



RESEARCH ARTICLE

## Previous year's reproductive state affects Spotted Owl site occupancy and reproduction responses to natural and anthropogenic disturbances

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### ABSTRACT

Understanding interactions among site occupancy, reproduction, vegetation, and disturbance for threatened species can improve conservation measures, because important aspects of vegetation and disturbances may be identified and managed. We used 9 yr of survey data collected at 168 sites to investigate dynamic site occupancy and reproduction in a declining population of California Spotted Owls (*Strix occidentalis occidentalis*) in southern California, USA. We used multistate models to examine the relationship among owl site occupancy, reproduction, high-severity wildland fire, and postfire logging, while accounting for variation in vegetation characteristics and variation in detectability. Both occupancy and reproduction were positively correlated with successful reproduction in the previous year. Tree cover (ha) in a site's 203-ha core area also was positively correlated with both occupancy and reproduction. We detected no effect of disturbance covariates on reproduction, given that a site was occupied. Fire and logging covariates were both negatively correlated with the probability of site occupancy, and the effect sizes of these disturbances were large in sites that were occupied by owls that were nonreproductive the previous year (reduced 0.19 by fire and 0.26 by post-fire logging), but small in sites that were occupied by owls that were reproductive the previous year (reduced 0.02 by fire and 0.03 by postfire logging). This study illustrates the important contribution of consistently occupied and productive breeding sites to this population of Spotted Owls, and demonstrates that both occupancy and reproduction at these productive sites exhibited negligible effects from disturbances. Our results suggest that sites with recent owl reproduction and sites with more tree cover in this study area should receive enhanced protection from management actions that modify vegetation utilized by Spotted Owls.

**Keywords:** Spotted Owl, occupancy, reproduction, fire, logging, southern California

### El estado reproductivo del año anterior afecta la ocupación de sitios y la respuesta reproductiva de *Strix occidentalis* a los disturbios naturales y antrópicos

### RESUMEN

Entender las interacciones entre la ocupación de sitios, la reproducción, la vegetación y los disturbios puede mejorar las medidas de conservación de las aves en peligro ya que importantes aspectos de la vegetación y de los disturbios pueden ser identificados y manejados. Empleamos 9 años de datos de muestreo colectados en 168 sitios para investigar la dinámica de ocupación de sitios y la reproducción en una población en disminución de *Strix occidentalis occidentalis* en el sur de California. Empleamos modelos de estado múltiple para examinar la relación entre la ocupación de sitios, la reproducción, los fuegos de gran intensidad de ambientes silvestres y el aprovechamiento forestal post-incendio, mientras consideramos las variaciones en las características de la vegetación y en la detectabilidad. La ocupación y la reproducción se correlacionaron positivamente con una reproducción exitosa en el año anterior. Las hectáreas de cobertura arbórea en un sitio de 203 ha de área núcleo también se correlacionaron positivamente con la ocupación y la reproducción. Considerando que un sitio estaba ocupado, no detectamos un efecto de las covariables del disturbio sobre la reproducción. Las covariables de fuego y aprovechamiento forestal estuvieron negativamente correlacionadas con la probabilidad de ocupación del sitio, y los efectos del tamaño de estos disturbios fueron grandes en los sitios que no fueron usados para reproducción en el año anterior (reducido 0.19 por fuego y 0.26 por aprovechamiento forestal post-incendio), pero fueron pequeños en los sitios usados previamente para reproducción (reducido 0.02 por fuego y 0.03 por aprovechamiento forestal post-incendio). Este estudio ilustra la contribución significativa de los sitios constantemente ocupados y usados para reproducción para esta población de *S. occidentalis*. La ocupación y la reproducción en estos sitios productivos no se vieron afectados por los disturbios. Nuestros resultados sugieren que los sitios reproductivos y los sitios con más cobertura arbórea en esta área de estudio deberían recibir una mayor protección a partir de acciones de manejo que modifiquen la vegetación utilizada por *S. occidentalis*.

**Palabras clave:** aprovechamiento forestal, fuego, ocupación, reproducción, *Strix occidentalis*, sur de California

## INTRODUCTION

Analyzing patterns of site occupancy and reproduction for territorial species can improve conservation measures, because characteristics of the landscape that are important to the species can be identified, measured, and, if possible, managed (Conroy et al. 1995, Dunning et al. 1995, Hurme et al. 2008). The importance of a territory, or breeding site, is best defined by the survival and reproduction of individuals who occupy the site through time (Van Horne 1983, Newton 1989, Franklin et al. 2000), but the site's capability to support occupancy or reproduction may be temporally dynamic as a result of natural and anthropogenic disturbance events (Sutherland 1998, Lee et al. 2012, 2013).

Methods are now well developed for using presence–absence survey data to estimate site occupancy and reproduction probabilities, while accounting for imperfect detectability and state misclassification and incorporating both time- and site-specific vegetation covariates (Nichols et al. 2007, MacKenzie et al. 2009, 2010). Multistate modeling provides a useful measure of productivity by estimating the probability that young are produced at a site, while accounting for imperfect detectability and examining the effects of a site's state during the previous year: (1) vacant, (2) occupied with no young, or (3) occupied with young. Within this framework, we examined the effects of vegetation and disturbance interactions on site occupancy and reproduction for an important indicator of late-seral forests, the California Spotted Owl (*Strix occidentalis occidentalis*), in southern California, USA.

Site occupancy and reproduction of California Spotted Owls are influenced by site-specific vegetation characteristics (Blakesley et al. 2005, Seamans and Gutiérrez 2007). Wildland fire is a major natural disturbance that has affected forests within the range of the Spotted Owl for millennia, with varying pattern, frequency, and intensity across forest types, regions, and time (Swanson et al. 2011). High-severity fires—also called stand-replacement or crown fires—cause widespread mortality of existing vegetation and result in a forest structure no longer dominated by live trees but by herbs, shrubs, and dead trees (Swanson et al. 2011). Only high-severity fires burn intensely enough to initiate ecological succession and restore essential habitat for a variety of fire-dependent and early-seral-stage species (Smucker et al. 2005, Kotliar et al. 2007, Hutto 2008, Fontaine et al. 2009), but data are scarce regarding the specific effects of this type of fire on wildlife characteristically associated with older forests, such as the Spotted Owl. Furthermore, high-severity burned forest is frequently logged—often called 'salvage logging'—which has additional effects on wildlife (Lindenmayer et al. 2004).

