canopy cover (Gutiérrez et al., 1995). The populations of all three subspecies have declined due to widespread historical and ongoing habitat loss, primarily from logging large, old trees

Fig. 1 California spotted owl in the central Sierra Nevada. Photograph reproduced with permission from Brett Hartl.

favored by the owls for nesting and roosting (USFWS, 2011, 2012; Conner et al., 2013; Tempel and Gutiérrez, 2013). More recently, invasion and competition by a related owl species from the Eastern United States, the barred owl (*S. varia*), into the range of the northern spotted owl (*S. o. caurina*) have been implicated in further declines of this subspecies (Kroll et al., 2010). Urban development was identified as a significant problem for California spotted owls (*S. o. occidentalis*) in southern California (LaHaye and Gutiérrez, 2005).

Changing Perceptions of Owl Habitat Use: An Old-Forest Icon in Burned Landscapes

For decades, studies on spotted owl habitat relations and correlations to survival and reproductive success were conducted in areas that had not experienced recent fire, where the "nonsuitable" owl habitat was typically a result of logging (Gutiérrez et al., 1992; Franklin et al., 2000; Seamans et al., 2002; Blakesley et al., 2005; Seamans and Gutiérrez, 2007a; Forsman et al., 2011; Tempel et al., 2014). As spotted owls are associated with dense, late-successional forests, biologists typically assumed that fires that burned at high intensity were similar to clearcut logging and had a negative impact on long-term survival of the species. Many land managers now believe that high-severity fires pose the greatest natural risk to owl habitat (Davis et al., 2016). Fire, however, is a different type of disturbance than logging. Before data were collected from spotted owls in burned forests, it was not unreasonable to assume that high-severity fire might eliminate habitat because it reduces canopy cover, kills trees, and consumes coarse woody debris—all of which comprise important structure for owls and their prey—but current research is revealing that a surprising number of spotted owl sites continue to be occupied and reproductively successful after experiencing fires of all intensities and that populations are quite resilient to fire. Further, spotted owls utilize complex early seral forests for foraging, providing evidence that severely burned forests can benefit spotted owls depending upon its extent and configuration (Bond et al., 2009; Comfort et al., 2016).

Spotted owls evolved in landscapes where severe fire was an important component historically (Baker, 2015), begging the question as to how these birds respond when severe fire affects habitat within their home ranges. Research on effects of wildfire on occupancy dynamics, survival and reproduction, and foraging habitat selection tells an interesting story, one that is not often heard beyond a small portion of the scientific community, but that provides compelling evidence for a new paradigm about severe fire and this key late-successional forest management species. The following discussion summarizes the available scientific literature on the effects of wildfire on different aspects of spotted owl demography, life history, and ecology, from studies using empirical data. Studies that modeled effects of simulated fires on spotted owl habitat and demography were not considered here.

Site Occupancy Dynamics

Spotted owls are territorial and have high site fidelity (Gutiérrez et al., 1995). Thus, occupancy of breeding territories is essential for successful survival and reproduction and for sustaining a population. The first peer-reviewed published study on spotted owl occupancy in burned landscapes was an examination of site and mate fidelity of northern, California, and Mexican spotted owls (*S. o. lucida*) 1 year after fire (Bond et al., 2002). Sixteen of 18 (89%) surviving owls (of all subspecies) were in the same breeding sites after fire, and all pairs were faithful to their prefire breeding site and mate.

Mexican spotted owl

Jenness et al. (2004) reported pre- and postfire occupancy of 64 Mexican spotted owl sites in mixed-conifer, pine (*Pinus* sp.), and pine-oak forests in four national forests in New Mexico and Arizona. The authors selected owl breeding sites in fires that burned from 1993 to 1996 and compared levels of occupancy (single, pair, failed reproduction and successful reproduction) in 1997 in 33 burned and 31 unburned sites, including 29 paired burned and long-unburned sites within 12 km of each other. Postfire

occupancy rates were not significantly different between burned and unburned sites and did not statistically differ with time since fire. The percent of high-severity fire in a burned site had no significant influence on whether the site was occupied. Postfire logging was minor in most of the fires.

California spotted owl

Roberts et al. (2011) compared longer-term effects of wildfire on occupancy of California spotted owls residing in burned (<15 years since fire) and long-unburned mixed-conifer forests in Yosemite National Park, the only study of this kind in an unmanaged landscape and the first to use modern statistical techniques to model occupancy probabilities (MacKenzie et al., 2006). This study compared occupancy of breeding sites in 16 randomly selected burned and 16 unburned "owl survey areas," each 3.75 km^2. A total of 19 owl pairs were monitored for a single year, and vegetation at owl sites was compared with sites that yielded no owl response to build detectability and occupancy models. The mean "owl survey area" that burned at high severity was 12%, with the greatest amount of high-severity burn in a survey area being 52%. Because this study was conducted in a national park, no postfire or recent prefire logging had occurred to confound results. The authors found no support for a model of occupancy rates that distinguished between burned and unburned sites. Occupancy and detection rates and densities of spotted owls were similar between burned and unburned sites. Vegetation structure was the main determinant of occupancy rather than whether or not the site had burned: the total basal area was higher at burned and unburned sites with owls than at sites without owls.

Lee et al. (2012) published an 11-year study of California spotted owl occupancy on national forest lands in the Sierra Nevada, the most extensive study of pre- and postfire occupancy ever conducted in this mountain range. This study also was the first in a burned landscape to use statistical methods for estimating rates of local extinction and colonization while accounting for imperfect detectability (MacKenzie et al., 2006) because multiple years of surveys were available. The authors used data collected by the US Forest Service to compile occupancy-survey histories at 41 breeding sites within six large fires that occurred from 2000 to 2007 throughout the Sierra Nevada and at 145 long-unburned control sites. Fires had no significant effect on occupancy probability (**Fig. 2**). The mean probability of colonization of burned sites was 0.381, similar to rates in long-unburned sites, which demonstrates the value of long-term monitoring to better understand wildfire effects on population dynamics, and underscores why managers must not presume a breeding site is permanently "lost" if owls are not detected immediately after fire. Based on simulation results, the authors recommended that managers should survey ≥200 burned and ≥200 long-unburned sites throughout the Sierra Nevada and that burned sites should be surveyed at least 2 years after fire to determine site occupancy prior to implementing postfire management activities.

