



UNIVERSITY OF CALIFORNIA PRESS
JOURNALS + DIGITAL PUBLISHING



Dynamics of Breeding-Season Site Occupancy of the California Spotted Owl in Burned Forests
(Dinámicas de la Ocupación de Sitio por *Strix occidentalis occidentalis* en la Estación Reproductiva
en Bosques Quemados)

Author(s): Derek E. Lee, Monica L. Bond and Rodney B. Siegel

Source: *The Condor*, Vol. 114, No. 4 (November 2012), pp. 792-802

Published by: [University of California Press](http://www.jstor.org/stable/10.1525/cond.2012.110147) on behalf of the [Cooper Ornithological Society](http://www.jstor.org/stable/10.1525/cond.2012.110147)

Stable URL: <http://www.jstor.org/stable/10.1525/cond.2012.110147>

Accessed: 17/07/2013 18:08

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



University of California Press and Cooper Ornithological Society are collaborating with JSTOR to digitize, preserve and extend access to *The Condor*.

<http://www.jstor.org>

DYNAMICS OF BREEDING-SEASON SITE OCCUPANCY OF THE CALIFORNIA SPOTTED OWL IN BURNED FORESTS

DEREK E. LEE¹, MONICA L. BOND, AND RODNEY B. SIEGEL

The Institute for Bird Populations, P. O. Box 1346, Point Reyes Station, CA 94956

Abstract. Understanding how habitat disturbances such as forest fire affect local extinction and probability of colonization—the processes that determine site occupancy—is critical for developing forest management appropriate to conserving the California Spotted Owl (*Strix occidentalis occidentalis*), a subspecies of management concern. We used 11 years of breeding-season survey data from 41 California Spotted Owl sites burned in six forest fires and 145 sites in unburned areas throughout the Sierra Nevada, California, to compare probabilities of local extinction and colonization at burned and unburned sites while accounting for annual and site-specific variation in detectability. We found no significant effects of fire on these probabilities, suggesting that fire, even fire that burns on average 32% of suitable habitat at high severity within a California Spotted Owl site, does not threaten the persistence of the subspecies on the landscape. We used simulations to examine how different allocations of survey effort over 3 years affect estimability and bias of parameters and power to detect differences in colonization and local extinction between groups of sites. Simulations suggest that to determine whether and how habitat disturbance affects California Spotted Owl occupancy within 3 years, managers should strive to annually survey ≥ 200 affected and ≥ 200 unaffected historical owl sites throughout the Sierra Nevada 5 times per year. Given the low probability of detection in one year, we recommend more than one year of surveys be used to determine site occupancy before management that could be detrimental to the Spotted Owl is undertaken in potentially occupied habitat.

Key words: California Spotted Owl, colonization, extinction, occupancy, site-occupancy modeling, *Strix occidentalis*.

Dinámicas de la Ocupación de Sitio por *Strix occidentalis occidentalis* en la Estación Reproductiva en Bosques Quemados

Resumen. Entender la manera en que los disturbios de hábitat, como los incendios forestales, afectan la extirpación y la probabilidad de colonización—el proceso que determina la ocupación del sitio—es crucial para desarrollar un manejo forestal adecuado para la conservación de *Strix occidentalis occidentalis*, una subespecie cuyo manejo es preocupante. Usamos datos de 11 años de monitoreo de la estación reproductiva de 41 sitios de presencia de *S. o. occidentalis* quemados en seis incendios forestales y 145 sitios en áreas no quemadas a lo largo de Sierra Nevada, California, para comparar las probabilidades de extirpación y colonización en sitios quemados y no quemados tomando en cuenta las variaciones en detectabilidad anuales y específicas de cada sitio. No encontramos efectos significativos de los incendios en estas probabilidades, sugiriendo que los incendios, incluso aquellos que queman en promedio 32% del hábitat adecuado con una alta severidad dentro de un sitio de presencia de *S. o. occidentalis*, no amenazan la persistencia de la subespecie en el paisaje. Empleamos simulaciones para examinar como diferentes asignaciones de esfuerzo de monitoreo a lo largo de tres años afectan la capacidad de estimación y sesgan los parámetros y el poder para detectar diferencias en colonización y extirpación entre los grupos de sitios. Las simulaciones sugieren que para determinar si y cómo los disturbios de hábitat afectan la ocupación de *S. o. occidentalis* a lo largo de tres años, los gestores deberían esforzarse para monitorear anualmente ≥ 200 sitios históricos de la especie afectados y ≥ 200 no afectados a lo largo de Sierra Nevada cinco veces por año. Dada la baja probabilidad de detección en un año, recomendamos que se use más de un año de monitoreo para determinar la ocupación antes de aplicar manejos que podrían ser negativos para *S. o. occidentalis* en sitios potencialmente ocupados.

INTRODUCTION

Reliable estimates of a population's vital rates are essential for wildlife conservation and management (Williams et al. 2002). Local extinction from occupied sites and colonization of unoccupied sites over time are the dynamic processes that govern changes in occupancy, and the rates of these processes provide

important information about the long-term sustainability of a population and effects of management (Mazarolle et al. 2005, MacKenzie et al. 2006). The development of statistical methods for estimating site occupancy and local rates of local extinction and colonization while accounting for imperfect detectability has increased the potential for understanding the

Manuscript received 9 September 2011; accepted 28 March 2012.

¹Current address: Wild Nature Institute, P. O. Box 165, Hanover, NH 03755. E-mail: derek@wildnatureinstitute.org

effects of natural processes and human disturbance on wildlife populations (MacKenzie et al. 2003, 2006, Kendall et al. 2009).

The California Spotted Owl (*Strix occidentalis occidentalis*) is a subspecies of management concern in the Sierra Nevada of California because it is strongly associated with older coniferous forests for nesting, roosting, and foraging (Gutiérrez et al. 1992, Blakesley et al. 2005, Seamans 2005). The California Spotted Owl is territorial, with high fidelity to breeding sites (Gutiérrez et al. 1995, Blakesley et al. 2006). Occupancy, site fidelity, adult survival, and reproductive success are positively associated with the amount of older conifer-dominated forest at a site (Blakesley et al. 2005, Seamans 2005, Seamans and Gutiérrez 2007). Modifications of old forests by logging and forest fire are believed by land and wildlife managers to be the greatest habitat-driven influences on California Spotted Owl populations (Verner et al. 1992, USFS 2004). Understanding how these habitat disturbances affect probabilities of local extinction from and colonization of breeding sites—the processes that determine occupancy—is critical for developing appropriate forest-management policies and activities to benefit the Spotted Owl. Moreover, managers with limited budgets need guidance on the amount of survey effort required to monitor Spotted Owl occupancy efficiently, so they can estimate detection probabilities and occupancy rates accurately with the minimum expenditure of effort.

The relationship between forest fire and the California Spotted Owl is relatively understudied although this natural disturbance has influenced the structure and function of habitat in California for millennia (Weatherspoon et al. 1992). The influence of fire on the occupancy dynamics of the California Spotted Owl's breeding sites is an important question for management and conservation of the subspecies, but the obvious logistical and political difficulties of conducting large-scale experiments with forest fire and a sensitive species necessitate collecting data opportunistically and taking advantage of natural experiments. The few existing studies of fire's effects on rates of occupancy of Spotted Owl sites have found no significant effects (Bond et al. 2002, Jenness 2004, Roberts et al. 2011), but all were limited either by small sample size or lack of prefire survey data. An experimental design in which occupancy rates are estimated at many burned and unburned sites both before and after forest fire would allow for a stronger inference that any observed changes in occupancy are due to fire (Smucker et al. 2005).

