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RESEARCH ARTICLE

Occupancy of California Spotted Owl sites following a large fire in the Sierra Nevada, California

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ABSTRACT

High-severity forest fire often is presumed to adversely affect the occupancy of territories by California Spotted Owls (*Strix occidentalis occidentalis*) because these owls are associated with mature and old-growth forests. We used single-season, multi-state occupancy statistics to estimate site occupancy probability for Spotted Owls at 45 historically occupied sites during the breeding season immediately following the 2013 Rim Fire, which was one of the largest forest fires on record in California. We quantified how occupancy probability was influenced by the amount of high-severity fire occurring in mature forested habitat within Protected Activity Centers (PACs). The model-averaged estimate of site-occupancy probability for at least a single owl was 0.922 ($\pm$SE $=$ 0.073), which was higher than other published occupancy probability estimates for this subspecies in either burned or long-unburned sites in the Sierra Nevada. Mean site-occupancy probability for pairs was 0.866 ($\pm$0.093), and most sites (33) were occupied by pairs. The amount of high-severity fire in the PAC did not affect pair occupancy. Occupancy probability by at least a single bird was negatively correlated with the amount of high severity fire in the PAC but remained $>$0.89 in 100% high-severity burned PACs. These data add to observations that California Spotted Owls continue to use post-fire landscapes, even when the fires were large and where large areas burned at high severity, suggesting that owls are not generally negatively impacted by high-severity fire. Based on this and other studies of Spotted Owls, fire, and logging, we suggest land managers consider burned forest within and surrounding PACs as potentially suitable California Spotted Owl foraging habitat when planning and implementing management activities, and we recommend against logging burned forest within at least 1.5 km of nests or roosts for the conservation and recovery of this declining subspecies.

Keywords: California Spotted Owl, *Strix occidentalis occidentalis*, occupancy, forest fire

Ocupación de sitios de *Strix occidentalis occidentalis* luego de un gran incendio en la Sierra Nevada, California

RESUMEN

Generalmente se supone que los incendios forestales de alta severidad afectan la ocupación de los territorios de *Strix occidentalis occidentalis* debido a que estos búhos se asocian con bosques maduros y primarios. Usamos estadísticos multiestado de ocupación de una temporada para estimar la probabilidad de ocupación de un sitio por *S. occidentalis* en 45 sitios históricamente ocupados, durante la temporada reproductiva que siguió inmediatamente al incendio Rim de 2013, uno de los incendios forestales más grandes registrados en California. Cuantificamos cómo la probabilidad de ocupación se vio influenciada por la cantidad de incendios de alta severidad en bosques maduros dentro de Centros de Actividad Protegida (PAC, por sus siglas en inglés). El estimado promedio de los modelos de probabilidad de ocupación de sitios para al menos un individuo fue de 0.922 ($\pm$EE $=$ 0.073), lo que es mayor que otras probabilidades de ocupación estimadas para esta subespecie en sitios con o sin incendios recientes en la Sierra Nevada. La probabilidad promedio de ocupación de sitios para parejas fue de 0.866 ($\pm$0.093), y la mayoría de los sitios (33) fueron ocupados por parejas. La cantidad de incendios de alta severidad en los PAC no afectó la ocupación de las parejas. La probabilidad de ocupación por al menos un individuo se correlacionó negativamente con la cantidad de incendios de alta severidad en los PAC, pero permaneció mayor a 0.89 en el 100% de los PAC severamente incendiados. Estos datos complementan las observaciones de que *S. o. occidentalis* sigue usando los paisajes incendiados, aún cuando los incendios fueron grandes y donde grandes áreas se incendiaron con alta severidad, lo que sugiere que los búhos generalmente no sufren un impacto negativo por los incendios de alta severidad. Basados en este y otros estudios sobre *S. occidentalis*, incendios y tala de bosques, sugerimos que los administradores de la tierra consideren los bosques incendiados dentro y alrededor de los PAC como hábitats de alimentación potencialmente apropiados para *S. o. occidentalis* durante la planeación e implementación de las actividades de manejo. No recomendamos la tala de los bosques incendiados en un radio menor a 1.5 km alrededor de los nidos y dormideros para la conservación y recuperación de esta subespecie en declive.

