



Research Article

Influence of Fire and Salvage Logging on Site Occupancy of Spotted Owls in the San Bernardino and San Jacinto Mountains of Southern California

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ABSTRACT Fire over the past decade has affected forests in the San Bernardino Mountains of southern California, providing an excellent opportunity to examine how this disturbance, and subsequent post-fire salvage logging, influenced California spotted owl (*Strix occidentalis occidentalis*) breeding-season site occupancy dynamics there and in the nearby San Jacinto Mountains. Using occupancy survey data from 2003 to 2011 for all-detections and pairs-only data, we estimated annual extinction and colonization probabilities at 71 burned and 97 unburned breeding-season sites before and after fire, while controlling for confounding effects of non-fire-related temporal variation and among-site differences in habitat characteristics. We found no statistically significant effects of fire or salvage logging on occupancy dynamics of spotted owls of southern California. However, we found some evidence that fire and logging effects could be biologically meaningful. For pairs data, the model-averaged mean of fire-related effects on colonization and extinction probabilities resulted in a 0.062 lesser site-occupancy probability in burned sites 1-year post-fire relative to unburned sites. Post-fire salvage logging reduced occupancy an additional 0.046 relative to sites that only burned. We documented a threshold-type relationship between extinction and colonization probabilities and the amount of forested habitat (conifer or hardwood tree cover types) that burned at high severity within a 203-ha core area around spotted owl nests and roost centroids. Sites where approximately 0–50 ha of forested habitat within the core area burned at high severity had extinction probabilities similar to unburned sites, but where more than approximately 50 ha of forested habitat burned severely, extinction probability increased approximately 0.003 for every additional hectare severely burned. The majority (75%) of sites burned below this threshold. Sites where high-severity fire affected >50 ha of forested habitat could still support spotted owls, so all burned sites should be monitored for occupancy before management actions such as salvage logging are undertaken that could be detrimental to the subspecies. We also recommend that managers strive to reduce human-caused ignitions along the wildland–urban interface, particularly at lower elevations where owl sites are at higher risk of extinction from fire. © 2013 The Wildlife Society.

KEY WORDS California spotted owl, fire severity, forest structure, occupancy modeling, population dynamics, *Strix occidentalis*.

Natural disturbances influence the structure and function of forested ecosystems and create spatial and temporal heterogeneity of wildlife habitats. Habitat alterations by fire have the potential to affect population dynamics of animals, particularly territorial species that demonstrate high breeding-site fidelity, such as the California spotted owl (*Strix occidentalis occidentalis*; Blakesley et al. 2006, Seamans and Gutiérrez 2007). Post-fire salvage logging is widespread

in burned spotted owl habitats, and this additional alteration may also affect this species.

The California spotted owl is an iconic subspecies of management concern because it is strongly associated with late-seral coniferous forests for nesting, roosting, and foraging (Bias and Gutiérrez 1992, Call et al. 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Blakesley et al. 2005). Modifications of older forest habitat from timber harvest and fire are believed to be primarily responsible for habitat-driven changes in spotted owl populations (Verner et al. 1992) although under certain circumstances, spotted owls may benefit from some degree of forest heterogeneity, for example, when openings of different seral stages were interspersed with older forest (sensu

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California spotted owl: Bond et al. 2009*b*; northern spotted owl [*S. o. caurina*]: Franklin et al. 2000, Olson et al. 2004). Understanding how habitat disturbances affect site-occupancy rates is essential for developing appropriate pre- and post-fire forest management practices to conserve spotted owls. Modeling of site-occupancy dynamics allows biologists to quantify the influence of site-specific habitat variables on site occupancy and local rates of site extinction and colonization while accounting for imperfect detectability (MacKenzie et al. 2003, 2006, 2009, 2010; Nichols et al. 2007; Seamans and Gutiérrez 2007).

Populations of California spotted owls in southern California are at the southern edge of their range, are highly insular, and are substantially smaller compared to those in the Sierra Nevada (Gutiérrez and Pritchard 1990; LaHaye et al. 1994, 2001). In southern California, spotted owls occur within forested islands located at upper elevations along a series of mountain ranges surrounded by extensive desert and semi-desert communities (LaHaye et al. 1994). Twenty-two isolated populations have been identified in central-coastal and southern California with the number of breeding-season sites per population ranging from 3 to 133 (Verner et al. 1992, LaHaye et al. 1994), the largest of which is in the San Bernardino Mountains (SBM). Spotted owl populations in the SBM and nearby San Jacinto Mountains (SJM) declined precipitously during demographic studies conducted from 1987 to 1998 (LaHaye et al. 2004), prompting serious concerns about the future of the subspecies in southern California (Loe and Beyers 2004). LaHaye and Gutiérrez (2005) proposed an array of possible causes for the declines, including fire, drought, recreational activities, air pollution, urbanization, and water diversions, but occupancy of sites was not quantitatively linked to any of these factors. Previous studies examining the effects of fire on occupancy of spotted owl breeding-season sites in the Sierra Nevada found no differences between burned and unburned sites in occupancy (Roberts et al. 2011) or in colonization and extinction rates (Lee et al. 2012). However, Lee et al. (2012) hypothesized that there may be a critical threshold proportion of habitat within a site that, if burned at high-severity, could adversely affect occupancy rates.

In the period 2003–2007, California spotted owl breeding-season sites in the SBM were more heavily affected by fire than during any time since the commencement of spotted owl studies in the region. After historically low rainfall and high temperatures beginning in 1998, wildfires burned 5,800 ha of conifer forests in 2003 (Bond et al. 2009*a*). In 2007, additional fires burned another 11,200 ha of conifer types (Keeley et al. 2009). These and other smaller fires in forested habitat during the period 2003–2007 constituted a widespread impact that occurred across many regularly monitored spotted owl territories.

Our objectives were to investigate if recent fires were associated with occupancy dynamics of southern California spotted owl breeding-season sites (hereafter sites) from 2003 to 2011, and to identify if occupancy is affected by a critical threshold of vegetation change due to high-severity fire and salvage logging within a site. We used a natural impact

assessment where a subset of all the owl sites surveyed annually from 2003 to 2011 were burned during that same time period, and a subset of those burned owl sites were subsequently salvage logged. We estimated local extinction and colonization probabilities at burned, burned and logged, and unburned sites both before and after fire, while including the possibly confounding effects of non-fire-related temporal variation and among-site differences in habitat characteristics, thus providing strong inference that observed changes in occupancy dynamics were likely due to fire and/or logging (Burnham and Anderson 2002, Stephens et al. 2005, Mundry 2011).

STUDY AREA

The San Bernardino and San Jacinto Mountains rise above the surrounding lowlands approximately 140–150 km east of Los Angeles, California. The SBM are in the Transverse Mountain Range and trend east–west, whereas the SJM are the northernmost terminus of the north–south trending Peninsular Ranges (Stephenson and Calcarone 1999). Climate of the study area was Mediterranean with most precipitation falling during the winter as rain at lower elevations and rain and snow at higher elevations. Average annual precipitation ranged from 500 to 1,000 mm with substantial local variability due to aspect, elevation, topography, rain-shadow patterns, and seasonal storm patterns (Minnich 1988).

In southern California, spotted owls inhabit lower montane forests, montane coniferous forests, and occasionally desert forests and woodlands (Gutiérrez et al. 1992, LaHaye et al. 1997). Lower montane forests ranged from 915 to 1,525 m (Stephenson and Calcarone 1999). Chaparral was the dominant vegetation over most of this landscape, although stands of bigcone Douglas-fir (*Pseudotsuga macrocarpa*) with an understory of canyon live oak (*Quercus chrysolepis*) often occurred in the steep, dissected drainages. Knobcone pine (*Pinus attenuata*) and sometimes Coulter pine (*P. coulteri*) formed open woodlands with dense chaparral in the understory. Montane coniferous forests ranged from 1,525 to 2,440 m and were dominated by Jeffrey pine (*P. jeffreyi*) or ponderosa pine (*P. ponderosa*). California black oak (*Q. kelloggii*) was a common understory tree in these forests. Mixed-conifer forests were prevalent in more mesic settings between 1,920 and 2,690 m and included combinations of Jeffrey and ponderosa pines, white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), and sugar pine (*P. lambertiana*; Stephenson and Calcarone 1999). The eastern, interior desert portions of the mountains were covered by pinyon pine (*P. monophylla*) and western juniper (*Juniperus occidentalis*) forests and woodlands. Spotted owl sites occurred on both private and public (San Bernardino National Forest, U.S. Forest Service) lands.