Vegetation disturbances such as timber harvest (Seamans and Gutiérrez 2007) and high-severity fire (Lee et al.

2013) may adversely affect the site occupancy dynamics of California Spotted Owls when alterations of forest within a territory exceed a certain threshold. Alternatively, these disturbances may have positive effects on occupancy (Lee et al. 2012) or reproduction (Franklin et al. 2000) by creating heterogeneity, such as complex early seral stands that are used for foraging (Bond et al. 2009) interspersed with older forest stands that are required for nesting and roosting (Gutiérrez et al. 1992).

Site occupancy and reproduction also could be correlated with the state of the site in the previous year. The probability of a site being occupied or supporting reproduction in a given year could be lower when young were produced the previous year because of 'resource depletion' in the territory (Carey et al. 1992, Ganey et al. 2014). Conversely, the probability of a site being occupied or supporting reproduction in a given year could be greater when young were produced the previous year if the site's capability to support occupancy and reproduction ('reproductive capability') is consistently high (Przybylo et al. 2001). The effect of the previous year's state also could vary among years in a complex interaction of state and time (MacKenzie et al. 2009, 2010), or could be absent (no effect of previous year's state).

We investigated dynamic site occupancy and reproduction of California Spotted Owls over a 9-yr period in relation to site-specific vegetation and topographic characteristics, and in response to the disturbances of high-severity wildland fire and postfire logging, in the San Bernardino and San Jacinto mountains of southern California, where populations have declined over the past 2 decades (LaHaye et al. 1994, 2004, Lee et al. 2013). We examined the influence of site- and year-specific covariates of the amount and structure of vegetation, which varied spatially because of climate and geography and temporally because of natural and human-caused disturbances. We performed multistate model selection and estimated the dynamic probability of annual occupancy and reproduction by Spotted Owls in known sites according to the reproductive state of the owls in the site in the previous year, and according to dynamic site-specific vegetation disturbance covariates that we used to classify sites as: (1) unburned, (2) burned and not logged postfire, or (3) burned and logged postfire. All burned sites were surveyed before and after fires, so that prefire occupancy and reproduction data existed for a before–after control–impact analysis (Popescu et al. 2012).

We did not know which owls occupied a given site in our study because birds were not individually marked. Thus, herein we consider occupancy, reproduction, and effects of previous year's state to be characteristics of the site, and these were our metrics of the site's capability to support reproduction in relation to disturbance covariates.

## METHODS

### Study Area

The San Bernardino Mountains (SBM) and San Jacinto Mountains (SJM) are located ~140–150 km east of Los Angeles, California. The climate is Mediterranean, with most precipitation (500–1,000 mm per year) falling during the winter as rain at lower elevations and as rain and snow at higher elevations (Minnich 1988).

In southern California, Spotted Owls inhabit isolated upper-elevation (915–1,525 m) forests surrounded by lower-elevation desert and semidesert vegetation (Gutiérrez and Pritchard 1990, Gutiérrez et al. 1992, LaHaye et al. 1994, 1997, 2001). Forest fires in these southern Californian forests occur largely as a result of human-caused ignition (Halsey 2005) and typically burn in a mosaic of severities (Weatherspoon et al. 1992, Stephenson and Calcarone 1999), with the largest high-severity fires burning under extreme Santa Ana weather conditions typical of the region (Keeley et al. 2009). Fire has been proposed as a factor in the regional Spotted Owl population decline (LaHaye and Gutiérrez 2005), although empirical evidence is lacking.

In the period 2003–2011, a large proportion (0.42) of Spotted Owl breeding sites in the SBM were affected by wildland fire, which occurred during drought conditions and warmer-than-average temperatures. Two large fires in 2003 and 2007, and several smaller fires during this period, burned through 71 of 181 owl sites that were regularly monitored by U.S. Forest Service biologists. Postfire logging occurred on a subset of 21 sites, and provided us with the opportunity to examine the effects of high-severity fire and postfire logging on Spotted Owl dynamic breeding site occupancy and reproduction from 2003 to 2011.

### Spotted Owl Surveys

We defined an owl site as a distinct geographical area deemed to be occupied by seeing or hearing a single or pair of territorial Spotted Owls during surveys from 1989 to 2001. From 1989 to 2001, 181 California Spotted Owl sites within the boundaries of the San Bernardino National Forest in the SBM and SJM (2,140 km<sup>2</sup>) were identified by annually surveying all forested stands (LaHaye et al. 2004, Gutiérrez et al. 2011). For our study, each year from 2003 through 2011, the U.S. Forest Service attempted to survey as many known Spotted Owl sites as possible from March 1 to August 31, following standardized methods described by Forsman (1983) and Franklin et al. (1996). The U.S. Forest Service provided us with the raw survey data, which we then used to construct an occupancy history database. Because we did not collect data ourselves, we acknowledge that there may be problems with the data that are unknown to us. We

analyzed the data from sites surveyed for >2 consecutive years from 2003 to 2011 ( $n = 168$  sites). Our population of interest was historical Spotted Owl sites that were subsequently burned (or not burned) by fire, so it was appropriate to use data from sites where occupancy status had been previously established, rather than from randomly selected sites where previous occupancy status was unknown (MacKenzie and Royle 2005).

Within each year, 2 types of surveys were conducted: (1) presence–absence surveys to initially locate owls in an area, and (2) reproductive surveys to find roosts and nests and to assess the reproductive status of owls detected during presence–absence surveys. All surveys were separated by >48 hr. The presence–absence surveys were conducted by imitating Spotted Owl vocalizations between dusk and dawn from a series of fixed calling stations. If a Spotted Owl responded during a nighttime survey, the presence–absence survey ended, and dusk or dawn reproductive surveys were conducted. Reproduction was estimated by feeding owls live mice (Forsman 1983, Franklin et al. 1996). Successful reproduction was documented when at least 1 owlet was observed outside the nest. A maximum of 6 presence–absence surveys and 4 reproductive surveys were conducted at Spotted Owl sites every year.

