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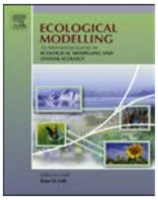

Using integrated population models to improve conservation monitoring: California spotted owls as a case study

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ABSTRACT

Integrated population models (IPMs) constitute a relatively new approach for estimating population trends and demographic parameters that makes use of multiple, independent data sources (e.g., count and mark-recapture data) within a unified statistical framework. In principle, IPMs offer several advantages over more conventional modeling approaches that rely on a single source of data, including greater precision in parameter estimates and the ability to estimate demographic parameters for which no explicit data are available. However, to date, the IPM literature has focused primarily on model development and evaluation, and few "real-world" applications have demonstrated that IPMs can strengthen inferences about population dynamics in a species of conservation concern. Here, we combined 23 years of count, occupancy, reproductive, and mark-recapture data into an IPM framework to estimate population trends and demographic rates in a population of California spotted owls (*Strix occidentalis occidentalis*). Using this framework, we observed a significant population decline, as evidenced by the geometric mean of the finite annual rate of population change ($\widehat{\lambda}_t = 0.969$, 95% CRI 0.957–0.980) and the resulting realized population change (proportion of the initial population present in 2012; $\widehat{\Delta}_{2012} = 0.501$, 95% CRI 0.383–0.641). The estimated decline was considerably greater than the approximately 30% decline estimated using conventional mark-recapture and occupancy approaches (Tempel and Gutiérrez, 2013). The IPM likely yielded a greater decline because it allowed for the inclusion of three years of data from the beginning of the study that were omitted from previous analyses to meet the assumptions of mark-recapture models. The IPM may also have yielded a greater estimate of decline than occupancy models owing to an increase in the number of territories occupied by single owls over the study period. All demographic parameters (adult and juvenile apparent survival, reproductive rate, immigration rate) were positively correlated with $\widehat{\lambda}_t$, but immigration was fairly high ($\widehat{imm}_t = 0.097$, 95% CRI 0.055–0.140) and contributed most to temporal variation in $\widehat{\lambda}_t$, suggesting that changes in owl abundance were influenced by processes occurring outside of our study area. More broadly, our results indicated that the IPM framework has the potential to strengthen inference in population monitoring and demographic studies, particularly for those involving long-lived species whose abundance may be slowly declining. In our case, the conservation implications from the results of the IPM suggested a decline in the population of owls that was steeper than previously thought.

1. Introduction

Many species are endangered by anthropogenic factors such as habitat loss and fragmentation, introduced species, climate change, and overexploitation (Wilcove et al., 1998; Fahrig, 2003; Moritz and Agudo, 2013), but detecting population declines and estimating rates of decline in rare species can be challenging (Thompson, 2004). Rare species are often widely distributed at low densities, which can lead to low precision in estimates of abundance and population trends because of small sample sizes. In addition, species of conservation concern are often characterized by "slow" life-history strategies where longevity has been selected at the expense of reproduction (Cardillo et al., 2005). Detecting population declines in such species can be challenging because long life spans and low mortality in adults can result in slow, but biologically important, declines. As a consequence, the status of many species of conservation concern remains uncertain despite the implementation of large-scale and labor-intensive population monitoring

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programs (e.g., Cam et al., 2003; Kendall et al., 2009; Blakesley et al., 2010).