Historical fire regimes in southern California's forests likely created a heterogeneous landscape that produced mixed patches of unburned, low-, moderate-, and high-severity burned forest (Weatherspoon et al. 1992). A century of intensive resource extraction, fire suppression, domestic

livestock grazing, and other management activities has led to changes in the structure and species composition of these forests (McKelvey and Johnston 1992, Minnich et al. 1995), but managers do not know whether or how this has altered pattern, frequency, and intensity of current fires.

The SBM and SJM ranges were isolated from each other by urban areas, deserts, and chaparral, all of which were unsuitable to spotted owls (LaHaye et al. 1994). Thus, dispersal of owls between mountain ranges was limited (LaHaye et al. 2001).

METHODS

Spotted Owl Surveys

All California spotted owl sites within the boundaries of the San Bernardino National Forest in the SBM and SJM were identified beginning in 1989 by annually surveying all forested stands (LaHaye et al. 2004). We defined an owl site as a distinct area within our geographic survey boundaries that was determined to be occupied prior to 2003 by seeing or hearing a single or pair of territorial spotted owls. Our population of interest consisted of previously identified owl sites that were subsequently burned (or not burned) by fire; therefore, using data from sites where occupancy status had been previously established is appropriate, rather than from randomly selected sites where previous occupancy status was unknown (MacKenzie and Royle 2005). Each year from 2003 through 2011, we attempted occupancy and reproductive surveys in all known spotted owl sites from 1 March to 31 August, following standardized methods described by Forsman (1983) and Franklin et al. (1996). Every year, the same experienced project manager (R. Tanner) trained field biologists in spotted owl survey and detection methods, and many of the biologists worked for multiple years on the project, thereby minimizing observer bias. Budgetary and safety constraints sometimes limited the number of sites surveyed in a given year. If the annual budget was insufficient to survey all sites, we prioritized sites potentially affected by management projects, but there was no systematic bias in selecting sites to survey in a given year. In other words, sites were neither included nor excluded from annual surveys based on prior occupancy history; sites with long periods of no detections continued to be surveyed as often as continuously occupied sites. The purposeful exclusion of a site from surveys in a given year was usually due to safety issues such as presence of a nearby marijuana (*Cannabis* spp.) plantation. We included in our analysis survey data from all known spotted owl sites in the SBM and SJM study areas that were surveyed for ≥ 2 consecutive years from 2003 to 2011 ($n = 168$).

Within a year, we used 2 types of surveys: 1) presence-absence surveys to initially locate owls in an area; and 2) reproductive surveys to locate roosts and nests and to assess the reproductive status of owls previously detected by presence-absence surveys. All survey visits were separated by >48 hours. We conducted presence-absence surveys to determine if spotted owls currently occupied previously identified sites by imitating spotted owl vocalizations while

thoroughly surveying designated areas between dusk and dawn. We accomplished survey coverage by calling from a series of fixed calling stations along roads and trails or by walking survey routes while calling continuously. We conducted up to 6 nighttime presence-absence surveys at each spotted owl site every year. If a spotted owl responded during a nighttime survey, we began conducting crepuscular (dusk and dawn) reproductive surveys. We conducted a maximum of 4 reproductive surveys to confirm occupancy and to assess reproductive status and success. We sexed owls based on their calls and behavior (Forsman 1983, Franklin et al. 1996). If we detected spotted owls at 1 site but then followed them back to an adjacent site during the same survey, we did not consider the first site to be occupied during that survey because owls were attracted to the surveyor's calls. We surveyed each site a maximum of 8 times (presence-absence and reproductive surveys combined), 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. This was comparable to the average maximum number of visits rule used by Olson et al. (2005) and the unspecified rule used by Kroll et al. (2010) to truncate their survey data.

Site-Specific Habitat Characteristics and Burned Vegetation Changes

To define which sites were burned, and to characterize habitat variation among all sites, we evaluated vegetation and physical attributes in a 203-ha circle around the most recently used nest tree location or roost centroid (as of 2003) in all spotted owl sites in 2003, and again post-fire in sites that burned between 2003 and 2007 (the last year that fires affected the owl sites in our dataset). Previous studies on spotted owls elsewhere in the species' range also have examined the effects of habitat variables on occupancy and vital rates in an approximately 200-ha circle surrounding nests and core roosts (Blakesley et al. 2005, Stralberg et al. 2008, Manley et al. 2009, Lee et al. 2012). This area is intended to represent regions of concentrated use by spotted owls and are described here as core areas. Average breeding-season home-range size previously was reported as 439 ha for California spotted owls in the SBM (fixed-kernel method; Zimmerman et al. 2001).

The United States Forest Service's Adaptive Management Services Enterprise Team (AMSET; Tahoe National Forest, Nevada City, CA) developed an attributed, landscape Geographic Information System (GIS) data set in 2003 that we supplemented with elevation and fire-related habitat covariates for our analysis. On a base map constructed from ortho-rectified, 1-m resolution infrared aerial photographs of the SBM and SJM taken in September 2003, AMSET plotted the most recent (as of 2003) nest locations or centroids of roost locations of 136 owl pairs in the SBM and 32 in the SJM. Within each 203-ha core area surrounding the nest or roost locations, AMSET delineated polygons of similar vegetation using on-screen infrared photographs and stereo pairs of color aerial photographs (at a scale of

1:15,840) over a background of black-and-white orthophotos. Mapping was carried out in ArcMap (ESRI, Inc., Redlands, CA). A new polygon was added whenever there was a minimum 10% change in vegetation composition or structure from the surrounding vegetation. On-screen templates assisted in standardizing some attributes. In each 203-ha core area, AMSET estimated hectares of each cover type: conifers, hardwoods, shrubs, herbs (grasslands and meadows), riparian, and non-vegetation. For each site, we also recorded elevation at the nest tree or geometric mean of the roost centroids.

We defined burned spotted owl sites as those where the 203-ha core area was inside or included the perimeter of one of the fires that occurred from 2003 to 2007. Using National Agricultural Imager Program (NAIP) imagery taken for the San Bernardino National Forest in October 2009, we re-attributed vegetation in core areas that burned between October 2003 and October 2007. Fires in southern California forests typically burn in a mosaic of severities (Weatherspoon et al. 1992, Stephenson and Calcarone 1999), but we only analyzed the owl habitat burned at high-severity within owl sites because this fire severity most concerns managers as being a threat to spotted owls (Loe and Beyers 2004). We defined owl habitat as conifer and hardwood tree cover types, and determined the hectares of habitat that burned at high severity between 2003 and 2007 by overlaying burn severity and vegetation maps and quantifying change in tree cover due to fire. High-severity fire resulted in areas where dominant vegetation had high to complete mortality due to fire. Post-fire tree removal occurred on private inholdings and on United States Forest Service lands adjacent to roads, which affected 21 of the core areas. We used aerial photographs obtained from Google Earth to impose a grid of 1-ha cells in a 203-ha circle around the nests or roost centroids and estimate the amount of the circle affected by extensive (i.e., clearcut) post-fire tree removal.

Statistical Analysis

We used raw survey data to compile occupancy histories for 168 California spotted owl sites. We found no substantial or systematic differences in average elevation or habitat values between the owl sites in SBM ($n = 136$) versus those in SJM ($n = 32$), and preliminary analysis revealed no difference in mean occupancy dynamics between SBM and SJM. Therefore, we pooled sites from both areas for analysis of fire effects on occupancy dynamics. Ninety-seven sites were not burned at any time, and 71 sites burned from 2003 to 2007. Twenty-one of the burned sites were subsequently salvage logged.