To assess demographic rates and explore ecological relationships, biologists have surveyed California Spotted Owl sites annually for more than 20 years in three areas of the Sierra Nevada (see Blakesley et al. 2010). In other areas of the Sierra Nevada, biologists with the U.S. Forest Service (USFS) surveyed historically occupied Spotted Owl sites prior to forest management such as logging. Over the past decade some known and repeatedly surveyed sites in national forests were

subsequently burned by forest fires. These surveys represent some of the best data available for investigating effects of fire on occupancy dynamics of California Spotted Owl sites.

We compiled a long-term (11-year) data set of surveys of California Spotted Owl sites throughout the Sierra Nevada, comprising 41 burned and 145 unburned control sites and including data from ≥ 3 years pre-fire for all burned sites. We used these data to determine whether rates of local extinction and/or colonization at burned and unburned sites differed before fire and for 5 to 7 years after fire, while accounting for annual and site-specific variation in detectability. We also quantified how fires affected vegetation characteristics at burned sites.

Additionally we used simulations to examine how different allocations of survey effort affected parameter estimability and bias and power to detect differences between groups of sites (i.e., burned and unburned). Our simulations continue the work of previous investigators in this field, providing guidance for research designed to examine differences in occupancy dynamics between groups of sites (objective ii in MacKenzie and Royle 2005). MacKenzie et al. (2002) provided early guidance for the number of occupancy surveys required for parameters to be estimated precisely. Field et al. (2005) used simulations to guide allocation of survey effort given budgetary constraints and concluded that three surveys per site are generally sufficient, but more surveys are required if the occupancy rate is high, as is the case with historical Spotted Owl sites (Olson et al. 2005, Dugger et al. 2011). Using simulations, MacKenzie and Royle (2005) provided additional guidance for allocating survey effort but in their simulations constrained detection probability to be constant through time, an assumption that may not be true for the Spotted Owl (Olson et al. 2005, Roberts et al. 2011, but see Seamans and Gutiérrez 2007). Bailey et al. (2007) further expanded these explorations and introduced software (GENPRES) for exploring study-design options and trade-offs in light of the realization that allocation of survey effort is sufficiently complex that designs should be evaluated on a case-specific basis. Following the methods of Bailey et al. (2007) we simulated 3 years of Spotted Owl occupancy data for two groups of sites with realistic but different parameter values, various numbers of surveys per year, and various numbers of sites.

METHODS

STUDY AREA

We obtained data on the California Spotted Owl's occupancy of burned and unburned sites throughout the Sierra Nevada, California. The Sierra Nevada is 650 km long, trends north-south, and composed of granitic rock. Its climate is Mediterranean, with cold, wet winters and hot, dry summers (Sierra Nevada Ecosystem Project 1996).

Sierran mixed-conifer forest was the dominant vegetation type in our study areas, with a canopy consisting largely of

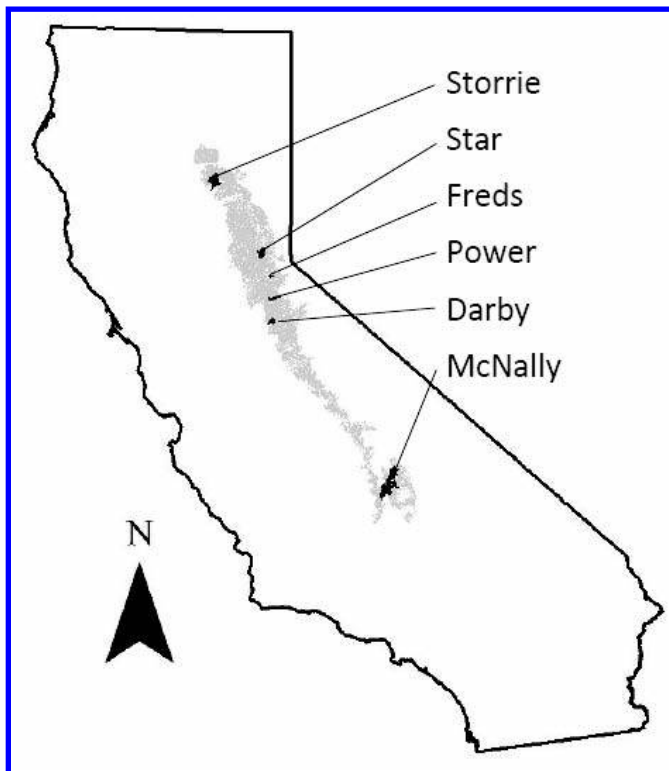


FIGURE 1. Location of six major fires (shaded black) that burned from 2000 to 2004 in California Spotted Owl habitat (conifer, mixed-conifer, and hardwood vegetation types [shaded gray]) in the Sierra Nevada, California.

ponderosa pine (*Pinus ponderosa*) or Jeffrey pine (*P. jeffreyi*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), incense-cedar (*Calocedrus decurrens*), and Douglas-fir (*Pseudotsuga menziesii*) and an understory of black oak (*Quercus kelloggii*), tanoak (*Lithocarpus densiflorus*), and bigleaf maple (*Acer macrophyllum*) (Sierra Nevada Ecosystem Project 1996). Higher-elevation sites were dominated by red fir (*Abies magnifica*).

Our sample of 41 burned Spotted Owl sites had been burned in the following six fires (north to south): the 2000 Storrie Fire in the Lassen and Plumas national forests, the 2001 Star Fire in the Tahoe and Eldorado national forests, the 2004 Freds and Power fires in the Eldorado National Forest, the 2001 Darby Fire in the Stanislaus National Forest, and the 2002 McNally Fire in the Sequoia National Forest (Fig. 1).

SPOTTED OWL OCCUPANCY DATA

The USFS provided us with records of occupancy surveys at California Spotted Owl sites that were conducted annually between 1 April and 31 August from 1997 to 2007 by methods described in its Spotted Owl inventory and monitoring handbook (USFS 1988). We used this window in time because (1) remotely sensed GIS data of fire severity were generally unavailable before about 2000, (2) we knew of six large fires after 2000 in which Spotted Owl sites were burned, and (3) we were striving for at least three years of pre-fire occupancy

data. We used these data to compile occupancy-survey histories for 41 sites throughout the Sierra Nevada that were influenced by fires and 145 sites unaffected by fire. We defined a site as a distinct area in which a single territorial Spotted Owl or pair had been detected. These sites could include multiple locations of roosts and nests. All sites had USFS-defined protected activity centers (PACs) associated with them. A PAC is an administratively designated polygon surrounding a California Spotted Owl nest or core roost area that delineates for management planning approximately 121 ha of forest dominated by the largest trees and highest canopy cover.

USFS biologists conducted or oversaw surveys in or near PACs at each site. Each site contained multiple permanent call stations. Surveys to elicit responses consisted of either 10 min of vocal imitations or playback of recorded Spotted Owl calls at these stations or >1 hr of vocalizing or playback at sites of historical nesting or roosting. The minimum time elapsed between consecutive surveys was 24 hr. We restricted our database to include only sites that had been surveyed in ≥ 3 years from 1997 to 2007, with at least 2 years being consecutive so colonization and local extinction rates could be estimated. We used data only from nighttime surveys conducted between dusk and dawn. To reduce the number of missing observations we used only the first five surveys in any single year. We defined a site as occupied if a Spotted Owl was detected whether or not it was paired.