The maximum number of surveys at any site in a year was 8, but both the median and mode number of visits across all sites each year was 6, so we truncated all within-year survey histories at 6 surveys for this analysis to reduce the number of missing observations (Olson et al. 2005, Kroll et al. 2010).

### Characteristics of Sites

We quantified site-specific vegetation covariates as hectares within a 203-ha circular ‘core area’ around the most recently used Spotted Owl nest tree location or roost centroid (geometric mean of roost locations) for the following variables: total tree cover; amount of coniferous, hardwood, and old-growth ( $\geq 5$  trees ha<sup>-1</sup> with crown diameter >9 m) forest; and area of riparian vegetation. The core area was approximately half of the average breeding-season home-range size for California Spotted Owls in the SBM (Zimmerman et al. 2001), and was intended to represent the area of most concentrated use by Spotted Owls during the breeding season (Blakesley et al. 2005, Lee et al. 2012, 2013). We also assigned a site-specific topographic covariate for elevation at the nest tree or roost centroid for each site. Table 1 shows the definitions of our temporal and vegetation covariates.

We used a landscape-level vegetation map developed by GIS analysts from the U.S. Forest Service’s Adaptive Management Services Enterprise Team (AMSET). The base map consisted of a layer of joined and orthorectified 1-m resolution infrared aerial photographs taken of the

**TABLE 1.** Temporal and vegetation covariates used in modeling detection, occupancy, and reproduction of California Spotted Owls in the San Bernardino Mountains, California, USA, 2003–2011. Predicted effects were: x = no prediction, but effect could be present; + = positive correlation predicted between covariate and parameter; – = negative correlation predicted; +/- = either positive or negative correlation predicted. If predicted effect is blank, the covariate was not modeled for that parameter.

Covariate name	Type	Definition	Predicted effect on parameter				
			$\delta$	$p1$	$p2$	$C\psi$	$CR$
<i>Survey</i>	Binomial	Within-year, survey-specific variation coded as 5 categorical dummy variables.	x	x	x		
<i>S</i>	Continuous	Linear within-year temporal trend according to survey.	x	x	x		
<i>S2</i>	Continuous	Quadratic within-year temporal trend according to survey.	x	x	x		
<i>S1diff</i>	Binomial	First survey in a year is different from subsequent surveys.	x	x	x		
.	Constant	Constant parameter value through time coded as an intercept only (used within and among years).	x	x	x	x	x
<i>Year</i>	Binomial	Year-specific annual variation coded as categorical dummy variables (7 variables in $C\psi$ and $CR$ ; 8 in $\delta$ , $p1$ , and $p2$ ).	x	x	x	x	x
<i>Y</i>	Continuous	Linear annual temporal trend.	x	x	x	x	x
<i>Y<sup>2</sup></i>	Continuous	Quadratic annual temporal trend.	x	x	x	x	x
<i>EO</i>	Binomial	Even-odd year effect where alternate years are coded 1 or 0.	x	x	x	x	x
<i>SB</i>	Binomial	Difference between SBM and SJM study sites.	x	x	x	x	x
<i>Elev</i>	Continuous	Site elevation standardized as (elevation – mean) / SD [mean = 0, range = –3 to 3].				+	+
<i>Rip</i>	Continuous	Amount of riparian vegetation computed as hectares in 203-ha core area [mean = 13, range = 0 to 96].	–	–	–	+	+
<i>Tree</i>	Continuous	Amount of tree cover computed as total hectares of conifer and hardwood tree cover in 203-ha core area [mean = 106, range = 44 to 149].				+	+
<i>OG</i>	Continuous	Late-seral stage ‘old growth’ trees in a 203-ha core area computed as hectares with $\geq 5$ large trees (>9 m crown diameter) [mean = 30, range = 0 to 148].				+	+
<i>HW</i>	Continuous	Amount (ha) of hardwood tree cover in 203-ha core area [mean = 63, range = 0 to 130].				+	+
<i>Burn</i>	Binomial	Intercept effect of fire between 2003 and 2011 coded 0 in unburned sites in all years, 0 in burned sites in prefire years, and 1 in burned sites in postfire years.	+	+	+	–	+/-
<i>Hisev</i>	Continuous	The amount of suitable forest vegetation burned at high severity within a 203-ha core area [mean = 44, range = 0 to 140].				+/-	+/-
<i>Hisev<sup>2</sup></i>	Continuous	The square of <i>hisev</i> , used to model occupancy and reproduction as a quadratic function of the amount of suitable forest vegetation burned at high severity.				+/-	+/-
<i>Salvage</i>	Continuous	Amount (ha) of burned forest clear-cut postfire [mean = 63, range = 0 to 150].				–	–

entire San Bernardino National Forest in 2002. Vegetation was mapped within the Spotted Owl core area circles with a minimum map unit of  $\sim 2$  ha.

We defined burned Spotted Owl sites as those in which the core area was inside or included the perimeter of one of the fires. M. Borchert and C. Hanson provided us with vegetation change data for our analyses. M. Borchert determined the number of hectares of tree cover that burned at high severity by overlaying burn severity and vegetation maps to quantify change in tree cover resulting from fire. High-severity fire induced changes in dominant vegetation by killing  $\geq 75\%$  of trees. C. Hanson quantified postfire logging using aerial photographs, obtained from Google Earth, by imposing a grid of 1-ha cells in the 203-ha circle around the nests or roost centroids and estimating the amount of the circle affected by extensive (i.e. clear-cut) postfire tree removal.

### GIS Map Accuracy Assessment

To confirm the GIS base map's accuracy in representing the vegetation variables in our analysis, we used field data collected by AMSET biologists within 81 variable-radius plots in 15 randomly selected owl sites. For each owl site, 6 plots were located at fixed distances in randomly selected directions from the most recently occupied nest tree. Plots ranged from a minimum distance of 50 m to a maximum distance of 500 m from the nest. At each plot, AMSET biologists estimated the number of large trees per acre and percent tree cover, and we compared these values (after conversion to hectares) with classifications of those covariates at the same locations from the landscape-level map. We considered percent tree cover to be accurate if the map's estimate was within 10% of the ground-plot estimate. Producer's accuracy was 63% for large tree density and 68% for percent tree cover, and user's accuracy was 58% for large tree density and 64% for percent tree cover. Our map accuracy was somewhat lower, but still comparable to other remotely sensed maps used to analyze Spotted Owl habitats (e.g., accuracy for mature conifer forests = 50–84%, Clark 2007; and 50–71%, Williams et al. 2011).