From the raw occupancy survey data, we created 2 datasets called all detections and pair, corresponding to different levels of site occupancy (Olson et al. 2005). We defined all-detections occupancy as any spotted owl detection at a site, regardless of pair or reproductive status (surveys with any spotted owl detection were coded as 1, no detection was coded as 0). The pair dataset only contained detections of pairs (surveys where we detected both members of a pair, an

adult of any sex with ≥ 1 juvenile, or ≥ 1 juvenile with no adult were coded as 1, all other surveys coded as 0). We analyzed all-detections and pair data in an identical procedure. Site occupancy in all-detections data represented the broadest definition of occupancy and indicated the use of a site by any spotted owl, whereas site occupancy by pairs represented a more conservative definition of occupancy and indicated the potential for a site to support breeding (Olson et al. 2005).

We used Program Presence 4.0 (USGS-Patuxent Wildlife Research Center, Laurel, MD 2006) to fit models and estimate survey-specific detection probabilities, initial occupancy, annual colonization probabilities, and annual extinction probabilities from occupancy survey histories following methods developed by MacKenzie et al. (2003) and MacKenzie and Royle (2005) for open populations. Detection (P) is the probability that an occupied site is correctly identified as such. Colonization (γ) is the probability that a site unoccupied in year $t - 1$ becomes occupied in year t . Extinction (ϵ) is the probability that a site occupied in year $t - 1$ is unoccupied in year t . We were most interested in the colonization and extinction processes that determine occupancy state in a given year, but the probability of occupancy (ψ) in year t can be calculated from occupancy in year $t - 1$, extinction, and colonization rates (MacKenzie et al. 2003).

We followed methods used by Olson et al. (2005), Kroll et al. (2010), Dugger et al. (2011), and Farber and Kroll (2012) to model spotted owl site-occupancy dynamics. We employed a multi-staged technique to rank models, and selected the best and competing models at each stage using an information theoretic approach (Burnham and Anderson 2002). First, we ranked models of detection probabilities to find the most parsimonious form of this parameter while holding colonization and extinction in their year-specific forms. We used the top-ranked model of detection from the first stage of the analysis in the second stage of ranking temporal models for local extinction and colonization probabilities. During the third stage of modeling, we ranked a set of pre-fire habitat covariate models for extinction and colonization probabilities. Finally, we ranked a set of fire and salvage-logging covariate models based on the best temporal and pre-fire habitat covariate models.

In this manner, we investigated the support for fire and logging effects while controlling for potentially confounding temporal variation as well as pre-fire site-specific (individual) vegetation and physical habitat variation. Our temporal and habitat covariates included effects previously reported to be associated with spotted owl detectability, habitat selection, or vital rates (Table 1). Annual temporal variation in all detection, colonization, and extinction parameters were modeled as year-specific (year), as well as a linear time trend (Y), quadratic time trend (Y^2), cubic trend (Y^3), and constant (\cdot). We expected that colonization and extinction probabilities could exhibit annual variation (year) due to variation in weather or prey populations (Franklin et al. 2000; Seamans et al. 2002; LaHaye et al. 2004; Glenn et al. 2010, 2011) and

Table 1. Definition of temporal and habitat covariates within a 203-ha circle around the nest tree or roost centroid for 168 California spotted owl sites in the San Bernardino and San Jacinto mountains of southern California from 2003 to 2011.

Covariate name	Type	Definition
year	Binomial	Annual variation coded as categorical dummy variables (8 variables in γ and ϵ , 9 in P)
Y	Continuous	Linear annual temporal trend
Y ²	Continuous	Quadratic annual temporal trend
Y ³	Continuous	Cubic annual temporal trend
altyr	Binomial	Alternate year temporal pattern, every other year coded 1, 0, 1, 0, etc.
fire	Binomial	Intercept effect of fire between 2003 and 2011 coded 0 in unburned sites for all years, 0 for burned sites in fire years before fire, and 1 for burned sites in years after fire
hisev	Continuous	Hectares of owl habitat vegetation in 203-ha core area burned at high severity between 2003 and 2011 coded as a site-specific continuous covariate (mean = 24, range = 0.2–119)
hisev ²	Continuous	The square of <i>hisev</i> , used to model extinction as a quadratic function of the amount of owl habitat vegetation burned at high severity between 2003 and 2011
log	Continuous	Hectares of post-fire salvage logging in 203-ha core area (mean = 63, range = 0–150)
elev	Continuous	Site elevation standardized as (elevation – mean)/SD (raw mean = 5,686, range = 2,620–8,820)
rip	Continuous	Index of riparian vegetation cover (mean = 13, range = 0–96)
tree	Continuous	Hectares of pre-fire owl habitat in 203-ha core area (mean = 106, range = 44–149)
survey	Binomial	Survey-specific variation coded as 6 categorical dummy variables per year
S	Continuous	Linear within-year temporal trend
S ²	Continuous	Quadratic within-year temporal trend
S ³	Continuous	Cubic within-year temporal trend

detection probability could vary because of survey-specific (survey) or annual (year) differences in survey staff, weather conditions such as wind, or other unmeasured factors. We also included alternate year structure (altyr) in annual temporal covariate models of colonization and extinction of pairs data because previous studies found patterns of alternate-year oscillations in reproductive output for California and northern spotted owls (LaHaye et al. 2004, Blakesley et al. 2010, Forsman et al. 2011). Breeding dispersal of California spotted owls is more prevalent after breeding failures (Blakesley et al. 2006, Gutiérrez et al. 2011), so an alternate-year reproduction cycle could mediate an alternate-year territory extinction pattern. An alternate-year pattern is also evident for long periods in year-specific survival rates of California spotted owls, although the authors did not test this model structure (Blakesley et al. 2010).

We modeled temporal variation in detection probabilities for within-year surveys as survey-specific (survey), as well as a linear time trend (S), quadratic time trend (S²), cubic trend (S³), and constant (.). Within each year, survey crews made efforts to survey all sites completely before beginning another iteration of surveys. Therefore, the first, second, third, etc., survey for all sites were close together in time and represented a seasonal continuum making temporal trends representative of seasonal variation in detectability. We did not include more detailed covariates of survey-specific variation such as observer, date- and site-specific weather conditions, or time of night because these covariates were not available.

In unburned landscapes, habitat selection of California spotted owls typically is associated with large trees and high canopy cover (Gutiérrez et al. 1992, Blakesley et al. 2005, Seamans 2005), so we predicted colonization would be positively, and extinction negatively, correlated with tree cover within 203 ha of the nest or roost centroid (tree). Spotted owls seek cool roosting sites during periods of warm

weather as an adaptation to heat stress (Barrows 1981), and radio-marked northern spotted owls in dry forests of southwestern Oregon selected foraging locations closer to perennial streams (Clark 2007); therefore, we predicted colonization would be positively, and extinction negatively, correlated with amount of riparian habitat (rip). We expected elevation-related gradients in vegetation type, prey biomass (Smith et al. 1999), and climate (LaHaye et al. 2004) to affect colonization and/or extinction probability (elev). The raw elev covariate consisted of large numbers, so we standardized this covariate to units of standard deviation (Table 1).

Our model set included year- and site-specific fire effects in detection, colonization, and extinction probabilities. We modeled detection, colonization, and extinction with and without an intercept effect (fire) for whether the site burned between 2003 and 2011. 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. Within a given season, sites are assumed to be closed to changes in occupancy; this assumption can be relaxed as long as changes occur at random (MacKenzie et al. 2006). All fires burned after surveys ended for the year, so fire did not affect within-season conditions in this study.

In colonization and extinction, we modeled covariates of vegetation changes due to high-severity fire as linear (*hisev*) and quadratic (*hisev*²) functions of the hectares of trees killed by fire within the 203-ha core area. We included quadratic covariates because we believed the relationship between the amount of habitat burned and occupancy dynamics could be nonlinear. Spotted owls may require a threshold amount of habitat in their core area that abruptly affects colonization or extinction probabilities rather than a smooth linear relationship. We modeled a site-specific colonization and extinction covariate of post-fire salvage logging (*log*) as a

linear function of the hectares of clearcut within the 203-ha core area.