Previous studies in unburned landscapes have investigated the effects of habitat variables on California Spotted Owl occupancy and vital rates at two spatial scales surrounding nests and core roost areas, 200 ha (circle of radius 800 m) and 400 ha (circle of radius 1128 m). The 200-ha circle marks approximately half the distance between nest sites of adjacent pairs in the Lassen National Forest in the northern Sierra Nevada (Blakesley et al. 2005), and the 400-ha circle marks half the mean distance between occupied sites in the Eldorado and Tahoe national forests in the central Sierra Nevada (Seamans and Gutiérrez 2007). These circles represent regions within an owl's home range that receive concentrated use. We used the smaller 200-ha circle to conservatively classify whether sites were "burned," but, to be inclusive about fire effects at the site, we used the larger 400-ha circle to describe the severity at which the vegetation burned.

Burned sites were those where a 200-ha circle around the best pre-fire owl location was inside or included the perimeter of one of six major forest fires that burned from 2000 to 2004. In defining a "best detection location" for the Spotted Owl at each site from available survey data we used the following hierarchical criteria: (1) most recent pre-fire nest site; (2) most recent pre-fire detection of a pair; (3) most recent pre-fire detection of a single owl. At 34 of the 41 burned sites the best pre-fire detection locations were within the perimeter of the fires. At the remaining seven sites, the best pre-fire detections were located outside but <400 m from the fire's perimeter.

We also compiled records of occupancy surveys from 1997 to 2007 at 145 unburned California Spotted Owl sites throughout the Sierra Nevada. We obtained available survey data from owl sites within the same national forests as the six fires but where the best detection location was >1500 m from the nearest fire. We defined sites this distance from any recent fire as “unburned” because previous studies in unburned landscapes of the central Sierra Nevada found California Spotted Owls’ occupancy rates were influenced by characteristics of the forest within 1128 m of their nest or core roost area (Seamans 2005, Seamans and Gutiérrez 2007), and the probability of an owl’s foraging is minimal beyond 1500 m from its nest or core roost area (Bond et al. 2009). These sites served as unburned controls that represented latitudes, altitudes, and pre-fire vegetation similar to those of burned sites. We excluded sites where the best pre-fire detection was 400–1500 m from the fire perimeter because we wished to distinguish clearly sites we defined as burned or unburned. Surveys at unburned sites followed the same field methods as at the burned sites and included sites in the Lassen and Plumas national forests in the north and the Eldorado and Tahoe national forests in the central Sierra Nevada. The majority (82%) of the unburned controls were from two areas of demography studies (Plumas–Lassen and Eldorado–Tahoe administrative studies). Our data do not encompass all Spotted Owl sites and surveys in the Sierra Nevada during our study period but rather consist of a subset of survey data that had been provided to the regional office of the USFS and that met our criteria for inclusion.

STATISTICAL ANALYSES

Occupancy analysis. Following MacKenzie et al. (2003), we used the program Presence 3.0 (Hines 2006) to fit models and estimate survey-specific detection probabilities, initial occupancy, and annual probabilities of colonization and local extinction from survey histories. Our analytical design allowed us to examine potential pre-fire differences between burned and unburned sites and determine whether differences existed between groups after fire. Our population of interest was historical Spotted Owl sites that subsequently were burned (or not burned) by fire, so it is 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). Unbalanced sample sizes (number of sites) in each category (burned or unburned) are not an issue in occupancy analysis, so long as numbers of sites in each category are adequate (MacKenzie et al. 2003).

We estimated the following four parameters. 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 . Local extinction (ϵ) is the probability that a site occupied in year $t - 1$ becomes unoccupied in year t . We were most interested

in colonization and local extinction processes that determine occupancy, but the probability of occupancy (ψ) in year t can be calculated from occupancy in year $t - 1$, local extinction, and colonization rates (MacKenzie et al. 2003).

We ranked models by Akaike’s information criterion (AIC) and used AIC weight as a measure of the strength of evidence supporting a given model (Burnham and Anderson 2002). We used a multi-stage (stepwise) approach to keep the number of models in our set reasonable (Lebreton et al. 1992, Doherty et al. 2012, Dugger et al. 2011). We began with the most highly parameterized form of general model [$\gamma(\text{year} + \text{fire}) \epsilon(\text{year} + \text{fire}) p(\text{year} \times \text{survey} + \text{dem})$] (notation defined below). First, we tested for pre-fire differences in detection, colonization, and local extinction between burned and unburned sites. Next, we constrained our model set in a stepwise manner beginning with detection probability. We then held p in its most parsimonious form while we constrained temporal variation in colonization and local extinction parameters. Finally, we added fire effects to the most parsimonious model of colonization and local extinction. We used likelihood-ratio tests to evaluate the significance of fire effects by comparing models that included fire effects against a null model with no fire effects. Because of uncertainty in model selection, we considered all models with $\Delta\text{AIC} \leq 2$ to be potentially the highest-ranking in a set. We used model-averaged parameter estimates to reduce bias and account for model-selection uncertainty in estimating and inferring final parameters for colonization, local extinction, and occupancy (Burnham and Anderson 2002, Doherty et al. 2012).

We modeled the pre-fire difference between burned and unburned sites in mean probabilities of colonization and local extinction as a time-varying individual (site-specific) categorical covariate, coded 0 for unburned sites in all years, 0 for burned sites post-fire, and 1 for burned sites pre-fire. Thus, models with pre-fire effects had structure for a pre-fire difference between burned and unburned sites in the mean estimates of probabilities of colonization and local extinction. We also examined a model in which mean probabilities of detection at burned and unburned sites differed. We found no evidence for a difference in detectability between burned and unburned sites ($\chi^2_1 = 0.64$, $P = 0.36$) and no pre-fire difference in rates of colonization ($\chi^2_1 = 1.95$, $P = 0.11$) or local extinction ($\chi^2_1 = 0.40$, $P = 0.51$). Therefore, we considered burned and unburned sites equivalent and proceeded with examination of fire effects.

To determine the most parsimonious form for detection probability, we first ranked 18 competing models of p while keeping ϵ and γ in the form [$(\text{year} + \text{fire})$] (Table 1). We modeled survey-specific detection within a season as a constant (\cdot), a linear trend (T), a quadratic trend (T^2), and a log-linear trend (\ln/T). We modeled annual probabilities of detection as a constant (\cdot) and as year-specific (year). We included an additional detection effect (dem) between sites that were part of intensive demography studies and all other sites because survey effort at

TABLE 1. Model-selection results for probabilities of detection (p) of the California Spotted Owl at sites in Sierra Nevada national forests, 1997–2007. Model notation is (year, survey, covariates), so $p(\text{year} + . + \text{dem})$ denotes annual variation with detectability constant for all surveys within a year and higher at demography-study sites. Local extinction (ϵ) and colonization (γ) were held in their most parameterized form during selection of the detection model [$\epsilon(\text{year} + \text{fire}) \gamma(\text{year} + \text{fire})$]. Weight (sum = 1.0) gives the relative strength of evidence that a given model is the best model in the set. K is the number of parameters in the model.

Detection model ^a	ΔAIC^b	Weight	K
$p(\text{year} + T + \text{dem})$	0.00	0.34	39
$p(\text{year} + \text{dem})$	0.81	0.23	38
$p(\text{year} + \ln T + \text{dem})$	1.00	0.21	39
$p(\text{year} + T^2 + \text{dem})$	1.16	0.19	40
$p(\text{year} + \text{survey} + \text{dem})$	5.44	0.02	43
$p(\text{year} \times \text{survey} + \text{dem})$	22.95	0.00	81
$p(\text{year} \times T + \text{dem})$	30.07	0.00	50
$p(\text{year} \times \ln T + \text{dem})$	32.49	0.00	50
$p(\text{dem})$	36.53	0.00	27
$p(. + T + \text{dem})$	36.93	0.00	28
$p(. + \ln T + \text{dem})$	37.64	0.00	28
$p(\text{year})$	37.72	0.00	37
$p(. + T^2 + \text{dem})$	38.09	0.00	29
$p(\text{year} + \text{survey})$	39.14	0.00	42
$p(. + \text{survey} + \text{dem})$	42.32	0.00	32
$p(\text{year} \times T^2 + \text{dem})$	43.72	0.00	62
$p(.)$	67.26	0.00	26
$p(\text{year} \times \text{survey})$	99.40	0.00	80

^aYear = year-specific variation, . = constant, survey = survey-specific variation, T = linear trend, T^2 = quadratic trend, $\ln T$ = natural log trend, dem = effect of demography-study site, fire = fire effect.