The 2013 Rim Fire near Yosemite National Park was the largest fire in recent recorded Sierra Nevada history, burning more than 100,000 ha. The fires burned through 45 known California spotted owl breeding sites in the Stanislaus National Forest and all sites were surveyed by US Forest Service personnel the following year. This provided an unparalleled opportunity to examine the effects of a large fire on spotted owl site occupancy within a single fire area, in a study area with relatively little private timber land compared with other recent large fires that also affected many owl sites (eg, Moonlight–Antelope Complex and King Fire). Increasing amounts of severe fire surrounding nest and roost sites decreased occupancy probability, but did not affect occupancy by pairs of owls (Lee and Bond, 2015a; **Fig. 3**).

Furthermore, single-season modeled occupancy rates 1 year after the Rim Fire were significantly higher than other previously published occupancy rates in both burned and long-unburned forests (Lee and Bond, 2015a; **Fig. 4**). The relatively high occupancy

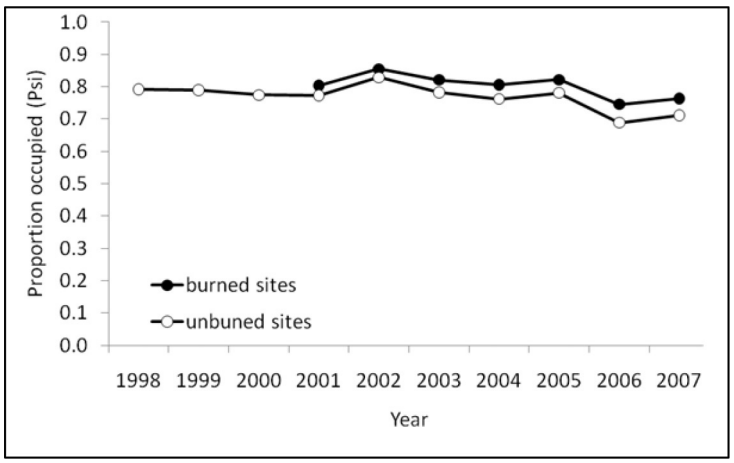

Fig. 2 Mean annual occupancy probabilities (*Psi*) of California spotted owls at unburned sites (*unfilled*) from 1998 to 2007 and sites burned by fires (*filled*) from 2001 to 2007 in Sierra Nevada national forests, California. Mean annual occupancy probabilities were derived from model-averaged estimates of colonization and extinction. Figure reproduced with permission from The Condor. Lee, D.E., Bond, M.L., Siegel, R.B., 2012. Dynamics of breeding-season site occupancy of the California spotted owl in burned forests. *Condor* **114**, 792–802.

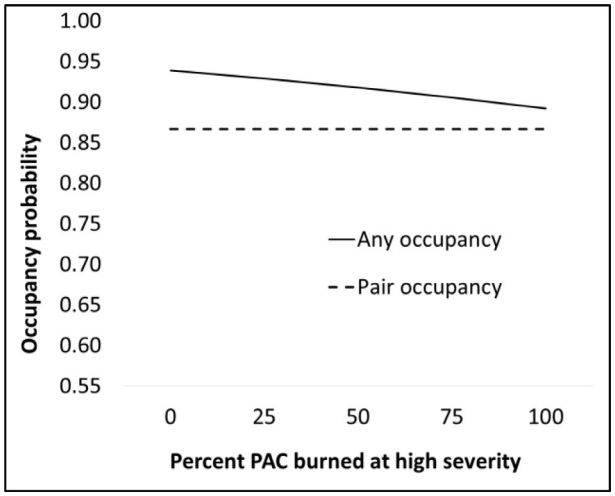

Fig. 3 Model-averaged site occupancy probability in 2014 for occupancy (*solid line*) and pairs (*dashed line*) in known California spotted owl sites burned in the 2013 Rim Fire. Site occupancy probability is presented as a function of the percent of the site's 121-ha protected activity center that was burned at high severity. Figure reproduced with permission from The Condor. Lee, D.E., Bond, M.L., 2015a. Occupancy of California spotted owl sites following a large fire in the Sierra Nevada. *Condor* **117**, 228–236.

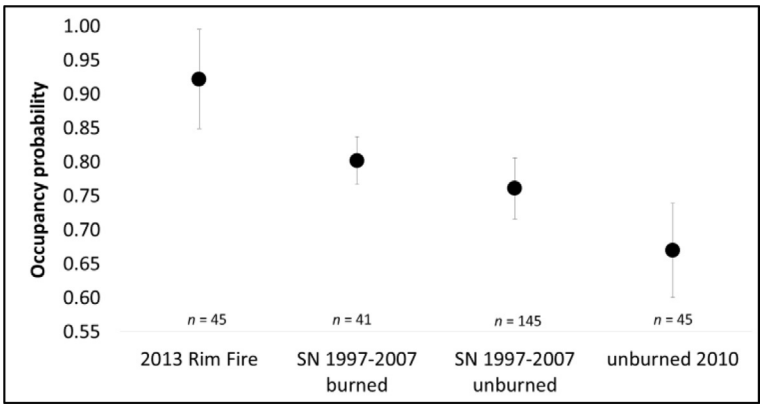

Fig. 4 Site occupancy probability (±SE) of known California spotted owl sites in the Sierra Nevada that were burned in the 2013 Rim Fire (data from Lee and Bond, 2015a), burned between 1997 and 2007 (data from Lee et al., 2012), unburned between 1997 and 2007 (data from Lee et al., 2012), and unburned in Eldorado and Tahoe National Forests in 2010 (data from Tempel and Gutiérrez, 2013).

rate could indicate either that owl sites in the Rim Fire area before and/or after fire were of above-average quality relative to the other fire areas or that owls remained in burned sites because of strong site fidelity.

A long-term (>20 years) demographic study of California spotted owls in the Eldorado and Tahoe National Forests of the central Sierra Nevada is providing a wealth of information on the effects of habitat, weather, and forest management activities. Tempel et al. (2014) examined the influence of timber harvest and wildfire on reproduction, survival, and occupancy over a 6-year timescale using data from 74 breeding sites, although only 12 sites experienced fire during the course of the study. Fire did not significantly affect survival, reproduction, or site extinction. The coefficient for the effect of fire on site colonization was strongly negative, but the standard error of the coefficient could not be estimated due to the very small sample of sites that were unoccupied after fire. Moreover, postfire logging at these sites confounded this result. The 2014 King Fire burned many additional spotted owl breeding sites in this demographic study area, and because much of the private land in this study area was postfire logged, current research is likely to yield important results on the influence of this widespread management activity on spotted owls.