To minimize potential biases, for both datasets (all detections and pair), within each stage of model selection, we ranked all possible combinations of covariates (Doherty et al. 2010). In detection, we examined every combination of temporal covariate for year- and survey-specific variation with and without fire effects (28 models). When modeling temporal variation in colonization and extinction, we examined every combination of annual variation covariates (22 models), pre-fire habitat covariates (19 models), and fire and salvage-logging effects (49 models).

To protect against spurious conclusions based only upon 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 calculated model-averaged parameter estimates by summing the individual model estimates multiplied by the associated Akaike's Information Criterion (AIC) model weight (Burnham and Anderson 2002). Model averaging produces real parameter estimates that account for the weight of evidence from our data for each model in the set, and these weighted averages result in real parameter estimates that are conservative and adjusted according to the amount of weight of evidence behind each model. Thus, even though the 95% confidence interval of point estimates of beta coefficients includes zero, the model-averaged real parameter estimates of burn or logging effects should be viewed as a conservative effect size that accounts for uncertainty and inference can be based on that model-averaged effect size. We used mean values of all individual covariates when computing mean model-averaged parameter estimates (Burnham and Anderson 2002). When presenting effects of a given covariate across its full range, we held all other covariates at their mean values. We computed unconditional estimates of variance, standard errors, and 95% confidence intervals (Buckland et al. 1997, Burnham and Anderson 2002). We determined specific covariate effects were statistically significant when the 95% confidence interval of the beta coefficient did not include zero. We calculated relative importance of variables by summing the weights from all models in a set that contained a variable of interest (Burnham and Anderson 2002). We ascertained potential biological significance by examining effect sizes among the 3 treatment groups (unburned, burned, burned and salvage logged) using model-averaged real parameters. Model averaging inherently presents parameter estimates based on the weight of evidence in the data for a given effect.

RESULTS

We analyzed 9,558 possible sampling events; 3,143 surveys (33%) were missing data (no survey done). Missing data were mostly the result of some sites not being surveyed in a given year because of budget or safety constraints (see the Methods Section). The mean number of California spotted owl sites surveyed each year (2003–2011) was 78 (SD = 23, minimum = 39) for unburned sites and 58 (SD = 13,

minimum = 38) for burned sites from 2004 to 2011 because the first fires burned in fall 2003. The mean number of sites surveyed each year that had been surveyed in the previous year (consecutive annual site surveys) was 76 (SD = 24, minimum = 39) for unburned sites and 52 (SD = 16, minimum = 31) for burned sites. In the last 8 years of the study (the years when burned sites were available), the mean annual proportion of surveyed sites that were in the burned group was 0.37 (SD = 0.09).

Vegetation Change and Site-Specific Covariates

The mean amount of pre-fire owl habitat (sum of conifer and hardwood types) within a 203-ha core area around the nest location or roost centroid in all 168 sites was 106 ha (SD = 24, range = 44–149). In our sample of 71 spotted owl sites burned from 2003 to 2007, the amount of owl habitat that burned at high severity within the core area around the pre-fire nest location or roost centroid was 24 ha (SD = 31, range = 0–119). Salvage logging was only detected when more than 20 ha of habitat burned at high severity in the core area, and occurred on 21 burned sites. Mean amount of salvage logging in burned sites was 63 ha (SD = 53, range = 0–150). Sites at higher elevations tended to support a greater amount of owl habitat pre-fire ($t = 2.77$, $P = 0.006$), but among burned sites the amount of owl habitat burned at high-severity within a core area was similar at all elevations ($t = -1.19$, $P = 0.23$).

Detection, Extinction, and Colonization

Top-ranked models for all detections and pairs data indicated evidence for time- and fire-related effects on colonization; time-, fire-, and logging-related effects on extinction (Table 2); and time- and fire-related effects on detection (for complete model selection results see Table S1, available online at www.onlinelibrary.wiley.com). Beta coefficients (β) and their standard errors from the highest-ranked models indicated that all parameters were estimable and reasonable. The 95% confidence intervals of beta coefficients for all fire and logging effects overlapped zero indicating these effects were not statistically significant (Tables 3 and 4), and the relative importance (cumulative AIC weights) of fire and logging variables was low (0.01) to moderate (0.42). Model-averaged real parameter effect sizes for mean detection, colonization, and extinction values indicated some evidence for potentially biologically significant effects, if we assume point estimates of beta coefficients are accurate (Fig. 1).

All detections.—The mean annual detection probability was 0.072 greater in burned sites versus unburned sites (burned $\bar{p} = 0.667$; unburned $\bar{p} = 0.595$). At unburned sites, mean colonization probability was 0.158 (SE = 0.041), and mean extinction probability was 0.172 (SE = 0.061). At burned sites, mean colonization probability was 0.067 (SE = 0.013), and mean extinction probability was 0.229 (SE = 0.004). Mean annual colonization probability was 0.090 lesser in burned sites relative to unburned sites, but colonization was unaffected by salvage logging (Fig. 1B). Mean annual extinction probability was 0.057 greater in burned sites relative to unburned sites, and 0.065 greater in salvage logged

Table 2. Top-ranked models of fire and logging effects on colonization and extinction probabilities for California spotted owl sites in the San Bernardino and San Jacinto mountains of southern California from 2003 to 2011. In all-detections data models, minimum Akaike's Information Criterion (AIC) was 3,618.68, and detection was modeled as $P(Y^3 + S^3 + \text{fire})$. In pairs data models, minimum AIC was 2,557.75, and detection was modeled as $P(\text{year} + S^3 + \text{fire})$. We included lower-ranked models with no fire effects for comparison.

Colonization ^a	Extinction ^a	ΔAIC	w_i^b	Model likelihood	K^c
All detections data					
(Y ² + tree + fire + hisev)	(Y ² + tree + elev + fire + log)	0	0.11	1	21
(Y ² + tree + fire + hisev)	(Y ² + tree + elev + fire + hisev ² + log)	0.81	0.07	0.67	23
(Y ² + tree + fire + hisev ²)	(Y ² + tree + elev + fire + log)	1.06	0.06	0.59	22
(Y ² + tree + fire + hisev)	(Y ² + tree + elev + fire)	1.21	0.06	0.55	20
(Y ² + tree + fire + hisev)	(Y ² + tree + elev + fire + hisev)	1.23	0.06	0.54	21
(Y ² + tree + fire + hisev)	(Y ² + tree + elev + fire + hisev + log)	1.60	0.05	0.45	22
(Y ² + tree + fire + hisev)	(Y ² + tree + elev + fire + hisev ²)	1.65	0.05	0.44	22
(Y ² + tree + fire + hisev + log)	(Y ² + tree + elev + fire + log)	1.98	0.04	0.37	22
(Y ² + tree + fire + hisev ²)	(Y ² + tree + elev + fire + hisev ² + log)	2.03	0.04	0.36	24
(Y ² + tree + fire + hisev)	(Y ² + tree + elev)	2.24	0.03	0.33	19
(Y ² + tree)	(Y ² + tree + elev + fire + log)	11.84	0	0	19
Pairs only data					
(tree + fire)	(Y + altyr + tree + elev + fire + hisev)	0	0.06	1	24
(tree)	(Y + altyr + tree + elev + fire + hisev)	0.08	0.06	0.96	23
(tree + fire)	(Y + altyr + tree + elev + fire + hisev + log)	0.16	0.06	0.92	25
(tree)	(Y + altyr + tree + elev + fire + hisev + log)	0.27	0.05	0.87	24
(tree + fire + hisev)	(Y + altyr + tree + elev + fire + hisev + log)	0.38	0.05	0.83	26
(tree + fire + hisev)	(Y + altyr + tree + elev + fire + log)	0.39	0.05	0.82	25
(tree + fire + hisev)	(Y + altyr + tree + elev + fire + hisev)	0.48	0.05	0.79	25
(tree + fire + hisev)	(Y + altyr + tree + elev + fire + hisev ² + log)	0.53	0.05	0.77	27
(tree + fire + hisev ²)	(Y + altyr + tree + elev + fire + hisev ² + log)	0.55	0.05	0.76	28
(tree + fire)	(Y + altyr + tree + elev + fire + hisev ² + log)	0.61	0.04	0.74	26
(tree)	(Y + altyr + tree + elev + fire + hisev ² + log)	0.63	0.04	0.73	25
(tree + fire + log)	(Y + altyr + tree + elev + fire + hisev)	0.67	0.04	0.72	25
(tree + fire + hisev ² + log)	(Y + altyr + tree + elev + fire + hisev ² + log)	1.45	0.03	0.48	29
(tree + fire + log)	(Y + altyr + tree + elev + fire + hisev + log)	1.48	0.03	0.48	26
(tree + fire)	(Y + altyr + tree + elev + fire + hisev ²)	1.53	0.03	0.47	25
(tree)	(Y + altyr + tree + elev + fire + hisev ²)	1.60	0.03	0.45	24
(tree + fire + hisev + log)	(Y + altyr + tree + elev + fire + hisev)	1.83	0.02	0.40	26
(tree + fire + log)	(Y + altyr + tree + elev + fire + hisev ² + log)	1.84	0.02	0.40	27
(tree + fire + hisev)	(Y + altyr + tree + elev + fire + hisev ²)	1.91	0.02	0.38	26
(tree + fire + log)	(Y + altyr + tree + elev + fire + hisev ²)	1.91	0.02	0.38	26
(tree + fire + hisev ² + log)	(Y + altyr + tree + elev + fire + hisev ²)	1.95	0.02	0.38	28
(tree)	(Y + altyr + tree + elev + fire + log)	2.01	0.02	0.37	23
(tree + fire)	(Y + altyr + tree + elev)	8.59	0	0.01	22