^bMinimum AIC = 4284.5.

these sites differed. After we determined the most parsimonious form for p we examined temporal and fire effects in ϵ and γ while holding p in its most parsimonious form (Table 2).

We modeled temporal pattern in local extinction and colonization as all possible combinations of constant (.), a linear trend (T), and with year-specific probabilities (year) in each parameter for a total of nine models of temporal variation in local extinction and colonization. The top two models of temporal variation in local extinction and colonization had ΔAIC values ≤ 2 (Table 2), so in the next step we added fire effects to both models.

We modeled the intercept effect of fire on extirpation and colonization (fire) as a time-varying individual (site-specific) categorical covariate, coded 0 for unburned sites in all years, 0 for burned sites pre-fire, and 1 for burned sites post-fire. Thus models with fire effects had structure for a post-fire difference between burned and unburned sites in the mean estimates of probabilities of colonization and local extinction. We ranked a total of nine models of fire effects (Table 3).

Within a given season, sites are assumed to be closed to changes in occupancy; this assumption can be relaxed as long

TABLE 2. Model-selection results for temporal variation in probabilities of colonization (γ) and local extinction (ϵ) of the California Spotted Owl at sites in national forests of the Sierra Nevada, 1997–2007. Detection was held in its most parsimonious form during selection of the local extinction and colonization model [$p(\text{year} + T + \text{dem})$]. Weight (sum = 1.0) gives the relative strength of evidence that a given model is the best model in the set.

Colonization ^a	Local extinction ^a	ΔAIC^b	Weight	K
$\gamma(T)$	$\epsilon(\text{year})$	0	0.52	28
$\gamma(.)$	$\epsilon(\text{year})$	1.24	0.28	27
$\gamma(\text{year})$	$\epsilon(\text{year})$	2.08	0.18	37
$\gamma(T)$	$\epsilon(.)$	8.39	0.01	18
$\gamma(T)$	$\epsilon(T)$	9.71	0.00	19
$\gamma(.)$	$\epsilon(T)$	10.6	0.00	18
$\gamma(.)$	$\epsilon(.)$	12.83	0.00	17
$\gamma(\text{year})$	$\epsilon(.)$	14.11	0.00	27
$\gamma(\text{year})$	$\epsilon(T)$	15.08	0.00	28

^aYear = year-specific variation, . = constant, T = linear trend.

^bMinimum AIC = 4280.1.

TABLE 3. Model-selection results for fire effects in probabilities of colonization (γ) and local extinction (ϵ) of the California Spotted Owl at sites in Sierra Nevada national forests, 1997–2007. Detection was held in its most parsimonious form during selection of the local extinction and colonization model [$p(\text{year} + T + \text{dem})$]. Weight (sum = 1.0) gives the relative strength of evidence that a given model is the best model in the set.

Colonization ^a	Local extinction ^a	ΔAIC^b	Weight	K
$\gamma(T)$	$\epsilon(\text{year} + \text{fire})$	0	0.25	29
$\gamma(T)$	$\epsilon(\text{year})$	0.23	0.22	28
$\gamma(.)$	$\epsilon(\text{year})$	1.47	0.12	27
$\gamma(.)$	$\epsilon(\text{year} + \text{fire})$	1.63	0.11	28
$\gamma(T + \text{fire})$	$\epsilon(\text{year} + \text{fire})$	1.82	0.10	30
$\gamma(T + \text{fire})$	$\epsilon(\text{year})$	2.23	0.08	29
$\gamma(\text{fire})$	$\epsilon(\text{year})$	3.46	0.04	28
$\gamma(\text{fire})$	$\epsilon(\text{year} + \text{fire})$	3.52	0.04	29
$\gamma(\text{year} + \text{fire})$	$\epsilon(\text{year} + \text{fire})$	4.60	0.03	39

^aYear = year-specific variation, . = constant, T = linear trend, fire = fire effect.

^bMinimum AIC = 4279.9.

as changes occur at random (MacKenzie et al. 2006). All fires began after 28 August, so all surveys within a given year were in identical pre- or post-fire condition and fire did not affect conditions within a season.

Vegetation changes. Sierran mixed-conifer forests are characterized by mixed-severity fire regimes resulting in a mosaic of lightly to severely burned patches at intermediate scales (Weatherspoon et al. 1992, Sierra Nevada Ecosystem Project 1996). The USFS defines fire severity according to vegetation effects by the following criteria: low severity = areas of surface fire with little change in cover and little mortality of the dominant vegetation; high severity = areas

where the dominant vegetation experienced great to complete mortality due to the fire; moderate severity = areas between low- and high-severity classes and representing a mixture of effects on the dominant vegetation (USFS Region 5 Remote Sensing Lab, McClellan, CA). Fires in Sierran mixed-conifer forests typically generate a mix of areas burned at low, moderate, and high severity (Odion and Hanson 2006, Miller et al. 2009), but at owl sites we described only the portions burned at high severity because this level most concerns managers as being a threat to California Spotted Owls (USFS 2004).

To qualitatively describe how high-severity fire affected suitable vegetation at burned Spotted Owl sites, we used the GIS extension FRAGSTATS (McGarigal et al. 2002). We defined suitable vegetation as conifer, mixed conifer–hardwood, or hardwood, the types the Spotted Owl typically uses (Gutiérrez et al. 1992). We calculated the area of pre-fire suitable vegetation and the proportion of suitable vegetation that burned at high-severity within a circle of radius 1128 m (400 ha) around the best detection location at each site.

Cover types and fire severity were derived from vegetation maps based on Landsat Thematic Mapper imagery developed by the USFS Pacific Southwest Region's Remote Sensing Lab and available from the GIS Clearinghouse (<http://www.fs.fed.us/r5/rsl/clearinghouse/>). Fire severity was estimated from relative difference normalized burn ratios (RdNBR), which are calibrated with the composite burn index and provide data on a fire's severity to vegetation (see Miller and Thode 2007, Miller et al. 2009).

Simulation analyses. We used the program GENPRES (Bailey et al. 2007) to investigate how different allocations of survey effort affect estimability and bias of parameters of local extinction and colonization. We also wanted to determine the power to detect differences in probabilities of local extinction and colonization between groups of sites under various scenarios of survey-effort allocation. We simulated 3 years of data for two groups (i.e., burned and unburned sites) with realistic values of underlying parameters derived from our data and other Spotted Owl studies (MacKenzie et al. 2009, Dugger et al. 2011). Initial occupancy was set at 0.95 in both groups. Detection probabilities varied annually ($p = 0.50, 0.60, 0.40$). Colonization rates were 0.30 for affected sites, 0.40 for unaffected sites. Local extinction rates were 0.05 for unaffected sites, 0.10 for affected sites. Thus, the effect sizes we examined were 0.10 for colonization ($\Delta\gamma$, a 25% proportional change and more than double our observed effect size), 0.05 for local extinction ($\Delta\epsilon$, a 100% proportional change and similar to our observed effect size).