Conventional approaches for estimating population trends typically make use of a single source of information such as mark-recapture, count, or presence–absence data (Williams et al., 2002; MacKenzie et al., 2006). For example, population growth can be estimated from mark-recapture data using "robust designs" when a study area has been surveyed on more than one occasion within primary sampling periods (Otis et al., 1978) or using a temporal symmetry model when only one survey has been conducted per primary sampling period (Pradel, 1996). In contrast, integrated population models (IPMs) represent a more recent analytical approach that can combine multiple data sources, including count, occupancy, mark-recapture, and reproductive data, into a unified framework (Besbeas et al., 2002; Abadi et al., 2010a). This approach offers several potential advantages over separate analysis of each dataset, including more precise estimates of population growth and the ability to estimate demographic parameters for which no explicit data are available (Schaub and Abadi, 2011). For example, IPMs can provide estimates of immigration rates without explicit data on the movements of individuals into a study area or population (Abadi et al., 2010). Reliable estimates of immigration are notoriously elusive, yet essential to determine if a population of interest is a sink population that would decline in the absence of recruitment from other populations or if regional processes affect local population dynamics (Pulliam, 1988; Thomas and Kunin, 1999; Peery et al., 2006). However, thus far, the IPM literature has been primarily about model development and evaluation, with few "real-world" applications demonstrating that IPMs can improve conservation monitoring (Gauthier et al., 2007; Schaub et al., 2007, 2010).

The California spotted owl (*Strix occidentalis occidentalis*) is a subspecies of conservation concern because it inhabits old forests which have high economic value. Thus, logging of these forests is a conservation concern because it may negatively affect the owl. However, the status (i.e., population trend) of California spotted owls in the Sierra Nevada has been uncertain for more than two decades despite the results of large-scale mark-recapture studies, partly because of a lack of precision for estimates of population change (Franklin et al., 2004; Blakesley et al., 2010; Tempel and Gutiérrez, 2013). A previous occupancy analysis of our study population indicated a decline in the number of occupied territories (Tempel and Gutiérrez, 2013), but this simple occupancy model did not account for factors that may impact population size (e.g., the proportion of territories occupied by single owls). Uncertainty about population status as a result of imprecise estimation contributed to decisions not to list the California spotted owl as a threatened species under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service, 2003, 2006). Moreover, uncertainty in the population trend of California spotted owls has challenged the assessment of two major forest-management plans implemented to protect owls and their habitat on public lands in the Sierra Nevada (Verner et al., 1992; U.S. Forest Service, 2004).

Here, we developed an IPM to estimate finite annual rates of population change (λ_t) and realized population change (Δ_t) over a 23-year period in a demographically open population of California spotted owls in the central Sierra Nevada (Seamans et al., 2001; Franklin et al., 2004; Blakesley et al., 2010). Our IPM incorporated data on population counts, mark-recapture histories, and reproduction, but it differed from previous IPM applications in that we first used a multi-state occupancy model to obtain annual "counts" of the number of adults and young produced, rather than using naïve counts that did not account for imperfect detection. This approach would produce stronger inferences about population trends if, for example, researchers became more proficient over time at locating individuals on their study area. In addition, incorporating these different sources of data into an IPM differed from all previous studies of spotted owl demographics that relied solely upon either mark-recapture or occupancy data to estimate population change (e.g., Gutiérrez, 1994; Forsman et al., 2011; Tempel and Gutiérrez, 2013). We structured the IPM such that it contained annual random effects for apparent adult and juvenile survival, reproductive rate, and immigration rate, which allowed us to evaluate the sensitivity of population growth to changes in vital rates. By using an IPM framework, we strove to improve precision in estimates of population change, understand the role of immigration to local population dynamics, and reduce uncertainty about the status of California spotted owls in the Sierra Nevada.

2. Materials and methods

2.1. Study area

We conducted our study on a contiguous 35,500-ha area on the Eldorado National Forest in the central Sierra Nevada, California, which has been the site of a long-term mark-recapture study of California spotted owls (Seamans et al., 2001; Franklin et al., 2004; Blakesley et al., 2010; Tempel and Gutiérrez, 2013). We surveyed the entire area each year regardless of land cover, topography, access, or land ownership. Approximately 60% of the study area was public land managed by the USFS, and 40% was private land managed by timber companies. The primary vegetation type on our study area was mixed-conifer forest, elevations ranged from 360 to 2400 m, and the climate was characterized by cool, wet winters and warm, dry summers.