^a Y = year effect, tree = hectares of tree cover (owl habitat) in core area, fire = binomial fire effect, hisev = hectares of owl habitat in core area burned with high severity, log = binomial post-fire salvage logging effect, elev = standardized site elevation, altyr = alternative year temporal pattern.

^b Akaike weights.

^c Number of parameters.

versus unlogged sites (Fig. 1C). Extinction probability increased, and colonization probability decreased as a function of the amount of owl habitat that burned at high-severity (Fig. 2A). When >30 ha of owl habitat burned at high severity, colonization probability was significantly lesser than in unburned sites (Fig. 2A); when >110 ha of owl habitat burned at high severity, extinction probability was significantly greater than in unburned sites (Fig. 2A). Colonization and extinction parameters were correlated with amount of owl habitat in the 203-ha core area (Fig. 4A), and extinction probability was negatively correlated with elevation (Table 3).

Initial occupancy for all sites was 0.625. The difference between unburned and burned sites was small in the first year post-fire, but because occupancy is calculated using annual colonization and extinction rates combined with the previous year's occupancy, the difference between burned and unburned sites grows over time (Fig. 3A). Thus, the mean annual site occupancy probability from 2004 to 2011 of

unburned sites was 0.477, for sites burned in 2003 mean occupancy was 0.306, and logged sites was 0.255. The relationships between the amount of habitat burned at high severity and the probabilities of colonization and extinction resulted in significant differences (no overlap of standard errors) in site occupancy probabilities when >50 ha of owl habitat burned at high severity in the 203-ha core area. Salvage logging reduced burned site occupancy probability an additional 0.051.

Pair data.—The mean annual detection probability was slightly greater in burned sites versus unburned sites (burned $\bar{p} = 0.151$; unburned $\bar{p} = 0.144$), but detection increased during the study period from 0.063 to 0.312. At unburned sites, mean colonization probability was 0.071 (SE = 0.041), and mean extinction probability was 0.138 (SE = 0.061). At burned sites, mean colonization probability was 0.055 (SE = 0.004), and mean extinction probability was 0.238 (SE = 0.033). Mean annual colonization probability was 0.015 lesser in burned sites relative to unburned sites, but

Table 3. All-detections data model-averaged beta coefficients (β), their unconditional standard errors (SE) and 95% confidence intervals (95% CI) for temporal, habitat, and fire-related covariates of occupancy dynamics at burned and unburned California spotted owls sites in the San Bernardino and San Jacinto mountains from 2003 to 2011.

Covariate ^a	β	SE	95% CI	
Initial occupancy	0.510	0.239	0.041	0.978
Colonization				
intercept	-2.459	0.771	-3.969	-0.948
Y	-0.722	0.000	-0.722	-0.722
Y ²	0.073	0.000	0.073	0.073
tree (pre-fire owl habitat)	0.039	0.014	0.011	0.067
fire	-0.529	0.399	-1.311	0.253
hisev	-0.029	0.019	-0.066	0.008
hisev ²	-0.00017	0.00007	-0.00030	-0.00004
log	0.00014	0.00101	-0.00184	0.00212
Extinction				
intercept	0.816	0.263	0.300	1.331
Y	0.426	0.000	0.426	0.426
Y ²	-0.061	0.000	-0.061	-0.061
tree (pre-fire owl habitat)	-0.052	0.013	-0.078	-0.026
elev	-0.131	0.150	-0.425	0.163
fire	0.379	0.304	-0.217	0.975
hisev	-0.007	0.005	-0.018	0.004
hisev ²	0.00033	0.00010	0.00013	0.00053
log	0.010	0.006	-0.001	0.022
Detection				
intercept	-1.224	0.197	-1.610	-0.838
S	1.249	0.099	1.055	1.444
S ²	-0.425	0.016	-0.455	-0.394
S ³	0.040	0.001	0.038	0.042
Y	0.179	0.049	0.084	0.275
Y ²	-0.007	0.005	-0.016	0.002

^a Y = year effect, tree = hectares of tree cover (owl habitat) in core area, fire = binomial fire effect, hisev = hectares of owl habitat in core area burned with high severity, log = binomial post-fire salvage logging effect, elev = standardized site elevation, S = within year temporal trend.

colonization was unaffected by logging (Fig. 1E). Mean annual extinction probability was 0.100 greater in burned relative to unburned sites, and 0.110 greater in logged versus unlogged sites (Fig. 1F). Extinction probability increased as a function of the amount of owl habitat that burned at high-severity (Fig. 2B). When >50 ha of owl habitat burned at high severity, extinction probability was significantly greater than in unburned sites (Fig. 2B). Colonization and extinction parameters were correlated with amount of owl habitat in the 203-ha core area (Fig. 4B), and extinction probability was negatively correlated with elevation (Table 4).

Initial occupancy for all sites was 0.403. Mean annual site occupancy probability from 2004 to 2011 of unburned sites was 0.346, of burned sites was 0.239, and logged sites was 0.185 (Fig. 3B). The relationships between the amount of habitat burned at high severity and the probabilities of colonization and extinction resulted in significant differences (no overlap of standard errors) in site occupancy probabilities where >50 ha of owl habitat burned at high severity in the 203-ha core area. Salvage logging reduced burned site occupancy probability an additional 0.054.

DISCUSSION

We found no statistically significant effects of fire or salvage logging on occupancy dynamics of spotted owls in the San Bernardino and San Jacinto mountains of southern

California. However, we found some weak to moderate evidence that fire and logging impacts could be biologically meaningful. Uncertainty in model selection and parameter estimation does not mean the effects are not real, only that they were difficult to detect in this study. If we assume the model-averaged effect sizes were accurate, compared to unburned sites, sites affected by fires had lesser colonization probabilities and greater extinction probabilities, resulting in lesser site occupancy. Furthermore, compared with unlogged burned sites, salvage-logged sites had greater extinction probabilities which further reduced site occupancy. We also quantified the relationship between colonization and extinction probabilities and the amount of habitat that burned at high severity in the 203-ha circular core area around the nest or roost centroid. When 0–50 ha of forested habitat burned at high severity, colonization and extinction probabilities—and thus site occupancy probabilities—were similar to unburned sites. However, when >50 ha of forested habitat burned severely, site occupancy probability decreased approximately 0.003 for every additional ha of forested habitat severely burned. The 50-ha threshold should be considered approximate, because error bars for the modeled relationship were large (Fig. 2A,B). The majority of sites (75%) burned below the 50-ha threshold. Post-fire salvage logging exacerbated the lesser site occupancy of burned versus unburned sites by decreasing occupancy probability an additional 0.05.