Our simulated effect sizes were much smaller than the documented effect of the Barred Owl (*S. varia*) on colonization ($\Delta\gamma \approx 0.42$) and local extinction ($\Delta\epsilon \approx 0.27$) of the Northern Spotted Owl (*S. o. caurina*) from its sites (Dugger et al. 2011). However, if a group of sites were affected by some disturbance that lowered colonization and raised local extinction

probabilities in the manner we simulated, the consequence would be occupancy of affected sites 10.4% lower after 3 years. Clearly, our simulations emulate biologically significant effects and a realistic trigger for management.

We simulated 3 years of surveys where all surveys were completed with no missing data. We assumed the two groups of sites were identical in every way except the effect of interest. We varied the number of sites surveyed in each group (50, 100, 200) and the number of surveys per year (2, 3, 5). We created 100 simulated data sets under each of the nine sets of conditions (number of sites and number of surveys) and analyzed them by the appropriate model, $\epsilon(g) \gamma(g) p(\text{year}, .)$. In this model local extinction and colonization differ by group (affected versus unaffected) with detection different in each year but constant within a given year.

We analyzed each of our simulated datasets with the appropriate model and determined estimability, bias, and power. We computed failure of estimability as the number of simulations with one or more parameters whose β coefficient standard errors equal zero and excluded simulations with estimability failures from subsequent analyses. Bias was calculated as the mean difference between the true generating parameter value and the estimate from each simulation. Power was calculated as the proportion of simulated data sets that successfully determined the true group differences in ϵ and γ were significant.

The values reported under Results are means \pm SD.

RESULTS

We analyzed data from 186 California Spotted Owl sites (41 burned and 145 unburned) from 1997 to 2007 with up to five surveys in each year. Sites in demography-study areas made up 27% of the burned sites (11/41) and 81% of the unburned sites (117/145). Out of 10 230 total possible instances of sampling, 6649 (65%) were missing data (no survey done). For sites that were surveyed at least once in a year, the median number of surveys was four at demography-study sites, three at other sites. The mean number of unburned sites surveyed each year was 71 ± 39 (1997–2007), of burned sites 21 ± 3 (2001–2007 because the first fires burned in fall 2000). In the last 7 years of the study (the years when burned sites were available), the proportion of surveyed sites that were in the burned group each year was 0.20 ± 0.06 .

DETECTION, LOCAL EXTINCTION, AND COLONIZATION

The best model of detection probability in our set included variation by year and an effect of demography-study area (Fig. 2). Within a given year, we found evidence that the probability of detection changed over time, with the highest-ranked model of survey-specific detection probability within a year being a positive linear trend (Table 1). We used the most

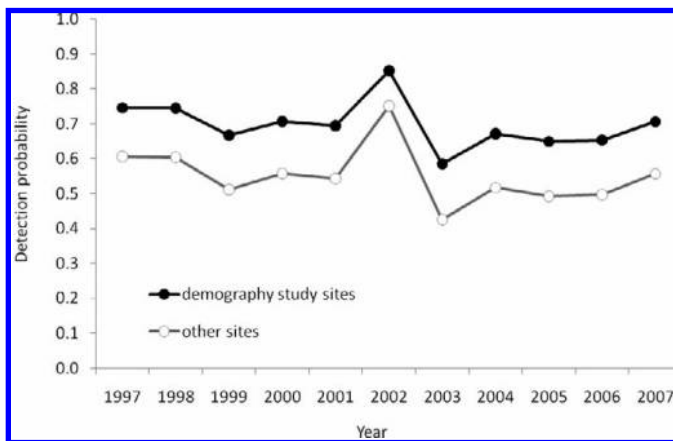


FIGURE 2. Annual probability of detection (p) of the California Spotted Owl at sites of demography studies (filled circles) and other sites (open circles) in national forests in the Sierra Nevada, California. Estimates are from the model $[\gamma(T) \varepsilon(\text{year} + \text{fire}) p(\text{year} + T + \text{dem})]$.

parsimonious form of the detection model for all subsequent model-ranking and estimation procedures. The mean annual probability of detection was 0.698 ± 0.069 at demography-study sites and 0.551 ± 0.084 at all other sites.

Temporal variation in probabilities of colonization and local extinction had two models with ΔAIC values < 2 (Table 2). Both top-ranked models had year-specific probabilities of local extinction, and probability of colonization was a negative linear trend or constant (Table 2). We added fire effects to both of these models in the next step of the analysis (Table 3).

We found no significant differences between burned and unburned sites in probabilities of colonization ($\chi^2_1 = 0.18$, $P = 0.86$) or local extinction ($\chi^2_1 = 2.23$, $P = 0.09$) (Fig. 3). Local extinction parameters for 1999 and 2001 were unestimable so we substituted mean values of each group for those years.

The model-averaged mean probability of colonization of unburned sites was 0.425 ± 0.073 , of burned sites 0.381 ± 0.051 , an effect size of 0.044 lower probability of colonization of burned sites. The model-averaged mean probability of local extinction from unburned sites was 0.137 ± 0.053 , from burned sites 0.094 ± 0.042 , an effect size of 0.043 lower probability of local extinction from burned sites. Model-averaged probabilities of colonization and local extinction resulted in derived site-occupancy probabilities that were slightly higher for burned sites than for unburned sites (Fig. 4). Mean occupancy from 2001–2007 was 0.761 ± 0.045 at unburned sites, 0.802 ± 0.035 at burned sites.

VEGETATION CHANGES

In our sample of 41 burned Spotted Owl sites, the area of pre-fire suitable vegetation (conifer, mixed conifer-hardwood, and hardwood types) within a 400-ha circle around the best pre-fire detection location was $280.2 \text{ ha} \pm 110.3$, range 28.2–398.8. The average proportion of suitable vegetation that burned at

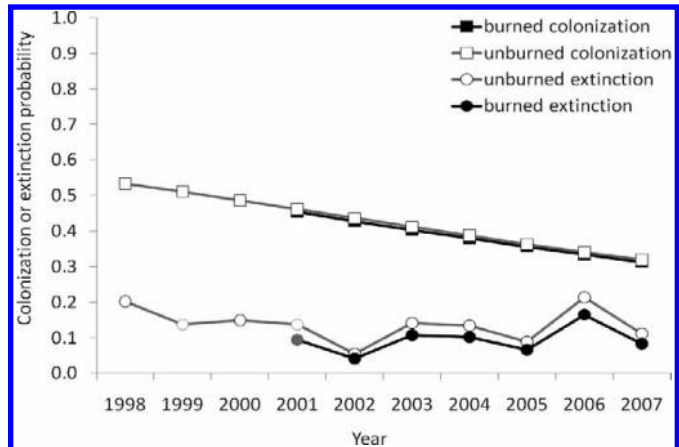


FIGURE 3. Model-averaged probabilities of colonization (squares) and local extinction (circles) of the California Spotted Owl at unburned control sites (unfilled) and sites burned by fires (filled) from 2001 to 2007 in national forests in the Sierra Nevada, California. Local extinction parameters for 1999 and 2001 were unestimable, so values for those years are the mean of all years.