### Statistical Analysis

We used raw survey data to compile occupancy histories for 168 California Spotted Owl sites. Our 9-yr dataset included 97 unburned control sites and 71 burned sites, of which a subset of 21 were logged postfire. We created occupancy histories in which each survey of each site was coded according to observed state: '0' for no Spotted Owls observed, '1' for  $>0$  adults observed, and '2' for  $>0$  owlets observed outside the nest. We used program Presence 4.0 (USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA) to fit models and estimate parameters from occupancy histories following methods developed by MacKenzie et al. (2009, 2010). Readers are directed to

those papers for more detail on the statistical foundation and methods.

We modeled the process that gave rise to our detection history data using the following notation and parameters (from MacKenzie et al. 2009, 2010):  $\psi$  = the probability that the area was occupied by the species during the first year of the study;  $R$  = the probability that successful breeders were present in the first year of the study, given that the area was occupied by the species;  $C\psi x_i$  = the probability that the area was occupied in year  $i$ , conditional upon state ( $x = 0, 1$ , or  $2$ ) in year  $i - 1$ ;  $CRx_i$  = the probability that successful breeders were present in year  $i$ , conditional upon state ( $x = 0, 1$ , or  $2$ ) in year  $i - 1$ ;  $p1_i$  = the probability of detecting adult nonbreeders or unsuccessful breeders in year  $i$ ;  $p2_i$  = the probability of detecting successful adult breeders in year  $i$ ; and  $\delta_i$  = the probability of correctly identifying reproduction (observing young) in year  $i$ , given presence ( $1 - \delta_i$  = the misclassification parameter).

**Model selection.** Because we had a large number of temporal and vegetation covariates to consider in detection, occupancy, and reproduction parameters, we adopted a multistage process to build models, similar to the methods in Olson et al. (2005), MacKenzie et al. (2010), and Dugger et al. (2011). We selected the best model within each stage using Akaike's Information Criterion adjusted for small sample size ( $AIC_c$ ) to rank models (Burnham and Anderson 2002), and the best model structure from a given stage was then used in subsequent stages. Model selection proceeded as follows (a full table of model selection is provided in [Supplementary Material Table S1](#)):

- (1) First, we tested for within-year, survey-specific temporal variability in detection probabilities ( $p1$ ,  $p2$ , and  $\delta$ ), while holding occupancy and reproduction in their fully time-dependent forms (*state \* year*). Detection probabilities could vary because of survey-specific differences in survey staff, weather conditions, and other unmeasured factors. We considered 5 different models of within-year temporal variation: survey-specific (*survey*), constant ( $\cdot$ ), linear trend ( $S$ ), quadratic trend ( $S^2$ ), and first survey different from all subsequent surveys (*s1diff*). These models are typical temporal models that have been used in previous occupancy analyses of Spotted Owls (Olson et al. 2005, Dugger et al. 2011).
- (2) We examined whether and how previous year's reproductive state was correlated with current year's occupancy and reproduction by ranking 6 state models. Each model's structure represented a competing hypothesis. The model (*year*) represented no correlation between previous year's state and current year's occupancy or reproduction, so all states were equivalent. The model (*state + year*) represented a

correlation between previous year's state and current year's occupancy or reproduction that was consistent through time, and the competing hypotheses of 'resource depletion' or 'reproductive capability' of a site were differentiated by whether sites that were previously occupied by nonreproductive vs. reproductive owls had greater occupancy and reproduction probabilities. If site occupancy and reproduction probabilities varied because of previous state, such that nonreproductive > reproductive, then 'resource depletion' would be supported. If the opposite (reproductive > nonreproductive) occurred, then 'reproductive capability' would be supported. The model ( $state * year$ ) indicated a complex interaction of state and time (MacKenzie et al. 2009, 2010).

- (3) We examined among-year annual temporal variability in detection probabilities ( $p1$ ,  $p2$ , and  $\delta$ ), while holding occupancy and reproduction in their previously determined best state- and time-dependent forms ( $state + year$ ). Parameters were modeled as year-specific ( $year$ ), a linear year trend ( $Y$ ), a quadratic year trend ( $Y^2$ ), an even-odd year effect ( $EO$ ), and constant (.). We expected that detection, occupancy, and reproduction probabilities could exhibit annual variation due to fluctuations in weather or prey populations, and similar temporal model structures have been detected in previous studies of Spotted Owl occupancy or reproduction (Franklin et al. 2000, Seamans et al. 2002, LaHaye et al. 2004, Blakesley et al. 2010, Lee et al. 2013).
  - (4) We tested for among-year annual temporal variability in occupancy and reproduction probabilities, while holding detection probabilities in their best previously determined structures. Parameters were modeled as in step 3 above.
  - (5) We tested for the effects of fire and study area covariates on detectability. We included site-specific covariates of detection probabilities for burned vs. unburned sites ( $burn$ ), and differences between study areas ( $SB$ ).
  - (6) We investigated prefire vegetation covariate models of occupancy probability. We included 6 site-specific core area vegetation covariate models of occupancy: hectares of tree cover ( $tree$ ), hectares of hardwood tree cover ( $HW$ ), hectares of late-seral 'old growth' ( $OG$ ), hectares of riparian vegetation ( $rip$ ), elevation ( $elev$ ), and differences between the San Bernardino and San Jacinto mountains ( $SB$ ).
- California Spotted Owls are typically associated with habitats characterized by large trees and high canopy cover (Gutiérrez et al. 1992, Blakesley et al. 2005, Seamans 2005), and previous work has documented occupancy dynamics related to the site-specific amount of tree cover and elevation (Lee et al. 2013). Therefore,

we predicted that occupancy would be positively correlated with the amount of tree cover ( $tree$ ) or 'old growth' ( $OG$ ) within 203 ha of the nest or roost centroid. We expected elevation ( $elev$ ) to be negatively correlated with occupancy probability because of gradients in vegetation type, prey biomass (Smith et al. 1999), and climate (LaHaye et al. 2004). Spotted Owls seek cool roosting sites during periods of warm weather as an adaptation to heat stress (Barrows 1981), and radio-tagged Northern Spotted Owls (*S. o. caurina*) in dry forests of southwestern Oregon select foraging locations closer to perennial streams (Clark 2007); therefore, we predicted that occupancy would be positively correlated with the amount of riparian vegetation ( $rip$ ). Our model set also included 3 models of occupancy with >1 vegetation covariate: ( $tree + elev$ ), ( $tree + rip$ ), and ( $tree + OG$ ); and 5 models of reproduction with >1 vegetation covariate: ( $tree + elev$ ), ( $tree + rip$ ), ( $tree + OG$ ), ( $tree + SB$ ), and ( $tree + elev + OG$ ).