Surveys by the US Forest Service at spotted owl breeding sites in southern California from 2003 to 2011 offered a unique opportunity to study the long-term fire effects in this especially fire-prone region, as more sites were influenced by wildfire during this period there than anywhere else in the range of the species. Lee et al. (2013) used survey data from 97 long-unburned and 71 burned breeding sites to examine the influence of fire and postfire logging on local rates of extinction, colonization, and occupancy probability. Postfire logging occurred on 21 of the burned sites.

None of the fire and logging coefficients were statistically significant, but model-averaged effect sizes suggested that high-severity fire that burned >50% of forest in the 203-ha core area was correlated with lower colonization, greater extinction, and

lower occupancy relative to unburned sites, for all detections as well as pairs only (Fig. 5). Postfire logging further increased extinction probability (Fig. 5). The majority (75%) of sites burned below the 50% threshold.

Spotted owls in two study areas continued to occupy burned forests in winter. Bond et al. (2010) documented three of five radiomarked California spotted owls in the southern Sierra Nevada roosted within a burned landscape overwinter. Ganey et al. (2014) reported four radiomarked Mexican spotted owls moving to burned overwintering areas in New Mexico.

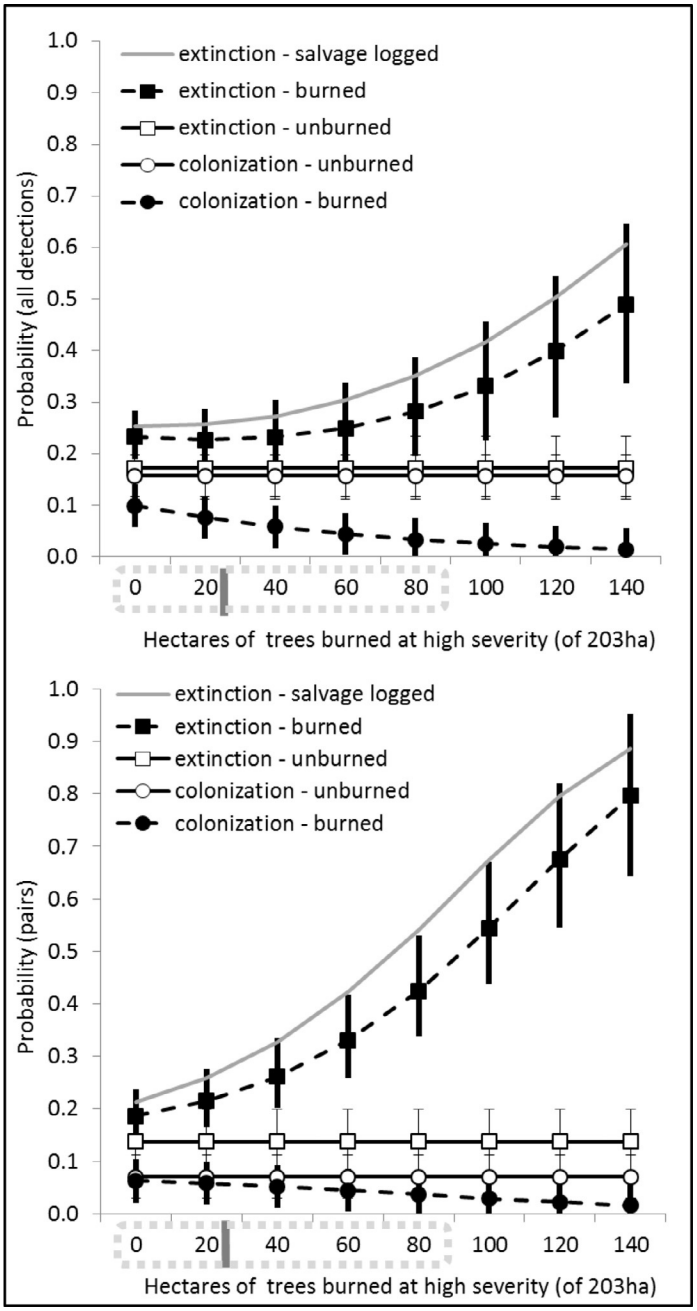

Fig. 5 Model-averaged relationship between site extinction probability and the hectares of suitable vegetation that burned at high severity within a 203-ha circle around the nest or roost centroid of California spotted owl sites in the San Bernardino and San Jacinto Mountains from 2003 to 2011 from all-detection (A) and pairs-only (B) data as calculated from model-averaged beta parameters. *Filled symbols* and *dashed lines* are burned owl sites (±SE), *open symbols* and *solid lines* are unburned sites (±SE), and *solid gray lines* represent burned and postfire-logged site extinction probabilities. *Vertical gray line* in *x*-axis indicates the mean amount of suitable vegetation that burned at high severity in all burned sites. *Dotted gray* rectangle in *x*-axis indicates 95% confidence interval of amount of suitable vegetation that burned at high severity in all burned sites. We set individual (site-specific) covariate values to the mean for each covariate. Figure reproduced with permission from Journal of Wildlife Management. Lee, D.E., Bond, M.L., Borchert, M.I., Tanner, R., 2013. Influence of fire and salvage logging on site occupancy of spotted owls in the San Bernardino and San Jacinto mountains of southern California. *Journal of Wildlife Management* **77**, 1327–1341.

Northern spotted owl

The only study to investigate the occupancy dynamics of northern spotted owls in burned landscapes was conducted in three fire areas and an adjacent long-unburned demographic study area in mixed-conifer and mixed-evergreen forests in the southern Oregon Cascade Mountains (Clark et al., 2013). The three fires all burned within 1 year of each other. Modeled occupancy rates of 103 spotted owl sites in the long-unburned area were compared with 40 burned sites before fire and after postfire logging. This extensive study also investigated survival rates and movements of 23 radiomarked owls in and just outside two of the fires (see *Survival*, later). Postfire logging was prevalent on private lands in all the fire areas; thus, it was not possible to quantify the influence of fire alone on occupancy dynamics and survival, but this research provided important insights into the effects of postfire logging on a federally threatened species whose numbers are continuing to decline (Forsman et al., 2011).

Extinction rates were greater after postfire logging in the burned area (Timbered Rock) than the long-unburned area (South Cascades; **Fig. 6**; Clark et al., 2013). Occupancy probability declined more steeply after postfire logging than in the unburned area (**Fig. 6**). The high rate of adult dispersal following postfire logging suggested that insufficient habitat remained at abandoned sites to support spotted owls. At all three fire areas, extinction probability of sites increased with greater amounts of combined area that was previously harvested, burned at high severity, or postfire logged.