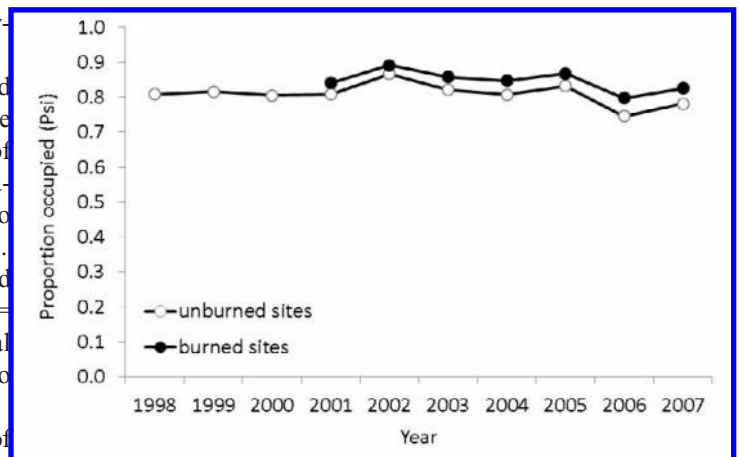


FIGURE 4. Mean annual probabilities of occupancy (ψ) of the California Spotted Owl at unburned sites (unfilled) from 1998 to 2007 and sites burned by fires (filled) from 2001 to 2007 in national forests in the Sierra Nevada, California. Mean annual probabilities of occupancy were derived from model-average estimates of colonization and local extinction.

high severity in the circle was 0.319 ± 0.234 , range 0.001–0.932. Over 50% of suitable vegetation was burned at high severity at 9 of 41 sites. Eight of these sites were surveyed after the fire, with Spotted Owls detected at 5 (63%).

SIMULATIONS

Our simulation results indicate that the number of sites surveyed and the number of surveys per season both had large effects on estimability, bias, and power. The failure rate of

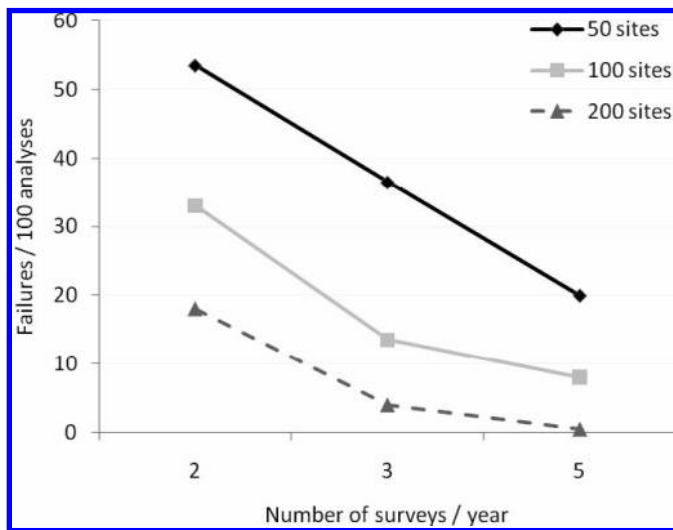


FIGURE 5. Failure rate of estimability under differing scenarios of spatial and temporal effort during 3 years of simulated Spotted Owl surveys. Failure is defined as any parameter SE = 0.

estimability was 54% under the lowest-effort scenario (50 sites, two surveys per year), but this was reduced by effort increased spatially or temporally (Fig. 5). Biases in parameter estimates were minimal in scenarios with ≥ 100 sites per group and ≥ 3 surveys per year (Fig. 6). Below this threshold of effort, estimates of initial occupancy tended to be biased low and estimates of colonization and local extinction rates were generally biased high (Fig. 6). Power to distinguish between groups with known differences was very low for colonization rate in all scenarios (Table 4). Power approximations for local

TABLE 4. Power to detect differences in local extinction ($\Delta\epsilon = 0.05$; $\epsilon = 0.05$ vs. 0.10) and colonization ($\Delta\gamma = 0.10$; $\gamma = 0.30$ vs. 0.40) between two groups of sites under differing scenarios of spatial (number of sites) and temporal (number of surveys per year) effort during 3 years of simulated surveys of Spotted Owl occupancy.

No. sites	No. surveys		
	2	3	5
$\Delta\epsilon = 0.05$			
50	16%	10%	22%
100	6%	40%	55%
200	27%	48%	80%
$\Delta\gamma = 0.10$			
50	16%	12%	22%
100	7%	12%	15%
200	22%	19%	29%

extinction rate were reasonable in scenarios with ≥ 100 sites per group and ≥ 3 surveys per year and good in the highest-effort scenario (Table 4).

DISCUSSION

Forest fire, particularly high-severity fire, is generally presumed to reduce occupancy by California Spotted Owls, on the basis of modifications to the forest canopy, basal area of live trees, and other vegetation and habitat elements. Our results do not support this presumption and instead corroborate and elaborate on previous studies of the Spotted Owl that found occupancy not diminished by forest fires of varying severities (Bond et al. 2002, Jenness et al. 2004, Roberts et al. 2011). We found no significant effect of fire on occupancy dynamics for up to 7 years post-fire and for the vegetation conditions of the sites in our study.

Bond et al. (2002) quantified post-fire site fidelity of all three subspecies of the Spotted Owl and found that 16 of 18 banded owls resighted after fire were at the same sites where they bred previously (89%); these rates were the same as those at unburned sites. Jenness et al. (2004) found rates of post-fire occupancy of the Mexican Spotted Owl (*S. o. lucida*) at 33 burned and 31 unburned sites were not significantly different and did not differ with time since fire. Moreover, the percentage of high-severity fire at a burned site had no significant influence on whether the site was occupied.

Roberts et al. (2011) were the first to model the effects of fire on rates of California Spotted Owl occupancy by incorporating detectability. They obtained unbiased estimates of single-season occupancy in Yosemite National Park at randomly selected burned and unburned areas and demonstrated no effect of fire on site occupancy.

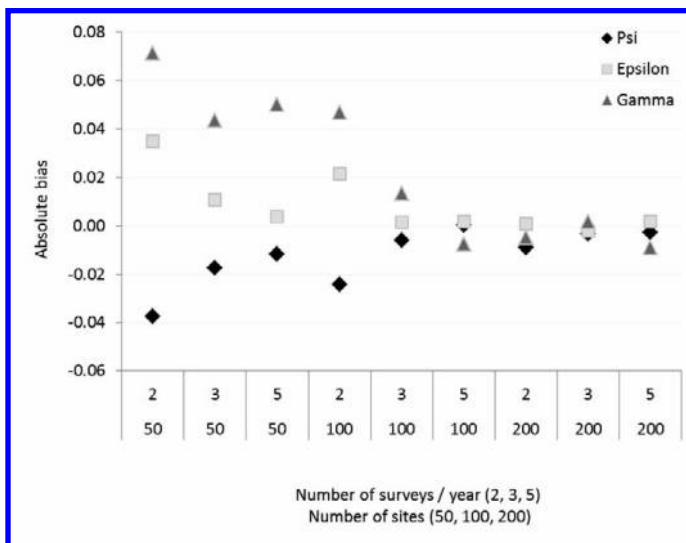


FIGURE 6. Bias of parameter estimates (0 = no bias) under differing scenarios of spatial (number of sites in each of two groups) and temporal (number of surveys per year) effort during 3 years of simulated Spotted Owl surveys. Psi = initial occupancy, epsilon = local extinction probability, gamma = colonization probability.

At our burned sites, an average of 32% of suitable vegetation burned at high severity, yet rates of colonization of and local extinction from these sites were not significantly different from those at unburned sites. Thus owls continued to occupy sites where nearly one third of their suitable habitat burned severely. Existing data for habitat selection in burned landscapes show that within fire-affected landscapes California Spotted Owls typically nest and roost in unburned, lightly burned, or moderately burned patches, while patches burned at high severity provide preferred foraging habitat (Bond et al. 2009). Fires in mixed-conifer forests of the Sierra Nevada typically result in 11–26% of vegetation burned at high severity (Odion and Hanson 2006, Miller et al. 2009). Our results indicate that fire, even fire that burns on average 32% of suitable habitat within a California Spotted Owl site at high severity, does not threaten the persistence of the subspecies on the landscape.