Palabras clave: incendios forestales, ocupación, *Strix occidentalis occidentalis*

INTRODUCTION

For more than 25 years, the California Spotted Owl (*Strix occidentalis occidentalis*) has been a species of concern throughout its range because it selects commercially valuable mature and older conifer forests for nesting, roosting, and foraging (Verner et al. 1992). Recent evidence from long-term demographic studies in the Sierra Nevada show that California Spotted Owl populations are declining significantly on managed national forest lands (Conner et al. 2013, Tempel and Gutiérrez 2013). At the same time, populations are apparently stable in Sequoia and Kings Canyon national parks where forests are largely unmanaged (Conner et al. 2013).

Forest fire has long been hypothesized to be a major threat to California Spotted Owls (Verner et al. 1992, USFWS 2006), but recent studies have shown that owls persist for years in landscapes burned by all fire intensities (Roberts et al. 2011, Lee et al. 2012, 2013). Despite this evidence, forest managers continue to assume that large areas of high-severity fire adversely affect Spotted Owl occupancy to the extent it renders forests unsuitable as habitat (USFS 2004). As a result, post-fire salvage logging is routinely proposed and permitted in severely burned forests, even within administrative designations established to conserve owl habitat, such as 121 ha Protected Activity Centers and 405 ha Home Range Core Areas surrounding nests and roost sites (USFS 2004).

In August 2013, the Rim Fire burned a large (>100,000 ha) area within and around the Stanislaus National Forest and Yosemite National Park, California. The year following the fire, biologists from the USDA Forest Service (USFS) conducted surveys in all previously occupied (occupied $\geq$1 year before the fire) California Spotted Owl sites (Protected Activity Centers, see Methods) within the Rim Fire area to determine site occupancy status. These data provided an excellent opportunity to estimate single-season occupancy of Spotted Owl breeding sites within one of the largest forest fires in recent Sierra Nevada history and to compare occupancy with previously reported rates in burned and long-unburned forests. The USFS also maps burn severity of vegetation, which we used as a site-specific covariate to determine how the amount of high-severity burned forest within Spotted Owl Protected Activity Centers affected occupancy status. This information is important for developing appropriate post-fire forest management policies and activities to conserve this declining management indicator species.

METHODS

Study Area and Species

The Rim Fire started near the confluence of the Clavey and Tuolumne rivers about 32 km east of Sonora, California, and burned primarily eastward into the Sierra Nevada (USFS 2014a). Elevations within the Rim Fire area ranged from 300 to 2,100 m. The fire area included a variety of habitats and vegetation age classes; forest types pertinent to Spotted Owls included Sierran mixed-conifer, white fir (*Abies concolor*), red fir (*A. magnifica*), montane hardwood-conifer, ponderosa pine (*Pinus ponderosa*), and Jeffrey pine (*P. jeffreyi*) (USFS 2014b).

The California Spotted Owl occurs in conifer and mixed conifer-hardwood forests in the Sierra Nevada, central and southern coastal, and southern interior mountain ranges of California (Gutiérrez et al. 1995). This nocturnal raptor primarily preys on small mammals but also eats insects, birds, and bats (Thrailkill and Bias 1989, Munton et al. 2002, Bond et al. 2013). California Spotted Owls are territorial with high site fidelity (Gutiérrez et al. 1995, Blakesley et al. 2006) and select nest and roost sites in older forests containing large live trees typically >61 cm diameter at breast height, with multi-layered structure, high canopy cover (>40% but typically >70%), and abundant large snags and downed logs (Call et al. 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Bond et al. 2004, Blakesley et al. 2005). Foraging habitat is more variable and can include forest areas with high canopy cover (Call et al. 1992, Gutiérrez et al. 1992), medium-sized forest (Williams et al. 2011), and forest burned at any severity (Bond et al. 2009).

Defining Spotted Owl Habitat and Protected Activity Centers (PACs)

The USFS manages wildlife habitat using a classification system based on the California Wildlife Habitat Relationships system (CWHR) developed by the California Department of Fish and Game (now California Department of Fish and Wildlife). The CWHR types 6, 5D, 5M, 4D, and 4M denote stands dominated by larger-sized trees and high canopy cover, and these CWHR types are considered highly and moderately suitable "Spotted Owl habitat" for the California subspecies (CDFG 2008). The USFS delineates for management purposes a 121 ha Protected Activity Center (PAC) consisting of Spotted Owl habitat CWHR types in as compact a unit as possible around owl detection locations on National Forest System lands (Verner et al. 1992). Owl detection locations are based on (1) the most recent documented nest site, (2) the most recent known roost site when a nest location remains unknown, and (3) a central point based on repeated daytime detections when neither nest nor roost locations are known (USFS 2004). In addition, a 405 ha Home Range Core Area (HRCA), consisting of Spotted Owl habitat CWHR types, is established around each owl detection location and includes the PAC.