Key Findings: Typically, severe fire does not have significant adverse effects on breeding-site occupancy by spotted owls, especially in sites occupied by pairs of owls. However, large amounts of high-severity fire in a core area can reduce occupancy probability, and postfire logging further increases site extinction and decreases site colonization. Studies are needed to determine thresholds for high-severity fire for Mexican and northern spotted owls and for California spotted owls in the Sierra Nevada.

Survival

Estimation of survival rates is possible only when animals can be individually identified and then later resighted. Spotted owls are captured and fitted with permanent colored leg bands that are then resighted in subsequent surveys.

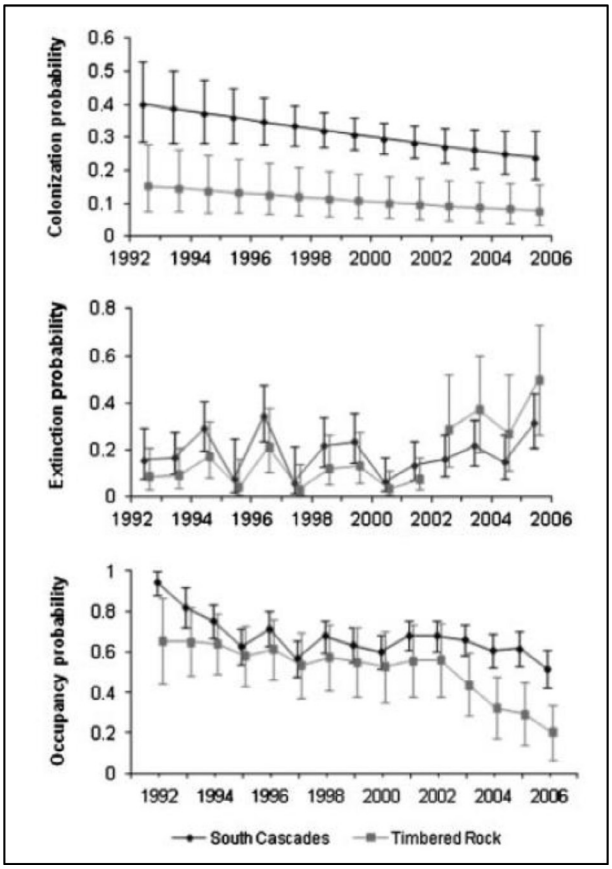

Fig. 6 Estimated extinction, colonization, and site occupancy probabilities (95% CI) of northern spotted owls at the Timbered Rock and South Cascades study areas in southwest Oregon, the United States, from 1992 to 2006. Figure reproduced with permission from Journal of Wildlife Management. Clark, D.A., Anthony, R.G., Andrews, L.S., 2013. Relationship between wildfire, salvage logging, and occupancy of nesting territories by northern spotted owls. *Journal of Wildlife Management* **77**, 672–688.

Table 1 Estimates (95% CI) of minimum postfire survival, site fidelity, and average number of fledglings per pair for 21 spotted owls that experienced fire in their territories in northwestern California, southern California, Arizona, and New Mexico, compared with overall averages for the four populations

	Estimates				
Parameter	*Postfire estimates*	S. o. caurina *NW CA*	*So. CA*	S. o. occidentalis *NM*	S. o. lucida *AZ*
Survival	0.86 (0.71–1.00) $n=21$	0.876 (0.84–0.91)	0.79 (0.76–0.81)	0.832 (0.78–0.89)	0.814 (0.72–0.91)
Site fidelity	0.89 (0.74–1.00) $n=18$	0.88 (0.85–0.92)	0.91 (0.88–0.94)	0.90 (0.85–0.95)	0.92 (0.85–0.99)
Average number of fledglings/pair	1.0 (0.62–1.38) $n=7$ pairs	0.62 (0.56–0.68)	0.64 (0.59–0.69)	0.77 (0.70–0.84)	0.93 (0.86–1.0)

Source: Bond ML, Gutiérrez RJ, Franklin AB, LaHaye WS, May CA, and Seamans ME (2002) Short-term effects of wildfires on spotted owl survival, site fidelity, mate fidelity, and reproductive success. Wildlife Society Bulletin 30: 1022–1028, with permission from Wildlife Society Bulletin.

Bond et al. (2002) examined short-term (1-year) postfire survival of 21 color-banded spotted owls in four separate study areas encompassing all subspecies: in mixed-conifer and mixed-evergreen forests of northwestern California, southern California, and New Mexico and in pine-oak forests in Arizona. All nest and roost areas were burned, and no postfire logging had occurred before owls were surveyed the year after fire. Vegetation burn severity maps were available for only eight of the 11 breeding sites. Four of the eight breeding sites where fire severities were mapped burned at low to moderate severity, and the other four burned 36–88% at high severity. Each breeding site was defined as a circle approximately 150–400 ha, depending on study area. The authors found that 18 of 21 (86%) individual owls were resighted after fire. These survival rates are the same as those for individuals in unburned sites (**Table 1**).

In a long-term demographic study of color-banded California spotted owls in the central Sierra Nevada, Tempel et al. (2014) found fire did not significantly affect survival.

Clark et al. (2011) examined the monthly survival rates of northern spotted owls 3–4 years after fire and postfire logging in two fire areas in southwestern Oregon. The authors color-banded and radiomarked 11 spotted owls inside and six owls adjacent to fire areas where much of the forest burned at high severity had been postfire logged. A third group of six owls had moved outside the perimeter after fire and subsequent logging. Owls that remained within the postfire logged landscape had lower survival rates than those reported throughout the range of the subspecies. Owls that moved had the lowest monthly survival rates of the three groups. Owls outside the burned and logged areas had the highest annual survival, but there was no evidence for an effect of fire severity on survival. The authors suggested past logging activities coupled with loss of habitat from severe fire followed by postfire logging contributed to the lower survival rates of owls in burned forests.

Key Findings: Spotted owl survival rates 1-year postfire (before postfire logging) were similar to survival rates in long-unburned forests, whereas monthly survival rates of northern spotted owls in postfire logged landscapes were lower than in long-unburned forests.

Reproduction

High annual variability in reproductive rates is typical of spotted owls and has been associated primarily with weather and to a lesser extent with habitat structure (Franklin et al., 2000; Seamans et al., 2002; Seamans and Gutiérrez, 2007b). While weather is a key factor, productivity also differs by site; thus, any impacts of wildfire on reproduction should account for prefire reproductive rates of the site and, ideally, be compared with long-unburned areas.