However, it is conceivable that there may be a critical threshold proportion of a site that, if burned at high severity, could adversely affect the owl's occupancy rates. Seamans and Gutiérrez (2007) identified just such a threshold in their examination of 66 California Spotted Owl sites, of which 36 were logged and 2 were burned at high severity over 15 years. They found that logging of ≥ 20 ha of mature conifer forest ($>70\%$ canopy cover dominated by trees >30.4 cm in diameter at breast height) within a 400-ha circle surrounding an owl site resulted in lower rates of colonization and higher rates of local extinction. Seamans and Gutiérrez (2007) did not report the mean area of mature forest in their 400-ha circles, but the range was 0–257 ha. In addition, dispersal of marked breeding birds of both sexes increased dramatically when $\geq 20\%$ of mature conifer habitat in the 400-ha circle was logged.

Thus logging of $\sim 20\%$ of mature conifer forest within the 400-ha circle surrounding a site appears to be a threshold beyond which California Spotted Owl occupancy declines and dispersal of breeding birds increases significantly, whereas when an average of 32% of suitable vegetation within the 400-ha circle burns at high severity, no such negative effect on occupancy is apparent. On the contrary, we found some evidence for a positive effect of high-severity fire in probabilities of local extinction from burned sites lower than from unburned sites, resulting in overall higher occupancy of burned sites. This disparity between the effects fire and logging suggests that “legacy” snags or other habitat components generally not left from logging (Swanson et al. 2011) may play an important role in maintaining habitat suitability for the Spotted Owl and is an issue that deserves further study.

Post-fire logging (e.g., salvage logging) may have affected rates of occupancy of the burned sites we studied. We did not have spatially explicit data on post-fire logging, but it occurred within 2 years after the fire near at least eight of our 41 burned sites. Seven of the eight sites that were later logged were occupied by California Spotted Owls after the fire but

none of the eight sites was occupied after logging. Thus post-fire logging may have adversely affected rates of occupancy of the burned sites, but our sample size was too small for this effect to be included as a covariate. We suggest that future studies examine the effects of fire on rates of occupancy of Spotted Owl sites without the confounding factor of post-fire logging.

Our 3-year simulations provide guidance to land managers and researchers designing population-monitoring programs or experimental systems. The power of survey data to detect a change in colonization and/or local extinction rates is related to survey effort and the proportional difference in rates between groups (Bailey et al. 2007). When a species' detectability is ~ 0.5 it is clear that parameter estimates that are useful for informing management require surveys at a minimum of 100 sites in each group and a minimum of 3 surveys per year. This survey effort is sufficient if the expected proportional effect size is $\sim 100\%$, as in our simulated effect of local extinction. Smaller proportional effect sizes will require more sites and more surveys (as evident in our proportional effect of simulated colonization of $\sim 25\%$) or studies of longer duration if groups and effect sizes are stable over long periods. The power to detect effects of the size and proportion we simulated in 3 years is achieved only with large numbers of sites in each group (≥ 200) and many surveys per year (≥ 5). These recommendations are for historically occupied sites, not randomly selected sites, in which case the number of required sites would be larger and related to occupancy rate.

On the basis of our simulations, and given our mean annual sample sizes (71 unburned and 21 burned sites per year), the failure rate for 3 years of data similar to our survey data was a $\sim 20\%$ chance of unestimable parameters. Additionally, the power of 3 years of data to detect simulated differences between groups in rates of colonization and local extinction was low, $\sim 22\%$. However, Olson et al. (2005) completed six analyses of historical Northern Spotted Owl sites in three study areas where $\leq 25\%$ of 146 surveyed sites were affected by Barred Owls, and the proportional effect sizes during a 13-year study were 7–37%. The authors were able to detect effects of the Barred Owl on occupancy probabilities in five out of six analyses (83%). Also, Seamans and Gutiérrez (2007) observed significant deleterious effects of habitat alteration in a study of 66 California Spotted Owl sites of which 38 were altered during a 15-year study. Thus smaller proportional effects can be detected with low numbers of sites over a longer time.

However, most efforts at management would benefit from more immediate feedback. More than 1470 known historically occupied Spotted Owl sites have been identified in the Sierra Nevada (USFS Region 5 Remote Sensing Lab, McClellan, CA), but management and natural disturbances will only affect a small subset of this total each year. Obtaining data from numbers of affected sites sufficient for meaningful

comparison with controls is possible in 3 years if enough survey effort is expended.

Our simulations suggest that historically occupied California Spotted Owl sites in the Sierra Nevada should be surveyed more frequently, preferably every year, if the effects of fire or management on occupancy are to be distinguished. Efforts should be made to compile all survey data in a regional database for ease of analysis. To further assess the effects of fire on local Spotted Owl persistence, managers should strive to survey ≥ 200 burned sites (or as many as exist) throughout the Sierra Nevada annually as well as ≥ 200 historically occupied unburned sites from among the >1470 known sites. Furthermore, given low detectability rates, we recommend more than one year of surveys be used to determine site occupancy before management that may be detrimental to the Spotted Owl is undertaken in potentially occupied habitat. When detectability is 0.55, as it was at sites not part of demography studies, almost half of all occupied sites would be misclassified as unoccupied by a single season of surveys. To inform management, all sites should be surveyed with a minimum of three visits per year to determine occupancy; five visits per year would provide a significant improvement in estimability and accuracy of parameters and power to detect effects. Meeting these recommendations would require a significant increase in survey effort in national forest lands outside demography-study areas but would provide a robust framework for inference about fire and other management effects throughout the Sierra Nevada.

ACKNOWLEDGMENTS

We thank USFS biologists and technicians throughout the Sierra Nevada for their efforts surveying for the Spotted Owl. We are grateful to district biologists R. Galloway, D. Lipton, T. Mark, A. Palmer, and W. Rannals and Pacific Southwest Region regional threatened and endangered species coordinator P. Krueger for providing the data for our analyses. J. Koltun at Geographic Resource Solutions and P. Nott at the Institute for Bird Populations assisted with GIS analyses, and anonymous reviewers offered helpful comments on the manuscript. This project was funded by grants from Environment Now and Resources Legacy Fund Foundation to The Institute for Bird Populations, and was conducted by the institute's Sierra Nevada Bird Observatory. This is contribution 408 of The Institute for Bird Populations.