The guiding USFS management document for the Sierra Nevada (USFS 2004) states that PACs are maintained regardless of California Spotted Owl occupancy status, but after a "stand-replacing event," habitat conditions are to be evaluated within a 2.4 km radius around the activity center. The PAC may be re-mapped to exclude high-severity fire areas or can be removed from the conservation network altogether (USFS 2004). The elimination of PAC protections enables areas to be logged following impact by high-severity fire (i.e. "salvage" logging). Prior to post-fire salvage logging in former PACs, portions of former PACs, or HRCAs, surveys for Spotted Owls are conducted in accordance with 1995 Pacific Southwest Region survey protocol (USFS 1995), but burned stands may be logged even if owls are detected during these surveys.

Data Collection and Analysis

We organized and analyzed survey data using a single-season, multi-state occupancy modeling approach (MacKenzie et al. 2006, 2009, 2010). We followed as much as possible the methods of data collection and analyses of MacKenzie et al. (2006, 2009, 2010) where suitably defined geographic units or "sites" are repeatedly surveyed for detections of the species of interest to define presence at a site in 1 of 2 "states." Here we use the term "site" to mean a PAC, which was our sampling unit (MacKenzie et al. 2006, 2009, 2010), and defined "state" as the detection of either a single or pair of owls. This allowed us full use of survey data while incorporating information about single- vs. pair-detection data (MacKenzie et al. 2006, 2009, 2010). Our population of interest was all historical Spotted Owl sites that were burned during the Rim Fire, so it was appropriate to use data from sites that were not randomly selected (MacKenzie and Royle 2005).

At our request, the USFS provided field data forms from Spotted Owl surveys conducted within the boundary of the Rim Fire. The standardized data forms contained the following information: survey location (PAC number and site name), date, observers, starting latitude and longitude, specific survey times, survey duration, weather and moon phase, age and sex of owls detected, detection type (seen or heard), latitude and longitude for nest and roost trees, and a detailed narrative about the survey. A narrative typically included the time and place that surveyors began broadcasting vocal lures, the time when an owl was seen or heard and the sex of the owl, the time a mouse was offered to an owl to assess reproduction and when the owl took the mouse, and the fate of each mouse (eaten, cached, offered to a mate or to young, or undetermined). The USFS also provided us with quadrangle maps associated with each survey that identified the survey routes and owl locations by sex if owls were detected. Although we did not conduct the surveys ourselves, we assumed that the USFS provided us with all available data forms for the PACs within the Rim Fire and that the data on the forms were accurate. Thus, we acknowledge that factors unknown to us could have affected the reliability of the data.

USFS biologists who gathered the data surveyed for Spotted Owls at all of the 45 historically occupied PACs within the Rim Fire using the 1995 Pacific Southwest Region survey protocol from 24 March through 5 August 2014 (USFS 1995). Surveyors used vocal lures at 3–11 ($\bar{x} = 6$) calling stations per PAC at night. Following a nighttime detection, they conducted daytime follow-up surveys by feeding owls live mice (1) to locate active nest trees, (2) to locate roosts of pairs and resident singles, and (3) to monitor reproduction (USFS 1995). Protocols required a minimum of 6 site surveys during a single year, with at least 4 of these surveys occurring before 30 June. If no detections were recorded during any survey, a site may be designated as not occupied. Six PACs in the Rim Fire were not surveyed enough times to meet protocol standards, but we included these in our analyses to avoid potential bias owing to censoring and because a minimum of 3 visits is generally sufficient when detection probability is >0.5 (MacKenzie and Royle 2005), as was the case for our pairs data (see Results).