Jenness et al. (2004) found that the number of successfully reproducing Mexican spotted owl sites did not differ between burned and unburned forests (**Fig. 7**). Spotted owls successfully reproduced at three sites with 8%, 31%, and 32% high-severity fire within a 1-km circle of their nest. Moreover, reproductively successful sites had a higher percentage of burned area than other occupied sites affected by fire (including single owls and nonreproducing pairs).

Bond et al. (2002) also found that productivity of burned California spotted owl sites was higher than overall annual rates of reproduction for long-unburned sites (**Table 1**). Fire was not a significant variable influencing reproduction of California spotted owls in the central Sierra Nevada (Tempel et al., 2014).

As described in the preceding text, Lee et al. (2013) found that more high-severity fire in a site's core use area reduced occupancy by spotted owls in southern California. Lee and Bond (2015b) used the same dataset to examine how the quality of a site influenced occupancy and reproduction after severe fire. Site quality was measured by whether the site supported a single owl, pair of owls, or pair of owls with offspring the previous year. The influence of severe fire on occupancy was minor in sites that had been occupied and reproductive the previous year (high quality), and if a site remained occupied, severe fire did not affect the probability of reproduction compared with unburned sites (Lee and Bond, 2015b). In other words, lower-quality sites that were often vacant

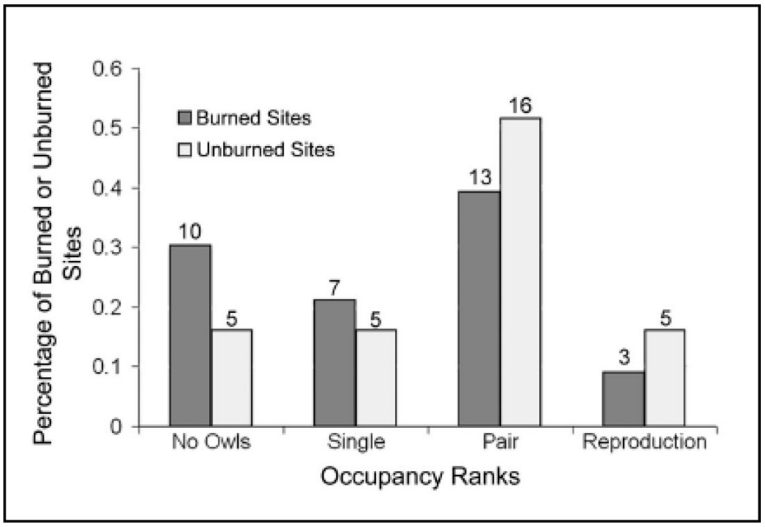

Fig. 7 Relative proportions of burned and unburned Mexican spotted owl sites that had no owls, a single bird, a pair, or confirmed reproduction. Figure reproduced with permission from Forest Science. Jenness, J.J., Beier, P., Ganey, J.L., 2004. Associations between forest fire and Mexican spotted owls. *Forest Science* **50**, 765–772.

and nonreproductive typically had lower occupancy with increasing amounts of severe forest fire, whereas in higher-quality sites that were consistently occupied and reproductive, the amount of severe fire that occurred in the core area had negligible effects on occupancy and reproduction. This was similar to the Rim Fire results that indicated that severe fire did not affect occupancy by pairs.

Key Findings: As long as sufficient suitable late-successional forest remains after fire to support a pair of spotted owls, owls in burned forests produced young at rates equal to owls in long-unburned forests. Increasing amounts of high-severity fire significantly reduced occupancy only in lower-quality sites that were often nonreproductive or vacant.

Nesting, Roosting, and Foraging in Burned Forests

Only one published study has documented roosting locations in burned forests (Bond et al., 2009). In this study, no nests were found in stands burned at high severity. California spotted owls roosted in all fire intensity classes 4 years after the McNally Fire in the Sequoia National Forest, southern Sierra Nevada, but most roosts were associated with low-severity fire. Only 1 of 60 roosts occurred in an area that burned at high severity, and owls selected roost sites burned at low severity and avoided sites burned at moderate severity. Roost sites averaged 63% canopy cover and had an abundance of large (average = 63 cm) trees. Thus, roosting habitat in burned landscapes was comparable with roosting habitat identified in unburned forests (Gutiérrez et al., 1995). These results underscore the importance of the burn severity mosaic of within an owl's home range.

Most studies of selection of habitat by spotted owls have focused on nesting and roosting habitat. Foraging habitat is just as critical for the persistence of owls, but is more difficult to identify because it requires radiotelemetry. Bond et al. (2009) were the first to quantify foraging habitat selection by spotted owls in a burned landscape. Selection studies compare how much owls used forest that burned at a particular severity with the availability of that burn severity. The authors banded and radiomarked seven California spotted owls occupying the McNally Fire 4 years after fire. Very little (<3%) of the foraging ranges of these owls had been postfire logged, so effects of high-severity fire were not confounded with postfire logging. All owls had access to sufficient amounts of unburned, low, moderate, and highly burned patches of forest in their home ranges from which to choose, so the authors could quantify whether owls selected or avoided any of these burn severities. The probability of an owl using a site for foraging was significantly greater in burned—especially high-severity burned—forests than unburned forest, after accounting for distance from nest (Fig. 8). Selection for a particular burn class occurred within 1.5 km from nest. Thus, recently burned complex early seral forest should be considered a potentially suitable foraging habitat for this subspecies.

Spotted owls in the McNally Fire area fed primarily on pocket gophers (*Thomomys* spp., 40.3% by biomass) and northern flying squirrels (*Glaucomys sabrinus*, 25.9% by biomass), whereas owls fed primarily on flying squirrel and woodrats (*Neotoma* spp.) in long-unburned study areas (Bond et al., 2013). The mean home-range sizes of the McNally Fire owls were similar to those recorded in unburned forests using similar time periods and methodology (Bond et al., 2013).

Bond et al. (in press) analyzed foraging habitat selection by eight California spotted owls in the Slide Fire in the San Bernardino National Forest of southern California 3 and 4 years after fire. Habitat selection with sensitivity analysis at three spatial extents of available habitat showed owls used forests burned at all severities in proportion to their availability, with the exception of significant selection for moderately burned forest farther from core areas.