LITERATURE CITED

- BAILEY, L. L., J. E. HINES, J. D. NICHOLS, AND D. I. MACKENZIE. 2007. Sampling design trade-offs in occupancy studies with imperfect detection: examples and software. *Ecological Applications* 17:281–290.
- BLAKESLEY, J. A., B. R. NOON, AND D. R. ANDERSON. 2005. Site occupancy, apparent survival, and reproduction of California Spotted Owls in relation to forest stand characteristics. *Journal of Wildlife Management* 69:1554–1564.
- BLAKESLEY, J. A., D. R. ANDERSON, AND B. R. NOON. 2006. Breeding dispersal in the California Spotted Owl. *Condor* 108:71–81.
- BLAKESLEY, J. A., M. E. SEAMANS, M. M. CONNER, A. B. FRANKLIN, G. C. WHITE, R. J. GUTIÉRREZ, J. E. HINES, J. D. NICHOLS, T. E. MUNTUN, D. W. H. SHAW, J. J. KEANE, G. N. STEGER, AND T. L. McDONALD. 2010. Population dynamics of Spotted Owls in the Sierra Nevada, California. *Wildlife Monographs* 174:1–36.
- BOND, M. L., R. J. GUTIÉRREZ, A. B. FRANKLIN, W. S. LAHAYE, C. A. MAY, AND M. E. SEAMANS. 2002. Short-term effects of wildfires on Spotted Owl survival, site fidelity, mate fidelity, and reproductive success. *Wildlife Society Bulletin* 30:1022–1028.
- BOND, M. L., D. E. LEE, R. B. SIEGEL, AND J. P. WARD JR. 2009. Habitat use and selection by California Spotted Owls in a postfire landscape. *Journal of Wildlife Management* 73:1116–1124.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multi-model inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.
- DOHERTY, P. F., G. C. WHITE, AND K. P. BURNHAM. 2012. Comparison of model building and selection strategies. *Journal of Ornithology* 152 (Supplement 2):317–323.
- DUGGER, K. M., R. G. ANTHONY, AND L. S. ANDREWS. 2011. Transient dynamics of invasive competition: Barred Owls, Spotted Owls, habitat, and the demons of competition present. *Ecological Applications* 21:2459–2468.
- FIELD, S. A., A. J. TYRE, AND H. P. POSSINGHAM. 2005. Optimizing allocation of monitoring effort under economic and observational constraints. *Journal of Wildlife Management* 69:473–482.
- GUTIÉRREZ, R. J., J. VERNER, K. S. MCKELVEY, B. R. NOON, G. N. STEGER, D. R. CALL, W. S. LAHAYE, B. B. GINGHAM, AND J. S. SENSER. 1992. Habitat relations of the California Spotted Owl, p. 79–99. In J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould Jr., and T. W. Beck [EDS.], *The California Spotted Owl: a technical assessment of its current status*. U. S. Forest Service General Technical Report PSW-133, Albany, CA.
- GUTIÉRREZ, R. J., A. B. FRANKLIN, AND W. S. LAHAYE. 1995. Spotted Owl (*Strix occidentalis*), no 179. In A. Poole and F. Gill [EDS.], *The birds of North America*. Academy of Natural Sciences, Philadelphia.
- HINES, J. E. [ONLINE]. 2006. PRESENCE 2—software to estimate patch occupancy and related parameters. Patuxent Wildlife Research Center, Laurel, MD. <<http://137.227.242.23/software/doc/presence/presence.html>> (9 September 2011).
- JENNESS, J. J., P. BEIER, AND J. L. GANEY. 2004. Associations between forest fire and Mexican Spotted Owls. *Forest Science* 50:765–772.
- KENDALL, W. L., S. J. CONVERSE, P. F. DOHERTY JR., M. B. NAUGHTON, A. ANDERS, J. E. HINES, AND E. FLINT. 2009. Sampling design considerations for demographic studies: a case of colonial seabirds. *Ecological Applications* 19:55–68.
- LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- MACKENZIE, D. I., AND J. A. ROYLE. 2005. Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology* 42:1105–1114.
- MACKENZIE, D. I., J. D. NICHOLS, G. B. LACHMAN, S. DROEGE, J. A. ROYLE, AND C. A. LANGTIMM. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- MACKENZIE, D. I., J. D. NICHOLS, J. E. HINES, M. G. KNUTSON, AND A. D. FRANKLIN. 2003. Estimating site occupancy, colonization and local extinction when a species is detected imperfectly. *Ecology* 84:2200–2207.
- MACKENZIE, D. I., J. D. NICHOLS, J. A. ROYLE, K. H. POLLOCK, L. L. BAILEY, AND J. E. HINES. 2006. Occupancy estimation and

- modeling: inferring patterns and dynamics of species occurrence. Elsevier, Oxford, United Kingdom.
- MACKENZIE, D. I., J. D. NICHOLS, M. E. SEAMANS, AND R. J. GUTIÉRREZ. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology* 90:823–835.
- MAZEROLLE, M. J., A. DESROCHERS, AND L. ROCHEFORT. 2005. Landscape characteristics influence pond occupancy by frogs after accounting for detectability. *Ecological Applications* 15: 824–834.
- MCGARIGAL, K., S. A. CUSHMAN, M. C. NEEL, AND E. ENE [ONLINE]. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. <http://www.umass.edu/landeco/research/fragstats/downloads/fragstats_downloads.html> (March 2011).
- MILLER, J. D., AND A. E. THODE. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta normalized burn ratio (dNBR). *Remote Sensing of Environment* 109:66–80.
- MILLER, J. D., KNAPP, E. E., KEY, C. H., SKINNER, C. N., ISBELL, C. J., CREASY, R. M. AND SHERLOCK, J. W. 2009. Calibration and validation of the relative differenced normalized burn ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. *Remote Sensing of Environment* 113:645–656.
- ODION, D. C., AND C. T. HANSON. 2006. Fire severity in conifer forests of the Sierra Nevada, California. *Ecosystems* 9:177–189.
- OLSON, G. S., R. G. ANTHONY, E. D. FORSMAN, S. H. ACKERS, P. J. LOSCHL, J. A. REID, K. M. DUGGER, E. M. GLENN, AND W. J. RIPLE. 2005. Modeling of site occupancy dynamics for Northern Spotted Owls, with emphasis on the effects of Barred Owls. *Journal of Wildlife Management* 69:918–932.
- ROBERTS, S. L., J. W. VAN WAGTENDONK, A. K. MILES, AND D. A. KELT. 2011. Effects of fire on Spotted Owl site occupancy in a late-successional forest. *Biological Conservation* 144:610–619.
- SEAMANS, M. E. 2005. Population biology of the California Spotted Owl in the central Sierra Nevada. Ph.D. dissertation, University of Minnesota, St. Paul, MN.
- SEAMANS, M. E., AND R. J. GUTIÉRREZ. 2007. Habitat selection in a changing environment: the relationship between habitat alteration and Spotted Owl territory occupancy and breeding dispersal. *Condor* 109:566–576.
- SIERRA NEVADA ECOSYSTEM PROJECT. 1996. Final report to Congress, vols. I, II, and III. Centers for Water and Wildland Resources, University of California, Davis, CA.
- SKALSKI, J. R., A. HOFFMAN, AND S. G. SMITH. 1993. Testing the significance of individual- and cohort-level covariates in animal survival studies, p. 9–28. *In* J. D. Lebreton and P. M. North [EDS.], *Marked individuals in the study of bird population*. Birkhauser Verlag, Basel, Switzerland.
- SMUCKER, K. M., R. L. HUTTO, AND B. M. STEELE. 2005. Changes in bird abundance after wildfire: importance of fire severity and time since fire. *Ecological Applications* 15:1535–1549.
- SWANSON, M. E., J. F. FRANKLIN, R. L. BESCHTA, C. M. CRISAFULLI, D. A. DELLASALA, R. L. HUTTO, D. B. LINDENMAYER, AND F. J. SWANSON. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment* 9:117–125.
- U.S. FOREST SERVICE (USFS). 1988. Spotted Owl inventory and monitoring handbook. U.S. Forest Service, Portland, OR.
- U.S. FOREST SERVICE (USFS). 2004. Sierra Nevada Forest Plan amendment, record of decision. U.S. Forest Service, Vallejo, CA.
- VERNER, J. K., S. MCKELVEY, B. R. NOON, R. J. GUTIÉRREZ, G. I. GOULD, AND T. W. BECK [TECH. COORDS.]. 1992. The California Spotted Owl: a technical assessment of its current status. U.S. Forest Service, Pacific Southwest Research Station, General Technical Report PSW-133, Albany, CA.
- WEATHERSPOON C. P., S. J. HUSARI, AND J. W. VAN WAGTENDONK. 1992. Fire and fuels management in relation to owl habitat in forests of the Sierra Nevada and southern California, p. 247–260. *In* J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, and T. W. Beck [tech. coords.], *The California Spotted Owl: a technical assessment of its current status*. U.S. Forest Service, Pacific Southwest Research Station, General Technical Report PSW-133, Albany, CA.
- WILLIAMS, B. K., J. D. NICHOLS, AND M. J. CONROY. 2002. Management of animal populations. Academic Press, San Diego.