We examined all USFS field data forms, notes, and associated maps depicting owl survey routes and detections or nondetections and created a database of the results of every survey for each site. We incorporated both nocturnal and daytime detections in our occupancy analysis to increase sample size. We attributed a state for each survey of each site as: pair detected, single owl detected, or no detection. To reduce the possibility of detecting an animal from a neighboring site, we excluded detections whenever surveyors suspected an owl came from another territory and recorded such suspicions in the narrative on the field forms. We did not consider nesting status or reproductive success as a state for occupancy modeling because surveyors had insufficient data to determine reproduction by owls at 14 of the 33 sites where pairs were detected. When a single male was detected at a site during a survey and, during a subsequent survey, a female was detected at that same site <400 m from the male's location or vice versa, we coded the second detection status as a pair following the 1995 Pacific Southwest Region survey protocol (USFS 1995). We used data from surveys conducted >72 hr apart to ensure independence and included results from complete surveys only (i.e. when >90% of all point stations were surveyed) and omitted surveys aborted because of inclement weather or other reasons.

We calculated a naïve occupancy estimate (number of sites with detections per total number of sites surveyed) and estimated site occupancy using single-season, multi-state site occupancy statistics. Naïve occupancy is the simple proportion of total sites surveyed where the species was detected. Owls may be present at a site but not detected, however, and the ability of surveyors to detect owls may vary throughout the season or depend on whether the site is occupied by a pair or a single owl. Surveyors may also misclassify a site as occupied by a single, when in fact a pair is present at the site. Estimation of site occupancy accounts for probabilities of detection and misclassification based on repeated surveys at a given site in a given year; thus, estimates of site-occupancy probabilities are unbiased by imperfect probabilities of detection and classification during a given survey (MacKenzie et al. 2006, 2009, 2010).

We modeled occupancy using Program Presence 4.0 (USGS-Patuxent Wildlife Research Center, Laurel, MD 2006) to analyze the survey histories of the 45 historical Rim Fire Spotted Owl sites and to estimate 5 parameters: probability a site was occupied (ψ1), probability a site was occupied by a pair (ψ2), detection probability of single occupancy (p1), detection probability of pair occupancy (p2), and probability of correct classification of pair-occupied sites (δ) (MacKenzie et al. 2010). For each survey, we coded owl detections as: 0 = no detection, 1 = single owl, and 2 = pair. We divided the survey season into 2-week sampling periods (i.e. 1–15 April, 16–30 April, etc.), and assigned the highest state detected within a sampling period to the site (e.g., see Tempel and Gutiérrez 2013).

We made a site-specific covariate of occupancy and detectability as the percentage of each owl PAC burned at moderately high to high severity (hereafter referred to as "high severity"). We obtained burn severity data from the Stanislaus National Forest's 2014 Biological Assessment, Evaluation, and Wildlife Report (USFS 2014b). The USFS mapped burn severity of vegetation after the Rim Fire using Landsat TM satellite imagery and RdNBR classification (Miller and Thode 2007, USFS 2014c). Areas with ≥75% basal area mortality were categorized as moderately high to high fire severity (USFS 2014c).

We first ranked temporal models of detection (p1 and p2) and classification (δ) as all possible combinations of survey-specific (t), constant (.), and linear temporal trend (T) structure. We then ranked all possible combinations of models of detection and classification probabilities using the percent of PAC area burned at high severity as a site-specific covariate, while maintaining the same temporal structure as the best-ranked temporal model. Finally, we ranked occupancy as a function of the site-specific covariate percent of PAC burned at high severity.

We ranked all models using Akaike's Information Criterion (Burnham and Anderson 2002). Site-specific covariates were standardized by subtracting each site's value from the mean and dividing by the standard deviation (Burnham and Anderson 2002). To protect against spurious conclusions based only on a single top model and to account for model selection uncertainty, we present all results as the model-averaged parameter estimates (Burnham and Anderson 2002, Doherty et al. 2010). We presented estimates as means (±SE).