- (7) We examined prefire vegetation covariate models of reproduction probability. We predicted that there would be site-specific, vegetation-related effects on reproduction, such that elevation ( $elev$ ) would be negatively correlated with reproduction (LaHaye et al. 1997, Blakesley et al. 2005), and that the following covariates would be positively correlated with reproduction: tree cover ( $tree$ ; Blakesley et al. 2005, Forsman et al. 2011), hardwood tree cover ( $HW$ ; LaHaye et al. 1997), 'old growth' ( $OG$ ; Blakesley et al. 2005), and riparian vegetation ( $rip$ ; Clark 2007).
- (8) We tested high-severity fire and postfire logging covariate models of occupancy probability. We ranked 6 models of fire and postfire logging effects. We modeled fire effects as a postfire change in intercept ( $burn$ ), and with continuous covariates of vegetation change from high-severity fire as linear ( $burn + hisev$ ) and quadratic ( $burn + hisev^2$ ) functions of the hectares of trees killed by fire within the core area. We modeled the intercept effect of fire between 2003 and 2011 as a time-varying, site-specific, categorical covariate that was coded 0 for unburned sites in all years, 0 for burned sites in years before the fire, and 1 for burned sites in years after the fire. All fires burned after surveys ended for the year, so fire did not affect within-season conditions in this study.

Linear and quadratic covariates of tree cover burned at high severity were previously shown to affect California Spotted Owl site occupancy in southern California (Lee et al. 2013). We included a site-specific covariate for postfire logging ( $burn + salvage$ ) as a linear function of the hectares of postfire clear-cut within the core area. Our model set also included ( $burn + hisev^2 + salvage$ ), and a null (no fire effects) model.

(9) Finally, we tested fire and postfire logging covariate models for reproduction probabilities that were the same as for occupancy probabilities in step 8 above.

We assessed support for models of the effects of vegetation, high-severity fire, and postfire logging on occupancy, reproduction, and detection parameters using  $AIC_c$  weights (Burnham and Anderson 2002, Doherty et al. 2010). The effect of a specific covariate was inferred to be significant when the 95% confidence interval of the beta coefficient did not include zero.

## RESULTS

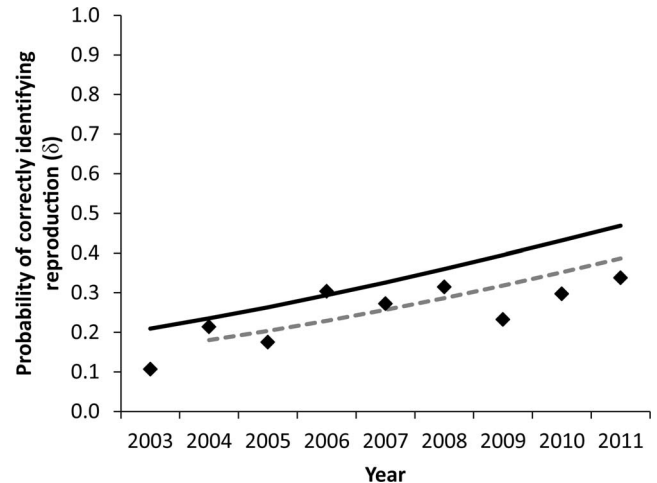
The mean number of Spotted Owl sites surveyed each year (2003–2011) that had also been surveyed in the previous year was 76 for unburned sites ( $SD = 24$ , minimum = 39) and 52 for burned sites ( $SD = 16$ , minimum = 31). In years after the first fire burned in 2003, the mean annual proportion of surveyed sites that were in the burned group was 0.37 ( $SD = 0.09$ ).

### Site-Specific Covariates

The mean amount of prefire tree cover within all (168) core areas was 106 ha ( $SD = 24$ , range = 44–149). The mean amount of tree cover that burned at high severity within the 71 burned core areas was 24 ha ( $SD = 31$ , range = 0–120). Postfire logging occurred on 21 burned sites. The mean amount of postfire logging in logged burned sites was 63 ha ( $SD = 53$ , range = 0–150). Sites at higher elevations tended to support a greater amount of tree cover prefire ( $t_{167} = 2.77$ ,  $P = 0.006$ ), but among burned sites the amount of tree cover burned at high severity within a core area was similar at all elevations ( $t_{70} = -1.19$ ,  $P = 0.23$ ).

### Detection

The top-ranked model of detection probability was  $\{\delta(Y + s1diff + burn + SB), p1(year + . + burn + SB), p2(year + s1diff + burn + SB)\}$ , which indicated that the probability of correctly identifying reproduction ( $\delta$ ) increased linearly across years (Figure 1), and that, within years, the probability of correctly identifying reproduction was significantly lower during the first survey than in all subsequent surveys (mean 1<sup>st</sup> survey  $\hat{\delta} = 0.012$ , mean 2<sup>nd</sup>–6<sup>th</sup> surveys  $\hat{\delta} = 0.331$ ). The probability of detecting owls given that they were unsuccessful or nonbreeders ( $p1$ ) varied annually (Figure 2), but was constant within years (mean  $\hat{p1} = 0.315$ ). The probability of detecting owls given that they were successful breeders ( $p2$ ) varied annually (Figure 2), and, within years, the probability of detecting owls during the first survey was significantly lower than in all subsequent surveys (mean 1<sup>st</sup> survey  $\hat{p2} = 0.756$ , mean 2<sup>nd</sup>–6<sup>th</sup> surveys  $\hat{p2} = 0.873$ ). Beta coefficients and 95%