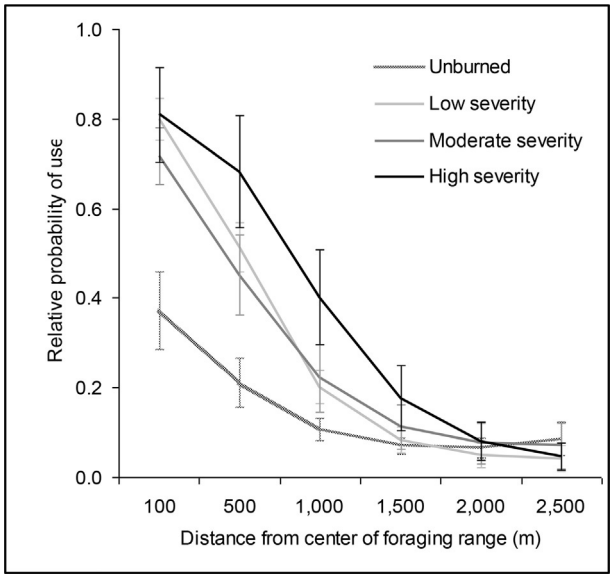

Fig. 8 Relative probability of use of a site for seven California spotted owls foraging at different distances from the center of the breeding range in forest burned at different intensities in the McNally Fire, Sequoia National Forest, 2006. Figure reproduced with permission from Journal of Wildlife Management. Bond, M.L., Lee, D.E., Siegel, R.B., Ward, J.P., 2009. Habitat use and selection by California spotted owls in a postfire landscape. *Journal of Wildlife Management* **73**, 1116–1124.

Comfort et al. (2016) examined foraging habitat selection by 23 northern spotted owls in the Timbered Rock Fire in southwest Oregon in relation to edges created by fire and postfire logging. Because postfire logging occurred immediately following fire on extensive private lands in the study area, and their remote-sensing methodology could not distinguish between fire and postfire logged areas, the authors created a combined burned–logged variable called the "disturbance severity." The edges between forested habitats and burned–logged areas were defined as "hard" edges. At smaller spatial scales (3.2 and 51.8 ha surrounding telemetry locations), increases in disturbance severity decreased the probability of use, but at larger spatial scales (829 ha), the opposite was true. The use of a location for foraging was maximized when about 20% of a 3.2-ha area surrounding the location was composed of hard edge. Thus, foraging owls selected some amount of edge, possibly because edges offer access for hunting small mammals while still providing adjacent closed-canopy habitat. Owls avoided areas with larger amounts of hard edge, but selected smaller amounts of edge, suggesting that small patches of high-severity fire surrounded by relatively undisturbed land are potentially suitable for foraging. Larger, more contiguous hard edges were described as intensively managed edges, that is, created by postfire logging.

A sample of four radiomarked Mexican spotted owls in the Sacramento Mountains, New Mexico, moved to wintering areas that had burned 4–6 years earlier and that had two to six times greater abundance and biomass of small mammal prey than nest core areas associated with those owls (Ganey et al., 2014). This study indicates that wintering areas provided important foraging habitats during an energetically stressful time of year.

Key Findings: Spotted owls appear to be mostly resilient to high-severity fire in their breeding sites and will take advantage of burned forest habitat for foraging when that habitat is close to the nest or roosts. Nests and roosts in burned landscapes were found in low-severity burned or long-unburned forested stands, underscoring the importance of the burn severity mosaic to provide for nesting, roosting, and foraging. Recently burned complex early seral forest should be considered a potentially suitable foraging habitat.

Fire Provides Spotted Owl Prey Species With Important Habitat

One reason why spotted owls remain in burned territories is that fire enhances habitat for some of their primary prey species. Primary prey for California spotted owls depends on elevation and includes small mammal species like woodrats, northern flying squirrels, pocket gophers, and deer mice (*Peromyscus maniculatus*; Verner et al., 1992; Munton et al., 2002; Blakesley et al., 2005). Many small mammal species are more abundant in shrub- and herb-dominated habitats, vegetation typical of recently burned complex early seral forests.

Due to their relatively large size, woodrats are a high-quality prey item for spotted owls. Chaparral is an important understory component of coniferous forests in the Sierra Nevada, and shrubs eaten by woodrats and needed for cover, such as *Ceanothus* spp., increase and flourish several years after high-severity fire.

Pocket gophers were the most important prey item by percent biomass for spotted owls in burned forests 4 years after the McNally Fire in the southern Sierra Nevada (Bond et al., 2013) and the second most important prey item for California spotted owls in a long-unburned landscape in the Sierra National Forest (Munton et al., 2002). Pocket gophers are uncommon in mature

and older forests with little or no herbaceous ground cover (Williams et al., 1992) and thus are likely to benefit from the habitat created by severe fire.

Deer mice increased significantly over time in moderate and severely burned mixed-conifer forests in the Butler II Fire in the San Bernardino Mountains of southern California over a 5-year postfire period (Borchert et al., 2014). Tevis (1956) captured nearly twice as many deer mice just 2.5 weeks after a postlogging burn as before in a Douglas-fir forest in northwestern California. Gashwiler (1959) also documented rapid increases in deer mice populations in forests following a postlogging prescribed burn. Tietje et al. (2008) found no difference in survival of three *Peromyscus* species among prescribed burned and unburned oak woodlands in coastal central California. In North America, generalist deer mice respond strongly and positively to high-severity fire in both shrubland and conifer forest types and are often the most abundant rodent after severe fire (Borchert et al., 2014).

Flying squirrels apparently suffer the greatest habitat loss from severe fire or take longer to recover from it than woodrats or forest-dwelling mice. Roberts et al. (2015) captured no flying squirrels in moderate and severely burned unmanaged forest stands in Yosemite National Park.

Key Findings: High-severity fire may increase habitat suitability for open-canopy spotted owl prey species, including woodrats, gophers, and deer mice, but may reduce suitability for flying squirrels.

Conclusions: An Emerging New Paradigm About Spotted Owls and Severe Wildfire

- Most spotted owl pairs generally survive and continue to reproduce in breeding sites that experienced severe fire across the range of the three owl subspecies.
- Lower-quality sites (often vacant and nonreproductive) have lower occupancy with increasing amounts of severe fire, whereas higher-quality sites (occupied and reproductive before fire) remain occupied at similar rates as long-unburned forests, regardless of amount of severe fire.
- Spotted owls nest and roost in forested stands with high canopy cover (unburned/low burned) even in burned landscapes.
- Spotted owls forage in severely burned stands.
- Home-range sizes are similar in burned and unburned landscapes.
- Postfire logging is correlated with site abandonment and reduces survival.
- Studies of spotted owls in burned forests not subjected to postfire logging are necessary in order to separate and understand the relative influence of each disturbance.