Occupancy Model Assumptions

Occupancy models rely on 4 major assumptions: (1) occupancy state is unchanged during the sampling season (also known as "closure"); (2) sites are independent, and animals do not move among sites; (3) there is no unexplained heterogeneity in detectability; and (4) there is no unexplained heterogeneity in occupancy. Regarding the first assumption, occupancy biases potentially occur in single-season models when sites are colonized or vacated during the sampling period (Kendall 1999, Otto et al. 2013), but we believe the closure assumption was not violated in our data because trend models for p were not highly ranked (Kendall 1999). Given our top model structures and our estimates of ψ and p, if colonization = 0.05 and extinction ranged from 0.0 to 0.1, then closure violation bias in ψ would be approximately +0.05 (Otto et al. 2013). Furthermore, random violations of closure do not bias estimators (Kendall 1999), but estimates in these cases correspond to sites being "used" by the species rather than "occupied" (MacKenzie et al. 2006, Kendall et al. 2013). Regarding the second assumption, some lack of independence among sites may have occurred because animals were free to move among nearby sites, but we were unable to quantify this because owls were not individually marked, although survey design and protocols should minimize this possibility. We also deleted records of owls that surveyors suspected were from outside the PAC being surveyed, but if we were not perfect in identifying such individuals, our estimates of occupancy could be biased high. For the third assumption, the standardized sampling design for Spotted Owl surveys should reduce detection heterogeneity (USFS 1995, Lee et al. 2012). We also included temporal and site-specific covariates to minimize unexplained variation in detectability (Popescu et al. 2012), but any extraneous heterogeneity in detectability would only negatively bias our occupancy estimates (MacKenzie et al. 2006). Finally, heterogeneity in occupancy is not known to cause excessively biased parameter estimates, but it can overestimate standard errors (MacKenzie et al. 2006). Our site-specific covariates also accounted for extra variation in occupancy and detectability due to fire, our main factor of interest; thus, our primary results are likely unbiased due to this effect (Popescu et al. 2012).

Because occupancy models rely on assumptions, problems with study design can bias resulting estimates and their interpretation. Tempel and Gutiérrez (2013) eliminated nocturnal detections >400 m from a site's nest or roost core area and used data from color-band resights to maximize independence among sites. USFS Spotted Owl surveyors often cannot determine nest and roost locations, and individual owls are not marked for identification because of logistical or budgetary constraints, but occupancy modeling was specifically developed to inform management using less expensive and less intensive presence–absence surveys than mark–recapture studies (MacKenzie et al. 2006). Here we provided analyses to inform post-fire forest management decisions affecting California Spotted Owls using data as they are typically collected under current USFS survey practices. The USFS survey data we used may have included some detections of owls from neighboring sites, but our estimates remain valid in terms of quantifying occupancy of PACs by owls and comparing with previous occupancy studies. The survey data also may have included some detections of nonresident "floater" owls, but these individuals are essential to the population as a source of breeding recruitment, and their use of sites should not be discounted (Franklin 1992). Any detected presence of owls from occupancy surveys, whether they are floaters or residential singles and pairs, should be interpreted as use, if not occupancy, of those forest stands (MacKenzie et al. 2006).

TABLE 1. Model selection results for multi-status, single-season occupancy modeling of California Spotted Owl breeding sites in the Rim Fire, 2014. Parameter notation: site-occupancy probability of at least one owl (ψ1), site occupancy probability of pairs (ψ2), survey-specific detection probabilities of singles (p1) and pairs (p2), and correct classification probability of pair-occupied sites (δ). ΔAIC = difference in a model's AIC relative to the AIC of the best-ranked model in the set (minimum AIC = 428.21), W = AIC Weight, a measure of the strength of evidence for a given model to be the best in the set, and k = number of parameters. "Burn" indicates a covariate model where parameter is a function of the percent of the site's PAC that burned at high severity.

Model	ΔAIC	W	k
ψ 1, ψ 2, p1(burn), p2(burn), δ(.)	0	0.23	7
ψ 1, ψ 2, p1(.), p2(burn), δ(.)	0.10	0.21	6
ψ 1(burn), ψ 2, p1(burn), p2(burn), δ(.)	0.22	0.20	8
ψ 1, ψ 2, p1(burn), p2(burn), δ(burn)	1.89	0.09	8
ψ 1(burn), ψ 2(burn), p1(burn), p2(burn), δ(.)	2.09	0.08	9
ψ 1, ψ 2, p1(.), p2(burn), δ(burn)	2.10	0.08	7
ψ 1, ψ 2, p1(.), p2(.), δ(.)	4.02	0.03	5
ψ 1, ψ 2(burn), p1(burn), p2(burn), δ(.)	5.11	0.02	8
ψ 1, ψ 2, p1(.), p2(.), δ(T)	5.79	0.01	6
ψ 1, ψ 2, p1(burn), p2(.), δ(.)	5.79	0.01	6
ψ 1, ψ 2, p1(.), p2(T), δ(.)	5.96	0.01	6
ψ 1, ψ 2, p1(.), p2(.), δ(burn)	5.99	0.01	6
ψ 1, ψ 2, p1(T), p2(.), δ(T)	7.79	0	7
ψ 1, ψ 2, p1(burn), p2(.), δ(burn)	7.86	0	7
ψ 1, ψ 2, p1(T), p2(T), δ(.)	7.96	0	7
ψ 1, ψ 2, p1(T), p2(.), δ(.)	9.43	0	6
ψ 1, ψ 2, p1(T), p2(T), δ(T)	9.74	0	8
ψ 1, ψ 2, p1(.), p2(t), δ(.)	11.18	0	14
ψ 1, ψ 2, p1(.), p2(t), δ(t)	12.94	0	15
ψ 1, ψ 2, p1(t), p2(.), δ(t)	16.10	0	15
ψ 1, ψ 2, p1(.), p2(.), δ(t)	16.63	0	14
ψ 1, ψ 2, p1(t), p2(t), δ(.)	24.97	0	23
ψ 1, ψ 2, p1(t), p2(t), δ(t)	37.59	0	32