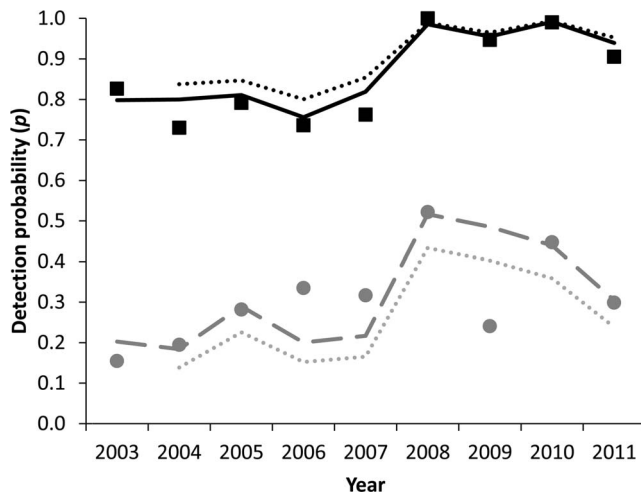
**FIGURE 1.** The probability of correctly identifying reproduction ( $\delta$ ) during surveys for California Spotted Owls in unburned sites (solid black line) increased linearly across years in the San Bernardino Mountains, California, USA. There was a lower probability of correctly identifying reproduction in sites that burned (dashed gray line). Linear estimates are from the top-ranked model (Supplementary Material Table S1). Black diamonds are annual estimates of  $\delta$  from the fully parameterized (state \* year) model of all parameters.

confidence intervals are presented in Supplementary Material Table S2.

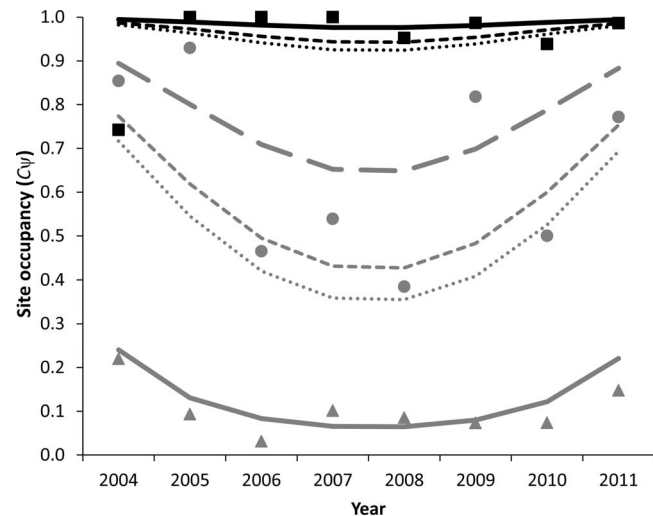
The probability of correctly identifying reproduction ( $\delta$ ) in burned sites was 0.068 lower than in unburned sites, the probability of detection of unsuccessful or nonbreeders ( $p1$ ) was 0.063 lower in burned sites relative to unburned sites, and the probability of detection of successful breeders ( $p2$ ) was 0.024 greater in burned sites relative to unburned sites (Figures 1 and 2). Although none of the effects of high-severity burns on detection probabilities were statistically significant (Supplementary Material Table S2), we retained these effects on detection probabilities when modeling occupancy and reproduction because they were present in most of the top detection probability models, and because ignoring covariates of detection probabilities can introduce biased results into the main effects of interest (Popescu et al. 2012). The SBM study area had significantly greater  $\delta$ ,  $p1$ , and  $p2$  than the SJM study area (Supplementary Material Table S2).

### Occupancy and Reproduction

**Influence of previous state.** Reproductive state in the previous year was significantly correlated with the current year's occupancy and reproduction (Supplementary Material Table S1, section 2). Occupancy and reproduction probabilities were consistently much greater for sites that were occupied by reproductive owls in the previous year vs. sites that were previously occupied by nonreproductive



**FIGURE 2.** The probability of detecting California Spotted Owls at occupied sites in which owls were either reproductive ( $p_2$ , solid black line) or nonreproductive ( $p_1$ , dashed gray line) in the San Bernardino Mountains, California, USA, 2003–2011. In sites that burned, there was a lower probability of detecting nonreproductive owls (dotted gray line) and a higher probability of detecting reproductive owls (dotted black line). Linear estimates are from the top-ranked model (Supplementary Material Table S1). Squares (■) and filled circles (●) are year-specific estimates of  $p_2$  and  $p_1$ , respectively, from the fully parameterized (state \* year) model of all parameters.



**FIGURE 3.** California Spotted Owl dynamic occupancy probability ( $C_{ij}$ ) at sites which in the previous year supported reproductive owls (state 2, solid black line), nonreproductive owls (state 1, long-dashed gray line), or were vacant (state 0, solid gray line) in the San Bernardino Mountains, California, USA, 2004–2011. There was a reduced probability of occupancy in sites that burned relative to unburned sites (state 2, short-dashed black line; state 1, short-dashed gray line), and site occupancy was further reduced by postfire logging (state 2, dotted black line; state 1, dotted gray line), but the effect sizes were much smaller in sites that previously supported reproductive owls (black lines). Linear estimates are from the top-ranked model (Supplementary Material Table S1). Squares (■), filled circles (●), and triangles (▲) are year-specific estimates of occupancy for the 3 states from the fully parameterized (state \* year) model of all parameters.

owls or vacant (Figures 3 and 4). This result supports the ‘reproductive capability’ hypothesis.

The top-ranked temporal model was  $C\psi(\text{state} + Y^2)$  and  $CR(\text{state} + \text{year})$ . Mean initial site occupancy probability was  $\hat{\Psi} = 0.65$ , and mean initial probability of reproduction was  $\hat{R} = 0.56$ . Mean state-dependent occupancy probability was  $\widehat{C\Psi} = 0.126, 0.759, \text{ and } 0.985$  for sites which in the previous year were vacant, held nonreproductive owls, and held reproductive owls, respectively. Mean state-dependent reproductive probability was  $\widehat{CR} = 0.048, 0.283, \text{ and } 0.819$  for sites which in the previous year were vacant, held nonreproductive owls, and held reproductive owls, respectively. The coefficient of variation (SD / mean across all years) in reproduction probability was  $R\ CV = 0.76, 0.56, \text{ and } 0.13$  for sites which in the previous year were vacant, held nonreproductive owls, and held reproductive owls, respectively.