Table 4. Pairs data model-averaged beta coefficients (β), their unconditional standard errors (SE), and 95% confidence intervals (95% CI) for temporal, habitat, and fire-related covariates of occupancy dynamics at burned and unburned California spotted owls sites in the San Bernardino and San Jacinto mountains from 2003 to 2011.

Covariate ^a	β	SE	95% CI	
Initial occupancy	-0.393	0.268	-0.918	0.131
Colonization				
intercept	-5.139	0.810	-6.727	-3.552
tree (pre-fire owl habitat)	0.048	0.015	0.019	0.078
fire	-0.133	0.414	-0.945	0.678
hisev	-0.005	0.021	-0.046	0.035
hisev ²	-0.00022	0.00007	-0.00035	-0.00009
Extinction				
intercept	1.790	0.263	1.274	2.306
Y	-0.097	0.099	-0.290	0.096
altyr	0.715	0.413	-0.095	1.525
tree (pre-fire owl habitat)	-0.068	0.042	-0.149	0.014
elev	-0.124	0.198	-0.512	0.264
fire	0.359	0.398	-0.422	1.139
hisev	0.014	0.015	-0.015	0.044
hisev ²	0.0004	0.0006	-0.0007	0.0015
log	0.015	0.012	-0.008	0.039
Detection				
intercept	-2.705	0.295	-3.282	-2.127
2004	0.087	0.304	-0.510	0.684
2005	-0.125	0.304	-0.722	0.472
2006	0.475	0.279	-0.072	1.022
2007	0.177	0.282	-0.375	0.730
2008	1.363	0.292	0.790	1.936
2009	1.223	0.277	0.680	1.767
2010	1.907	0.292	1.334	2.479
2011	1.490	0.289	0.923	2.057
S	1.734	0.135	1.470	1.999
S ²	-0.443	0.023	-0.487	-0.399
S ³	0.035	0.002	0.032	0.039
fire	0.076	0.158	-0.234	0.387

^a tree = hectares of tree cover (owl habitat) in core area, fire = binomial fire effect, hisev = hectares of owl habitat in core area burned with high severity, Y = year effect, altyr = alternative year temporal pattern, elev = standardized site elevation, log = binomial post-fire salvage logging effect, S = within year temporal trend.

We found that spotted owl sites in the SBM and SJM that burned tended to occur at lower elevations than sites that did not burn. The increase in fires at lower elevations in the SBM and SJM over the past decade was almost entirely a result of human-caused ignitions (Halsey 2005), compounded by drier conditions and warmer-than-average temperatures. Owl sites at lower elevations often are found in patchily distributed bigcone Douglas-fir-canyon live oak forests (Smith 1995). Because this forest type typically intergrades with chaparral along its margins, it is particularly vulnerable to high-severity fires (Lombardo et al. 2009).

Our results for fire-related effects on occupancy contrast with similar studies of the same subspecies in the Sierra Nevada (Roberts et al. 2011, Lee et al. 2012). Lee et al. (2012) used 11 years of breeding-season survey data from 41 burned California spotted owl sites (1997–2007) in the Sierra Nevada where on average 32% of owl habitat in a 200-ha circle around core areas burned at high severity (D. Lee, unpublished data), and found no significant effects of fire on extinction or colonization probabilities. In southern California, an average of 23% of owl habitat in a 203-ha circle around core areas burned severely, which was less than in the Sierra Nevada, yet some evidence for fire and logging effects was documented. Many of the spotted owl sites in the Sierra

Nevada differ from sites in southern California with respect to vegetation, elevation, climate, and fire regime, thus fire effects likely differ as well. The Sierra Nevada are farther north, higher in elevation, hold massive snowpack that irrigates lower elevations throughout the dry summer (Kattelmann 1996), and support a larger, more contiguous population of spotted owls relative to southern California's meta-populations (LaHaye et al. 1994). Furthermore, spotted owl surveys in the Sierra Nevada study were primarily associated with timber-harvest projects in mixed-conifer habitats, whereas the southern California study areas incorporated sites in all forested habitats within the SBM and SJM (Gutiérrez and Pritchard 1990, LaHaye et al. 1994), including vegetation types not typically monitored for spotted owls in the Sierra Nevada, such as pure hardwoods and conifer-hardwood forests associated with chaparral (Smith 1995). Moreover, southern California owl sites associated with vegetation such as bigcone Douglas-fir-canyon live oak forests have no corollary in the Sierra Nevada.

Effects of fire on occupancy dynamics in the Sierra Nevada compared with southern California may also be related to extent of pre-fire forested habitat within core areas. Colonization and extinction parameters in this study were