RESULTS

All 45 sites were surveyed ≥3 times from 28 March to 5 August 2014. The median number of surveys was 5, the mean number of surveys was 6, and maximum number of surveys was 10. At one site (Middle Fork Tuolumne), 2 pairs were detected during a survey and the USFS delineated a new site (Mather), so we included these as 2 distinct sites for determining the naïve occupancy. A male owl was detected at one site (Brushy Creek), but surveyors speculated the male was from a nearby site, so we considered the status of this site to be 0 = no detection. We calculated a naïve occupancy rate of 0.848 ± 0.053 (39/46). Naïve occupancy rate of pairs was 0.717 ± 0.066 (33/46).

In our estimated occupancy analysis we excluded the owl pair detected at the new Mather site because it lacked survey data. The top-ranked model was constant occupancy, detection, and classification, with the site-specific covariate describing percent of PAC burned at high severity affecting detectability but not occupancy (Table 1). The model-averaged estimate of site-occupancy probability for at least a single owl (ψ1) was 0.922 (±0.073), after accounting for detection and classification probabilities. Mean site-occupancy probability for pairs (ψ2) was 0.866 (±0.093). Detection (p) was 0.196 for singles (±0.122) and 0.613 for pairs (±0.038). Probability that pair-occupied sites were correctly classified (δ) was 0.555 (±0.046).

Model-averaged estimates of occupancy showed a slight decrease in occupancy as the percent of PAC burned at high severity increased (ψ1 β = –0.216 ± 0.155), but occupancy when the PAC burned at 100% high severity remained higher than 0.89, and no decrease was evident for sites occupied by a pair (Figure 1). Detection probability for both singles and pairs decreased as a function of the covariate describing percent of PAC burned at high severity (p1 β = –0.871 ± 0.884; p2 β = –0.223 ± 0.087). An average of 37% (SD = 35%, range 0–100%) of the area of pre-fire 121 ha PACs burned at high severity.

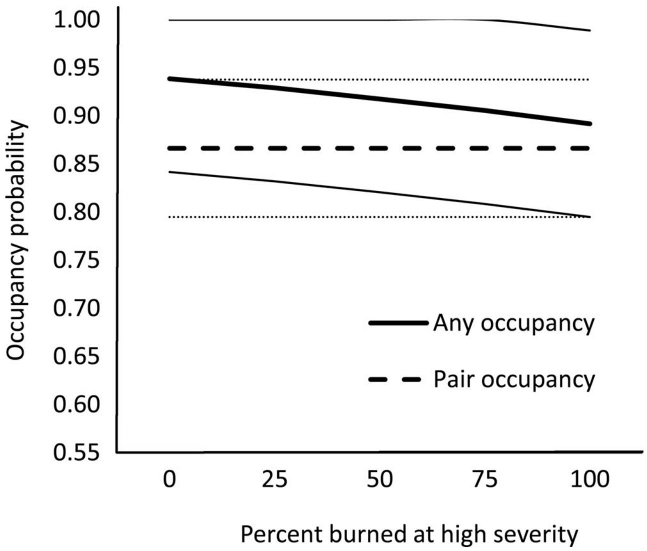

FIGURE 1. Model-averaged site occupancy probability in 2014 for occupancy by at least a single owl (thick solid line) and pairs (thick dashed line) in known California Spotted Owl sites burned during the 2013 Rim Fire. Site occupancy probability is presented as a function of the percent of the site's 121 ha Protected Activity Center that was burned at high severity. Thin solid lines and thin dotted lines are ±1 SE for any occupancy and pair occupancy, respectively.