**Prefire vegetation.** The top-ranked vegetation covariate model of occupancy was  $C\psi(\text{tree} + \text{elev})$ , and the second-ranked model was  $C\psi(\text{tree})$ .  $CR(\text{tree})$  was the only statistically significant vegetation covariate of occupancy or reproduction (Supplementary Material Table S2).

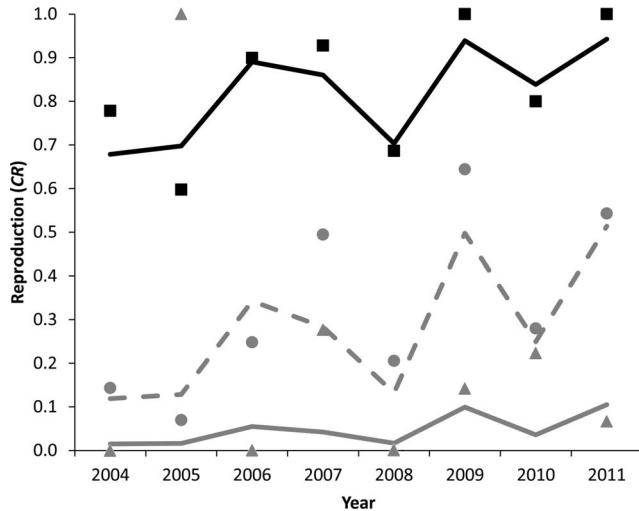
**Fire and logging.** The top-ranked model of the effects of fire on occupancy revealed significantly lower occupancy in burned vs. unburned sites, and showed that occupancy was further significantly reduced according to

how much of the core area was logged postfire (Figure 3, Supplementary Material Table S2). The occupancy of sites that supported reproductive owls the previous year was reduced 0.02 by fire and 0.03 by postfire logging. The occupancy of sites that were occupied by nonreproductive owls the previous year was reduced 0.19 by fire and 0.26 by postfire logging. The top-ranked model of fire and logging effects on reproduction indicated no significant effects of either covariate (Supplementary Material Table S2). The final, top-ranked model was  $\{C\psi(\text{state} + Y^2 + \text{tree} + \text{elev} + \text{burn} + \text{salvage}), CR(\text{state} + \text{year} + \text{tree}), \delta(Y + s1\text{diff} + \text{burn} + SB), p1(\text{year} + \text{burn} + SB), p2(\text{year} + s1\text{diff} + \text{burn} + SB)\}$ .

## DISCUSSION

Our study used multistate modeling of dynamic site occupancy and reproduction of California Spotted Owls in southern California to examine the effects of previous reproductive state and site-specific vegetation characteristics on responses to wildland fire and postfire logging for this important management indicator species.





**FIGURE 4.** Dynamic probability of reproduction (CR) of California Spotted Owls at sites which in the previous year supported reproductive owls (state 2, solid black line), nonreproductive owls (state 1, dashed gray line), or were vacant (state 0, solid gray line) in the San Bernardino Mountains, California, USA, 2004–2011. Linear estimates are from the top-ranked model (Supplementary Material Table S1). Squares (■), filled circles (●), and triangles (▲) are year-specific estimates of occupancy for the 3 states from the fully parameterized (state \* year) model of all parameters.

### Effects of Previous State

Both occupancy and reproduction probabilities of California Spotted Owls were much greater at sites that were occupied by breeding owls in the previous year (Figures 3 and 4), after accounting for variation in vegetation characteristics. This result supports predictions from the ‘reproductive capability’ hypothesis. We interpret this to indicate the presence of sites that were consistently occupied by successfully reproductive owls over time. It could be that variation in geography or vegetation influenced a site’s habitat and prey base and led to these sites being consistently occupied and productive regardless of the reproductive abilities of the individual owls present, or that individuals with high reproductive abilities occupied the sites with the best habitat and that this combination of individual and habitat attributes led to consistent occupancy and reproduction. Our inferences cannot extend to individual owls when our sampling unit was the site, but one can expect positive correlations between individual and site reproductive capability when intrinsically superior individuals settle preferentially in the sites with the best habitat (Fretwell 1972, Lomnicki 1988). Additionally, many avian species, including California Spotted Owls, exhibit a pattern of greater fidelity to breeding sites for individuals that were reproductively successful than for those that were not (Greenwood and Harvey 1982, Blakesley et al. 2006, Gutiérrez et al. 2011).

Our methods attempted to account for variation in site vegetation characteristics while examining evidence for ‘reproductive capability’ vs. ‘resource depletion’ effects, but our GIS map for vegetation was not highly accurate. Thus, the ‘reproductive capability’ effect could result from variation in site-specific characteristics that we could not account for with our vegetation covariates.

Our results differ from those of 2 similar studies of a population of California Spotted Owls in the central Sierra Nevada (Eldorado study area), where previous year’s reproductive state was not an important determinant of occupancy or reproduction (MacKenzie et al. 2009, 2010). Our methods were based directly upon the methods of those 2 studies, so comparisons are valid. Differences in habitat–demography relationships, mediated by the different vegetation, climate, and anthropogenic impacts in the 2 regions, could explain the observed patterns. One possibility may be that the Sierra Nevada population is at or above carrying capacity while the southern California population is below carrying capacity, in which case we would expect demographic patterns to be obscured in the Sierra Nevada relative to southern California (Pulliam 2000). Spotted Owl populations have declined in the Sierra Nevada (Tempel and Gutiérrez 2013, Conner et al. 2013), but it is likely that the amount of habitat has also declined because of extensive commercial logging (Seamans and Gutiérrez 2007), therefore the Sierra Nevada population could be at or above carrying capacity while also at a substantially lower population size than previously documented. California Spotted Owl populations in southern California have declined as well (LaHaye et al. 1994, 2004, Lee et al. 2013), but forests here are much less affected by recent commercial logging, and more affected by drought, water diversions, and urbanization (LaHaye and Gutiérrez 2005).