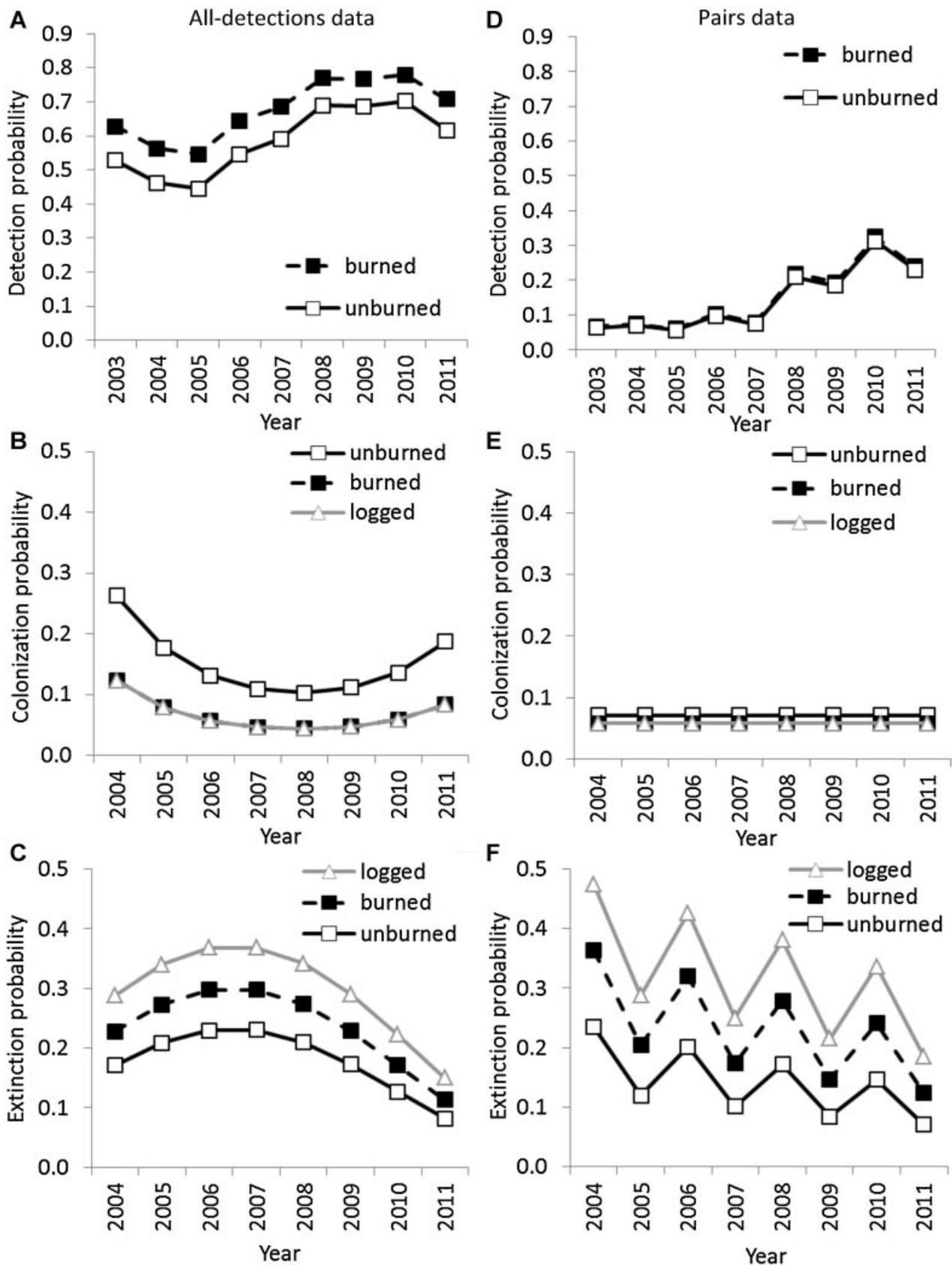


Figure 1. Annual modeled estimates of detection (A and D), colonization (B and E), and extinction (C and F) probabilities from all-detection (A–C) and pairs-only (D–F) data for burned and unburned California spotted owl sites in the San Bernardino and San Jacinto mountains from 2003 to 2011 as calculated from model-averaged beta parameters. We calculated burned sites as having burned in 2002 (detection) or 2003 (colonization and extinction). We set individual (site-specific) covariate values to the mean for each covariate.

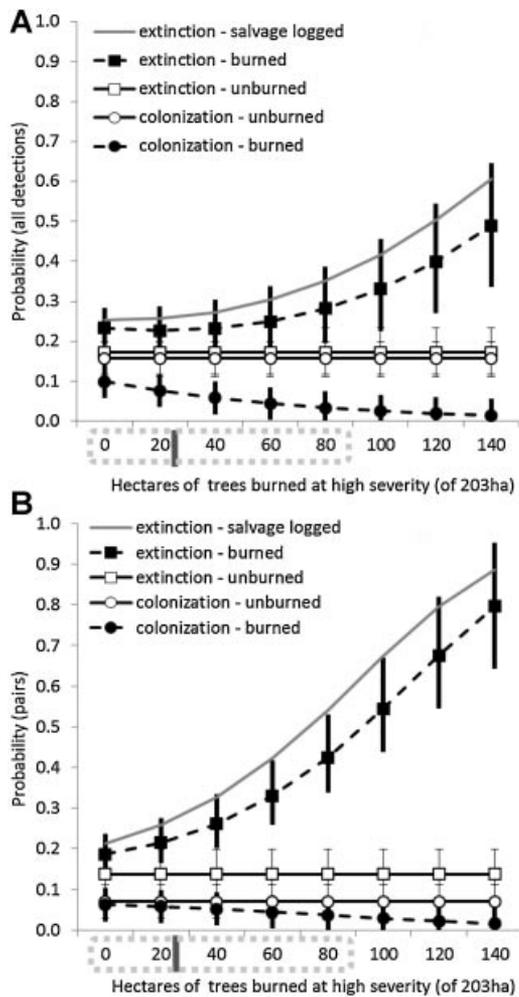


Figure 2. Model-averaged relationship between site colonization and extinction probability and the hectares of owl habitat that burned at high severity within a 203-ha circle around the nest or roost centroid of 71 California spotted owl sites in the San Bernardino and San Jacinto mountains from 2003 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 (\pm SE), open symbols and solid lines are unburned sites (\pm SE), and solid gray lines represent burned and salvage-logged site extinction probabilities. Vertical gray line in x -axis indicates the mean amount of owl habitat that burned at high severity in all burned sites. Dotted gray rectangle in x -axis indicates 95% confidence interval of amount of owl habitat that burned at high severity in all burned sites. We set individual (site-specific) covariate values to the mean for each covariate.

correlated with amount of forested habitat within the core area. The amount of pre-fire forested habitat in the core area averaged 180 ha ($SD = 20$) in the Sierra Nevada (D. E. Lee, Wild Nature Institute, unpublished data), but only 106 ha ($SD = 24$) in southern California. Core areas of southern California sites also had a greater proportion of hardwoods compared with Sierra Nevada core areas (D. E. Lee, unpublished data), which tend to burn at higher severities than conifer types (Bond et al. 2009a). The smaller amount of pre-fire forested habitat within spotted owl core areas in southern California translated into fewer hectares remaining unburned or lightly burned post-fire compared with the Sierra Nevada, perhaps explaining the potential impacts of

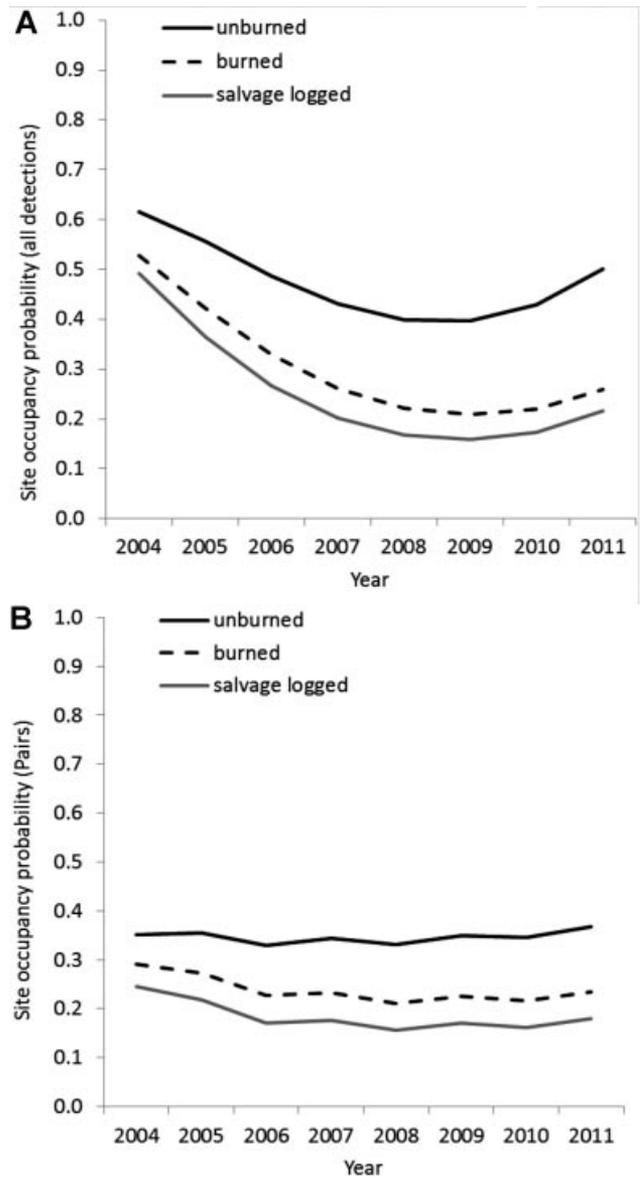


Figure 3. Annual estimates of southern California spotted owl site occupancy probability in unburned sites, sites that burned, and sites that were burned and salvage logged in San Bernardino and San Jacinto mountains. We computed estimates from estimates of initial occupancy, and annual colonization and extinction probabilities from the model-averaged parameters for all-detection (A) and pairs-only (B) data. We calculated burned sites as having burned in 2003. We set individual (site-specific) covariate values to the mean for each covariate.

severe fire on site occupancy we observed in southern California.