Contrary to current perceptions and recovery efforts for the spotted owl (USFWS, 2011, 2012), high-severity fire does not appear to be an immediate, dire threat to owl populations that requires massive landscape-level fuel-reduction treatments to mitigate fire effects (see, eg, Hanson et al., 2009). Empirical studies conducted from 1 to 15 years after fires demonstrate that most burned sites occupied by spotted owl pairs remain occupied and reproductive at the same rates as long-unburned sites, regardless of the amount of high-severity fire in core areas. Burned sites where owls are not detected immediately after fire are often recolonized later, demonstrating the folly of concluding those sites permanently "lost" to spotted owls. Large amounts of high-severity fire within owl core areas could harm populations over the long term, because lower-quality sites—those that have a higher probability of extinction after fire—may be important opportunities for colonization by "floater" owls (those without mates and territories) and for recruitment (young owls entering the breeding population). At the same time, however, severe fire may benefit adult and juvenile survival by creating foraging habitat with abundant small mammal prey, but only if fire-killed trees are not logged after fire. Moreover, in any given fire, relatively few owl sites experience levels of high-severity fire greater than the territory threshold above which occupancy probability was reduced, although confirming the specific threshold remains a research priority for northern and Mexican spotted owls and for California spotted owls in the Sierra Nevada. Potential harm to spotted owls by the temporary loss of late-successional nesting and roosting habitat from high-severity fire is certainly compounded and exacerbated by postfire logging, prefire fuel treatments, urbanization, and drought and increasingly warmer temperatures.

Harvesting timber to lower risk of fire has adverse effects on spotted owls (eg, Tempel et al., 2014), whereas fire itself has both costs and benefits depending on many factors. It is important to critically weigh these costs and benefits, especially since spotted owls evolved in landscapes shaped by wildfires (Baker, 2015). Odion et al. (2014) simulated changes in northern spotted owl habitat over a 40-year period following fire and the type of thinning typically proposed by federal land managers. The simulation showed that thinning over large landscapes would remove 3.4–6.0 times more late-successional forest over time in the Klamath and dry Cascades than forest fires would, even given a future increase in the amount of high-severity fire.

Many complex and interacting factors influence the population dynamics of spotted owls and the capacity of a site to support successful breeding after wildfire: amount of pre- and postfire nesting, roosting, and foraging habitat, abundance and accessibility of prey, and individual heterogeneity of the owls, to name just a few. How these complex interactions ultimately affect populations is a topic ripe for additional research, but studies must take place in areas that do not experience the confounding effects of postfire logging.

References

Baker WL (2015) Historical northern spotted owl habitat and old-growth dry forests maintained by mixed-severity fires. *Landscape Ecology* 30: 655–666.

Blakesley JA, Noon BR, and Anderson DR (2005) Site occupancy, apparent survival, and reproduction of California spotted owls in relation to forest stand characteristics. *The Journal of Wildlife Management* 69: 1554–1564.

Bond, M. L., Bradley, C. and Lee., D. E. (in press). Foraging habitat selection by California spotted owls after forest fire in southern California. J. Wildl. Manag. http://dx.doi.org/10.1002/jwmg.21112.

Bond ML, Gutiérrez RJ, Franklin AB, LaHaye WS, May CA, and Seamans ME (2002) Short-term effects of wildfires on spotted owl survival, site fidelity, mate fidelity, and reproductive success. *Wildlife Society Bulletin* 30: 1022–1028.

Bond ML, Lee DE, Siegel RB, and Ward JP (2009) Habitat use and selection by California spotted owls in a postfire landscape. *The Journal of Wildlife Management* 73: 1116–1124.

Bond ML, Lee DE, and Siegel RB (2010) Winter movements by California spotted owls in a burned landscape. *Western Birds* 41: 174–180.

Bond ML, Lee DE, Siegel RB, and Tingley MW (2013) Diet and home-range size of California spotted owls in a burned forest. *Western Birds* 44: 114–126.

Borchert MI, Farr DP, Rimbenieks-Negrete MA, and Pawlowski MN (2014) Responses of small mammals to wildfire in a mixed conifer forest in the San Bernardino mountains, California. *Bulletin of the Southern California Academy of Sciences* 113: 81–95.

Clark DA, Anthony RG, and Andrews LS (2011) Survival rates of northern spotted owls in post-fire landscapes of southwest Oregon. *Journal of Raptor Research* 45: 38–47.

Clark DA, Anthony RG, and Andrews LS (2013) Relationship between wildfire, salvage logging, and occupancy of nesting territories by northern spotted owls. *The Journal of Wildlife Management* 77: 672–688.

Comfort EJ, Clark DA, Anthony RG, Bailey J, and Betts MG (2016) Quantifying edges as gradients at multiple scales improves habitat selection models for northern spotted owl. *Landscape Ecology* . http://dx.doi.org/10.1007/s10980-015-0330-1.

Conner MM, Keane JJ, Gallagher CV, Jehle G, Munton TE, Shaklee PA, and Gerrard RA (2013) Realized population change for long-term monitoring: California spotted owl case study. *The Journal of Wildlife Management* 77: 1449–1458.

Davis, R. J., Hollwn, B., Hobson, J., Gower, J. E., Keenum, D. (2016). Northwest forest plan—the first 20 years (1994–2013): Status and trends of northern spotted owl habitats. General technical report PNW-GTR-929. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 54 p.

DellaSala DA, Bond ML, Hanson CT, Hutto RL, and Odion DC (2014) Complex early seral forests of the Sierra Nevada: What are they and how can they be managed for ecological integrity? *Natural Areas Journal* 34: 310–324.

Forsman ED, Anthony RG, Dugger KM, Glenn EM, Franklin AB, White GC, Schwarz CJ, Burnham KP, Anderson DR, Nichols JD, Hines JE, Lint JB, Davis RJ, Ackers SH, Andrews LS, Biswell BL, Carlson PC, Diller LV, Gremel SA, Herter DR, Higley JM, Horn RB, Reid JA, Rockweit J, Schaberel J, Snetsinger TJ, and Sovern SG (2011) *Population Demography of Northern Spotted Owls*. Studies in Avian Biology No. 40, Cooper Ornithological Society, University of California Press: Berkeley, CA, USA 1985–2008.

Franklin AB, Anderson DR, Gutiérrez RJ, and Burnham KP (2000) Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs* 70: 539–590.

Ganey JL, Kyle SC, Rawlinson TA, Apprill DL, and Ward JP Jr (2014) Relative abundance of small mammals in nest core areas and burned wintering areas of Mexican spotted owls in the Sacramento Mountains, New Mexico. *Wilson Journal of Ornithology* 126: 47–52.