### Effects of Disturbance

Site-specific vegetation covariates, including our disturbance variables of interest, high-severity fire and postfire logging, were important factors affecting detection and misclassification probabilities. It is now well established that vegetation and other site-specific covariates should be included in model selection procedures for detection and other ‘nuisance’ probabilities, in order to produce unbiased estimates of occupancy and reproduction (Popescu et al. 2012, Lee et al. 2012, 2013). It is particularly important to examine the influence of a study’s main effect of interest upon ‘nuisance’ parameters if researchers hope to produce robust results (Popescu et al. 2012).

In southern California, we found that high-severity fire and postfire logging were correlated with a significant reduction in Spotted Owl site occupancy probability, but that the negative effects were small in sites that supported reproductive owls the previous year (reduced 0.02 by fire

and 0.03 by postfire logging, respectively) and pronounced in sites that were occupied by nonreproductive owls the previous year (reduced 0.19 by fire and 0.26 by postfire logging; Figure 3). As with the influence of prior reproductive state, the effects of high-severity fire on Spotted Owl site occupancy also differed between southern California and the Sierra Nevada. Burned sites in the Sierra Nevada had slightly greater occupancy relative to unburned sites (Lee et al. 2012). Although the mean percentage of high-severity burned tree cover in owl core areas was similar between the 2 regions, owl sites in the Sierra Nevada had substantially greater amounts of prefire tree cover and thus retained more postfire unburned or lightly burned closed-canopy nesting and roosting habitat, potentially explaining the differences in the effects of fire on occupancy between the 2 areas (Lee et al. 2012, 2013). Further, vegetation and climate differ substantially between the regions.

Reproduction in occupied sites in our study area was unaffected by high-severity fire and postfire logging during the study period. Our results agree with previous studies on reproduction of Spotted Owls after fire, indicating that productivity in occupied burned sites is no different from (Jenness et al. 2004, Clark 2007), or may be greater than, productivity in occupied unburned sites (Bond et al. 2002). Our multistate modeling using 9 yr of owl survey data for 168 sites in 2 mountain ranges that experienced multiple fires corroborates results from earlier studies in other regions. Our and other studies suggest that, in Spotted Owl breeding sites with habitat characteristics that support occupancy, reproductive rates are similar in both burned and unburned areas.

We found no significant effect of elevation on reproduction, but elevation was found to be a significant factor in previous studies of Spotted Owl reproduction (LaHaye et al. 1997, Blakesley et al. 2005). The number of young fledged per pair could have been greater at lower elevations in our study, but our multistate modeling quantified reproduction at a site as binomial (0 or 1). Thus, the probability of successfully reproducing at lower-elevation sites is not greater than at higher-elevation sites, but more juveniles per pair apparently are fledged at lower elevations in this region (LaHaye et al. 1997). These lower-elevation owl sites were more vulnerable to high-severity fire during our study period (Lee et al. 2013). Therefore, we recommend strengthening efforts to reduce human-caused ignitions at the wildland–urban interface in the lower elevations of the San Bernardino and San Jacinto mountains to reduce the potential for high-severity fire to exceed critical thresholds in owl sites.

### **Importance of Productive Breeding Sites**

This study illustrates the important contribution of productive breeding sites to this population of Spotted

Owls. Zimmerman et al. (2003) noted that Spotted Owls in our study population tended to occupy sites where they were more likely to replace themselves. Although fire and postfire logging covariates were associated with reduced site occupancy, the effect sizes of these disturbances in the sites where owls reproduced the previous year were small. We were unable to quantify whether owls rearranged themselves according to an ideal despotic distribution after disturbance because we did not have data on individual survival and fecundity (*sensu* Franklin et al. 2000), but the greater overall productivity at sites where young were produced the previous year compared with sites where breeding did not occur, regardless of disturbance, indicates that some sites were more important than others.

The majority of Spotted Owl core areas in the SBM and SJM experienced high-severity fires that were below the critical threshold that reduced occupancy (>50 ha forested area in the 203-ha core), even during this period of extreme drought and elevated fire activity (Lee et al. 2013). Severe fire that burned owl core areas throughout the Sierra Nevada from 2000 to 2007 also did not reduce site occupancy (Lee et al. 2012), and severely burned forests in the southern Sierra Nevada that were not logged after fire had a greater probability of use by foraging Spotted Owls than unburned forests (Bond et al. 2009). Therefore, the occurrence of high-severity forest fire does not necessarily translate into adverse effects on California Spotted Owls.

In contrast, prior studies have demonstrated that Spotted Owls and other species have been adversely affected by logging projects intended to reduce the future risk of high-severity fire, including postfire logging and green-tree thinning. California Spotted Owls in the Sierra Nevada avoided foraging and showed reduced occupancy in recently implemented landscape-scale logging projects designed as firebreaks (Stephens et al. 2014), and Northern Spotted Owls avoided foraging in stands that were logged postfire (Clark 2007). In addition, many avian species that colonize postfire forests were significantly less abundant in postfire-logged patches (Saab et al. 2007, Hanson and North 2008, Hutto 2008, Cahall and Hayes 2009). Therefore, we urge managers to consider that the purpose and need for postfire logging, and for fuels treatments intended to reduce the risk of high-severity fire, conflicts with conservation of the Spotted Owl and other species.

Assessments of Spotted Owl sites based on recent reproductive output can provide an efficient and accurate measure of the relative contribution of specific sites to population growth (Sergio and Newton 2003, Peery and Gutiérrez 2012), and can enable managers to prioritize conservation efforts at sites that support high levels of reproduction (Sergio et al. 2009). In southern California, where both demographic and site-occupancy data strongly indicate a declining owl population, sites with successfully reproducing owls likely are making consistent, relatively

large contributions to overall population growth (Runge et al. 2006). Our results indicate that occupancy of these important sites that consistently supported reproductive owls exhibited negligible effects from high-severity fire. Protective measures should be in place for all known Spotted Owl sites, but sites with recent owl reproduction and sites with higher amounts of tree cover in the 203-ha core area should receive enhanced protection from management actions that modify vegetation utilized by Spotted Owls, including fuels treatments and postfire logging.

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