DISCUSSION

We examined the short-term response of California Spotted Owls to a large wildfire using survey data collected by USFS biologists. We documented high occupancy probabilities for historical California Spotted Owl sites during the first breeding season after the Rim Fire. Our estimated site occupancy probability after the Rim Fire was greater than estimates from burned and long-unburned sites previously reported for the subspecies in the Sierra Nevada, although there were some differences in methods among studies. Lee et al.'s (2012) estimated annual occupancy in sites throughout the Sierra Nevada from 1997 to 2007 was 0.80 in burned forests and 0.76 in forests without recent fire and encompassed longer-term effects of up to 7 years post fire. Tempel and Gutiérrez (2013) estimated 0.67 occupancy probability in the most recent year of their study (2010) in forests of the central Sierra Nevada that were largely unaffected by recent fire.

Our occupancy estimates for California Spotted Owls after the Rim Fire could be higher, lower, or the same as pre-fire occupancy. Occupancy status was known for only 9 of the 45 sites 1 year prior to the Rim Fire and for 6 sites 2 years prior to fire (USFS personal communication). The paucity of these data preclude modeling for occupancy estimates, but naïve occupancy estimates of the 13 sites surveyed during any of the 2 pre-fire years showed: 2 sites with no detections before the fire were occupied by pairs after the fire; 1 territorial single had a mate after the fire; 8 were occupied by pairs both before and after the fire; 1 territory with a pair had a single bird after the fire; and 1 territory with a single bird before the fire became unoccupied after the fire. Therefore, 3 sites had upgraded occupancy status post-fire, 2 had downgraded occupancy status, and 8 were unchanged, which supports the hypothesis that the Rim Fire was not detrimental to Spotted Owls in the short term. We were unable to examine effects of the Rim Fire on California Spotted Owl reproduction with these data, but data from other study areas have shown no effect of fire on reproductive success in occupied burned sites (Bond et al. 2002, Roberts 2008, Lee and Bond personal communication). Longer-term monitoring of owl sites in the Rim Fire—particularly monitoring of reproduction—without the confounding effect of post-fire salvage logging within home ranges will be essential to elucidate the influence of fire-induced vegetation changes on California Spotted Owls.

Our results indicate that forests within the Rim Fire area contained adequate amounts of Spotted Owl habitat for continued post-fire occupancy in the first breeding season following the fire. Site occupancy probability is positively correlated with habitat quality when animals tend to consistently occupy the highest-quality habitats (Rodenhouse et al. 1997, Sutherland 1997, Sergio and Newton 2003) and is likely the case for California Spotted Owls in the Sierra Nevada because site occupancy, reproductive output, and apparent survival are all positively correlated with the amount of Spotted Owl habitat in a 200–800 ha area surrounding the nest (Blakesley et al. 2005). The high occupancy rates in this study could indicate that Spotted Owl territories of the Rim Fire area are (or were, prior to fire) of above-average quality relative to other burned and long-unburned sites throughout the Sierra Nevada. However, the high site fidelity of the subspecies (Gutiérrez et al. 1995, Blakesley et al. 2006) could also mean that some owls may have remained in burned territories that are no longer of high habitat quality because they had occupied the site in the previous year. Importantly, vegetation changes and subsequent changes in prey species composition and/or abundance as a result of the Rim Fire began 6 months before surveys were initiated, providing resident owls time to evaluate post-fire habitat conditions and distribute themselves accordingly (Zimmerman et al. 2003). We believe the high rates of occupancy 1 year after the Rim Fire compared favorably with other study areas, and that the post-fire increase in naïve occupancy status compared with pre-fire suggested that the burned sites retained sufficient suitable owl nesting, roosting, and foraging habitat, at least in the short term. Longer-term monitoring of these sites will determine the temporal durability of our observed high occupancy rates.

Estimated occupancy by at least a single bird in the Rim Fire was negatively correlated with amount of high-severity fire in the PAC. Spotted owls likely occupy sites according to an ideal despotic distribution, with the highest-quality sites claimed by the most dominant pairs (Fretwell 1972, Zimmerman et al. 2003). Thus, high-severity fire may have reduced occupancy only in lesser-quality sites. The amount of high-severity fire in the PAC did not affect pair occupancy, and the majority of sites (33 of 46 of the naïve estimate) were occupied by pairs. Notably, 6 pair-occupied PACs had >70% habitat burned at high severity. Thus, the occurrence of even high levels of high-severity fire within these PACs did not alter or reduce habitat such that occupancy of the site by pairs was immediately affected.