Gashwiler JS (1959) Small mammal study in west-central Oregon. *Journal of Mammalogy* 40: 128–139.

Gutiérrez RJ, Verner J, McKelvey KS, Noon BR, Steger GN, Call DR, LaHaye WS, Bingham BB, and Senser JS (1992) Habitat relations of the California spotted owl. In: Verner J, McKelvey KS, Noon BR, Gutiérrez RJ, Gould GI Jr., Beck TW, and Tech. Coords (eds.) *The California Spotted Owl: A Technical Assessment of Its Current Status*, pp. 79–98. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station Gen. Tech. Rep. PSW-GTR-133.

Gutiérrez RJ, Franklin AM, and LaHaye WS (1995) Spotted Owl (Strix occidentalis). In: Poole A, Gill F, (eds.) *The birds of North America,* No.179. Washington, DC: The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union.

Hanson CT, Odion DC, DellaSala DA, and Baker WL (2009) Overestimation of fire risk in the Northern Spotted Owl recovery plan. *Conservation Biology* 23: 1314–1319.

Hutto RL (2006) Toward meaningful snag-management guidelines for postfire salvage logging in North American conifer forests. *Conservation Biology* 20: 984–993.

Jenness JJ, Beier P, and Ganey JL (2004) Associations between forest fire and Mexican spotted owls. *Forestry Sciences* 50: 765–772.

Kroll AJ, Fleming TL, and Irwin LL (2010) Site occupancy dynamics of northern spotted owls in the eastern Cascades, Washington, USA, 1990–2003. *The Journal of Wildlife Management* 74: 1264–1274.

LaHaye, W. L. and Gutiérrez., R. J. (2005). The spotted owl in southern California: ecology and special concerns for maintaining a forest-dwelling species in a human-dominated desert landscape. USDA Forest Service general technical report PSW-GTR-195.

Lee DE and Bond ML (2015a) Occupancy of California spotted owl sites following a large fire in the Sierra Nevada. *Condor* 117: 228–236.

Lee DE and Bond ML (2015b) Previous year's reproductive state affects spotted owl site occupancy and reproduction responses to natural and anthropogenic disturbances. *Condor* 117: 307–319.

Lee DE, Bond ML, and Siegel RB (2012) Dynamics of breeding-season site occupancy of the California spotted owl in burned forests. *Condor* 114: 792–802.

Lee DE, Bond ML, Borchert MI, and Tanner R (2013) Influence of fire and salvage logging on site occupancy of spotted owls in the San Bernardino and San Jacinto mountains of southern California. *The Journal of Wildlife Management* 77: 1327–1341.

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LA, and Hines JE (2006) *Occupancy Modeling and Estimation*. San Diego, CA: Elsevier.

Munton, T. E., Johnson, K. D., Steger, G. N. and Eberlein, G.P. (2002). Diets of California spotted owls in the Sierra National Forest. USDA Forest Service, Pacific Southwest Research Station general technical report PSW-GTR-183, Albany, CA.

Odion DC, Hanson CT, DellaSala DA, Baker WL, and Bond ML (2014) Effects of fire and commercial thinning on future habitat of the northern spotted owl. *The Open Ecology Journal* 7: 37–51.

Roberts SL, Van Wagtendonk JW, Miles AK, and Kelt DA (2011) Effects of fire on spotted owl site occupancy in a late-successional forest. *Biological Conservation* 144: 610–619.

Roberts SL, Kelt DA, van Wagtendonk JW, Miles AK, and Meyer MD (2015) Effects of fire on small mammal communities in frequent-fire forests in California. *Journal of Mammalogy* 96: 107–119.

Seamans ME and Gutiérrez RJ (2007a) Habitat selection in a changing environment: The relationship between habitat alteration and spotted owl territory occupancy and breeding dispersal. *Condor* 109: 566–576.

Seamans ME and Gutiérrez RJ (2007b) Sources of variability in spotted owl population growth rate: Testing predictions using long-term mark-recapture data. *Oecologia* 152: 57–70.

Seamans ME, Gutiérrez RJ, and May CA (2002) Mexican spotted owl (*Strix occidentalis*) population dynamics: influence of climactic variation on survival and reproduction. *Auk* 119: 321–334.

Swanson ME, Franklin JF, Beschta RL, Crisafulli CM, DellaSala DA, Hutto RL, Lindenmayer DB, and Swanson FJ (2011) The forgotten stage of forest succession: Early-successional ecosystems on forested sites. *Frontiers in Ecology and the Environment* 9: 117–125.

Tempel DJ and Gutiérrez RJ (2013) Relation between occupancy and abundance for a territorial species, the California spotted owl. *Conservation Biology* 27: 1087–1095.

Tempel DJ, Gutiérrez RJ, Whitmore SA, Reetz MJ, Stoelting RE, Berigan WJ, Seamans MA, and Peery MZ (2014) Effects of forest management on California spotted owls: implications for reducing wildfire risk in fire-prone forests. *Ecological Applications* 24: 2089–2106.

Tevis L (1956) Effects of a slash burn on forest mice. *The Journal of Wildlife Management* 20: 405–409.

Tietje WD, Lee DE, and Vreeland JK (2008) Survival and abundance of three species of mice in relation to density of shrubs and prescribed fire in understory of an oak woodland in California. *The Southwestern Naturalist* 53: 357–369.

U.S. Fish and Wildlife Service (2011) *Revised Recovery Plan for the Northern Spotted Owls (*Strix occidentalis caurina*)*. Portland, Oregon, USA: U.S. Fish and Wildlife Service xvi + 258 p.

U.S. Fish and Wildlife Service (2012) *Final Recovery Plan for the Mexican Spotted Owls (*Strix occidentalis lucida*)*. First Revision Albuquerque, New Mexico, USA: U.S. Fish and Wildlife Service 413 p.

Verner, J. K., McKelvey, S., Noon, B. R., Gutiérrez, R. J., Gould, G. I., Beck, T.W. and Technical coordinators. (1992). The California spotted owl: A technical assessment of its current status. USDA Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-133, Albany, CA.

Williams DF, Verner J, Sakai HF, and Waters JR (1992) General biology of major prey species of the California spotted owl. In: Verner J, McKelvey KS, Noon BR, Gutierrez RJ, Gould GI Jr., Beck TW, and Tech. Coords (eds.) *The California Spotted Owl: A Technical Assessment of Its Current Status. U.S. Forest Service, Pacific Southwest Research Station, General Technical Report PSW-133*, pp. 207–221 285. USFS, Albany, California, USA.