Post-fire salvage logging is a widespread practice that affects spotted owl habitat. Few studies have specifically examined this effect, but those that did reported adverse effects on foraging and occupancy rates of spotted owls elsewhere in the range of the species. In the Klamath Province in Oregon, northern spotted owls selected stands for foraging that were lightly or moderately burned and used severely burned stands in proportion to their availability, but avoided areas that were salvage logged after the fire

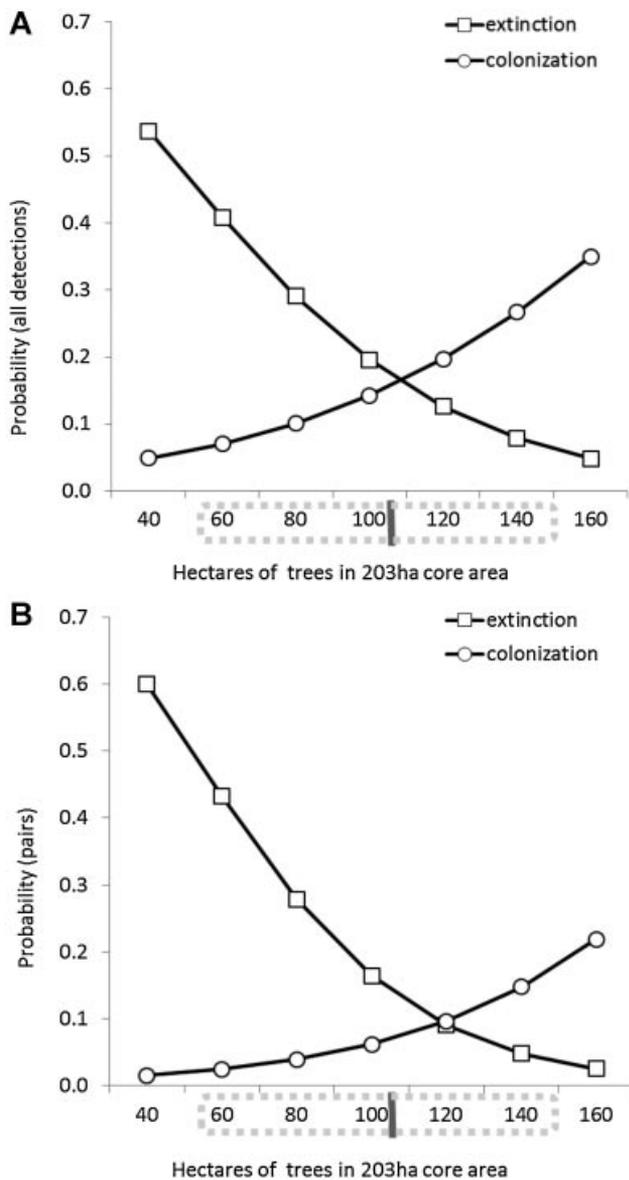


Figure 4. Model-averaged relationship between site colonization (circles) and extinction (squares) probabilities and the hectares of owl habitat (trees) within a 203-ha circle around the nest or roost centroid of California spotted owl sites in the San Bernardino and San Jacinto mountains from 2003 to 2011 from all-detection (A) and pairs-only (B) data. Vertical gray line in *x*-axis indicates the mean amount of owl habitat in all sites. Dotted gray rectangle in *x*-axis indicates 95% confidence interval of amount of owl habitat in all sites.

(Clark 2007). In a sample of 8 burned California spotted owl sites in the Sierra Nevada that were subsequently logged, 7 were occupied post-fire, but none were occupied after logging (Lee et al. 2012).

This study is the first to examine the discrete effects of severe fire and salvage logging on occupancy dynamics of spotted owls. Salvage logging in our southern California study area occurred mainly on private inholdings and as fuel wood cutting and hazard-tree removal along roads on United States Forest Service lands, rather than within the larger commercial salvage-logging projects typically conducted in the Sierra Nevada or the Pacific Northwest. Yet, even in the

absence of large-scale salvage-logging projects in southern California, post-fire tree removal in spotted owl cores was extensive enough to increase extinction probabilities and reduce occupancy relative to unlogged burned sites. Clark et al. (2013) examined effects of fire and logging on occupancy dynamics of northern spotted owls, but their analysis did not differentiate between the 2 disturbances.

Temporal factors also influence occupancy dynamics of California spotted owls. Weather conditions, particularly cold, wet conditions during winters (Nov–Mar) and nesting seasons (Mar–Apr), heavily influence annual variation in demographic rates of this species (Franklin et al. 2000; LaHaye et al. 2004; Olson et al. 2004; Glenn et al. 2010, 2011; Peery et al. 2011). Our annual estimates indicated that both burned and unburned sites experienced a drastic increase in extinction and decrease in colonization during the 2006 breeding season when snowfall in March and April was significantly greater than in any other year from 2003 to 2011 (>2.3 standard deviations above the mean). The elevated rate of extinction persisted through the 2007 breeding season for the all-detection data. We posit that this unusually extreme spring weather adversely affected demographic processes, which was reflected in greater site extinction and lesser colonization rates. LaHaye et al. (1994) documented a precipitous decline in site occupancy in the SBM, from more than 0.90 in 1987 to approximately 0.60 in 1992, among sites that were mostly unaffected by fire. Our all-detections estimate of unburned site occupancy from 2003 to 2004 was 0.61, but occupancy declined sharply in 2005 to 2009 before rebounding to 0.501 in 2011 (Fig. 3A). Our estimate of pair site occupancy was nearly constant during the study period (Fig. 3B). The alternate-year pattern we found in pairs extinction probability could be related to the alternate-year patterns found in California spotted owl reproduction and survival (Blakesley et al. 2010). This pattern in spotted owl demographic rates has been hypothesized to be related to cyclic small mammal populations, or to 1 irruptive small mammal year after a poor year (or years) resulting in a synchronized boom in owl reproduction that sets in motion an alternate-year pattern because of costs of reproduction that mediate a 2-year breeding cycle (Forsman et al. 2011). The alternate-year pattern attenuates as new recruits and stochastic effects increase the number of non-synchronized breeders.

The smaller, insular populations of the spotted owl in southern California are likely more vulnerable to extinction (Noon and McKelvey 1992, LaHaye et al. 1994) and thus may be more adversely affected by fires than populations in the Sierra Nevada. Often, populations at the edge of a species' range exhibit more variable occupancy dynamics than populations near their biogeographic core (Gaston 2009). In southern California, lower-elevation spotted owl sites appear to be most at risk, but these also are considered some of the most productive owl habitats. LaHaye et al. (2001) documented breeding spotted owls in lower-elevation bigcone Douglas-fir-oak habitat in the SBM produced more fledglings per nest, and Smith (1995) estimated relatively high densities of owls in these habitats. The higher

incidence of fires and greater risk of extinction in these sites is cause for concern.

MANAGEMENT IMPLICATIONS

We found no statistically significant effects of fire or salvage logging on occupancy dynamics of spotted owls of southern California. However, we found some evidence that fire and logging impacts could be biologically meaningful. The potential effect of fire on spotted owl occupancy in our southern California study area was most evident where >50 ha of owl habitat burned at high severity in the 203-ha core area. However, the majority of sites (75%) burned below this threshold. Bond et al. (2009b) documented California spotted owls in the southern Sierra Nevada selectively foraged in severely burned stands over unburned when those habitats were available, suggesting a possible fitness benefit from smaller high-severity burns within a site. We caution that our results not lead to conclusions that all sites with >50 ha of high-severity fire can no longer be occupied by spotted owls, as occupancy is site-specific, probabilistic, and influenced by factors other than fire. Burned sites, even those subjected to large areas of high-severity fire, should continue to be monitored for occupancy before management actions such as salvage logging are undertaken that could be detrimental to spotted owls. Post-fire salvage logging has the potential to increase extinction rates relative to burned sites, therefore California spotted owls will benefit from retaining fire-killed trees within core areas unless non-occupancy has been confirmed by protocol-level surveys conducted over multiple years (Lee et al. 2012). In southern California, the amount of owl habitat within spotted owl site core areas was correlated with colonization and extinction. Thus, forested habitat should be safeguarded from human-caused alteration wherever possible. Conserving maximum amounts of owl habitat, including large trees and dense canopy cover, could provide resiliency to potential adverse effects of severe fire. Finally, higher-elevation owl sites had more owl habitat relative to lower-elevation sites, but owls at lower-elevation sites are known to produce comparatively more offspring. Therefore, the risk of severe fire and site extinction is greater at lower elevations. The most effective management action may be to increase efforts aimed at reducing the rate of human-caused ignition in southern California mountains, especially at lower elevations. Because of the myriad differences between southern California and the rest of the species' range, our inferences are not directly applicable to spotted owls or their habitats outside of southern California.

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