Studies from the Sierra Nevada indicate that the "complex early seral forest" created by high-severity fire, with its structural complexity such as abundant snags and downed logs, pockets of surviving trees, montane chaparral patches, and natural conifer regeneration (DellaSala et al. 2014), may provide habitat for the small mammal prey of California Spotted Owls (Bond et al. 2009, 2013). Additionally, even within high-severity fire areas, considerable numbers of overstory trees can survive the fire, often containing no green needles immediately after fire when satellite imagery is taken for fire-severity mapping but flushing with new foliage 1 year post-fire (Hanson and North 2009). The USFS (2014c) mapped areas with ≥75% basal area mortality as high severity in the Rim Fire, therefore incorporating some moderately burned stands with surviving overstory trees into the high-severity category. Thus, a substantial amount of vegetation heterogeneity can occur even within areas mapped as high severity, potentially contributing to habitat structure used by Spotted Owls, and residual pockets of surviving trees can serve as Spotted Owl nesting areas (LaHaye and Gutiérrez 1999).

Our findings add to the growing body of research that fire, even high-severity fire, is not a major threat to the persistence of California Spotted Owls in the Sierra Nevada (Bond et al. 2002, 2009, Roberts 2008, Roberts et al. 2011, Lee et al. 2012). No difference in occupancy rates was detected between 41 burned and 145 long-unburned breeding sites throughout the Sierra Nevada up to 7 years post-fire in managed national forests (Lee et al. 2012), and occupancy rates were similar between burned (within 2–15 years) and long-unburned randomly selected survey areas in unmanaged forests in Yosemite National Park (Roberts et al. 2011). Further, radio-tagged California Spotted Owls in the southern Sierra Nevada selected forest patches burned at high severity for foraging within 1.5 km of their core nest and roost areas 4 years after fire (Bond et al. 2009), and radio-tagged Mexican Spotted Owls (*S. o. lucida*) moved to wintering areas that burned 4–6 years earlier and had a greater abundance and biomass of small mammal prey than nest core areas (Ganey et al. 2014), demonstrating that high-severity fires can provide foraging benefits during both breeding and nonbreeding seasons.

In contrast to fire, multiple studies show that logging is detrimental to this declining subspecies (Seamans and Gutiérrez 2007, Tempel et al. 2014), even when the largest trees and a minimum of 40% canopy cover is retained (Stephens et al. 2014). Post-fire logging also apparently reduces site occupancy; Lee et al. (2012) reported 7 sites that were burned and later salvage-logged were occupied by owls after the fire but not after logging. Tempel et al. (2014) compared occupancy dynamics in 12 burned sites relative to 62 unburned sites over 7 years and concluded that burned sites had lower colonization rates, but this inference suffered from small sample size (5 of 9 sites burned in the largest fire remained occupied every year post-fire so were unavailable for colonization), and post-fire salvage logging occurred in the remaining sites (M. Bond personal communication), which confounded the effects of fire with logging.

Our results indicate that managers should not immediately assume Spotted Owls vacate burned sites, even with large areas of high-severity fire in a PAC. We believe it is valid to reconfigure PACs after high-severity fire to incorporate and conserve closed-canopy nesting–roosting–foraging habitat because this important habitat type can be patchily distributed in the vicinity of owl nests or roosts, especially after fire. However, conservation of burned foraging habitat is also likely necessary to maintain site occupancy. Results from this and other studies suggest that the most prudent course of action is to forgo logging activities in burned forests within 1.5 km of the post-fire nest or roost core to provide easily accessible potential foraging habitat within the larger home range (Bond et al. 2009). Lee et al. (2012) recommended a minimum of 2 years of adequate occupancy surveys to demonstrate that owls are no longer occupying a site, but the probability that unoccupied burned sites were recolonized by owls was 0.381 per year (±0.051), so even post-fire unoccupied sites stand a good chance of being utilized in the future. Therefore, we also suggest retaining burned sites within the PAC network for the conservation and recovery of this declining subspecies. Overall, we encourage land managers to recognize fire as a natural rejuvenating process of Sierra Nevada forests (DellaSalla et al. 2014) and to no longer assume burned forest is unsuitable California Spotted Owl habitat when planning and implementing management activities in PACs and HRCAs.

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