2.2. Spotted owl surveys

We conducted annual surveys for spotted owls from 1986 to 2012 during their breeding season (1 April–31 August). Although the entire study area was not fully surveyed until 1993 because of funding constraints (Tempel and Gutiérrez, 2013), we used all data from 1990 to 2012 because our analytical approach could accommodate data from years where we had lower survey effort. For example, we used a Bayesian analysis for the multi-state occupancy model (see Section 2.3.1) and imputed the true state of each sampling unit (i.e., territory) for each iteration of the Markov chain (MacKenzie et al., 2009). Thus, the number of adults and the number of young that they produced were estimated at territories that were not surveyed in a given year.

Spotted owl surveys consisted of imitating owl vocalizations (vocal lures) for 10 min at designated survey stations or while walking along survey routes. We determined the sex of spotted owls responding to vocal lures by the pitch of their 4-note territorial calls; males have a lower-pitched call than females (Forsman et al., 1984). If we detected spotted owls on nocturnal surveys, we then conducted diurnal surveys to locate and band unmarked individuals, resight marked individuals, and assess reproduction (Franklin et al., 1996). We banded adult owls with a locking, numbered metal band on one leg and a unique combination of color band and color tab on the other leg (Franklin et al., 1996). We banded juvenile owls with a numbered metal band on one leg and a non-unique cohort band on the other leg, but we replaced the cohort band with a unique band and tab combination if we later recaptured the juvenile as an adult.

2.3. Analytical design

We used an age-structured population IPM structurally identical to the model developed by Abadi et al. (2010a) for the little owl (*Athene noctua*). The data used in the IPM consisted of annual population counts of adults (y), annual counts of the number of young

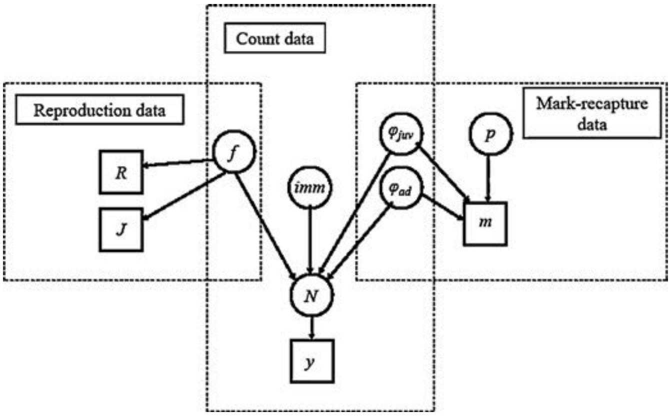

Fig. 1. Graphic representation of an integrated population model for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990–2012 (modeling framework adapted from Abadi et al., 2010a). R = number of adults assessed for reproduction; J = number of young produced, f = number of young produced per adult, imm = immigration rate (number of immigrants per adult), φ_{juv} = juvenile apparent survival probability, φ_{ad} = adult apparent survival probability, m = capture–recapture data, p = recapture probability, y = population count data, N = population size.

produced (J), and mark-recapture data for fledglings and adults (m) (Fig. 1). The IPM provided estimates of adult and juvenile apparent survival, reproductive rates, immigration rates, and population size. Immigration rates can be estimated within this framework despite the lack of explicit data on immigration. Rather than using raw counts of the number of owls detected each year, we first used a multi-state occupancy model that incorporated imperfect detection (MacKenzie et al., 2009) to obtain annual estimates of the number of adults (y) and number of young produced (J). As a result, R (the number of adults for which reproduction was assessed) in Fig. 1 was equal to y. We then used the estimates of y and J from the multi-state occupancy model as input data for the IPM, along with the mark-recapture data.

2.3.1. Multi-state occupancy model

We implemented a state-space modeling approach similar to MacKenzie et al. (2009). State-space models contain two components—a submodel for the latent, state process (e.g., the occupancy model described below) and a submodel for the observation process in which the observed data are conditional on the unobserved or partially observed state process (Buckland et al., 2004). The sampling units for the multi-state occupancy model were the owl territories; we considered a territory to be a site where spotted owls were observed either roosting or nesting at some point during the study. Each territory could be in one of five states: 0 = no spotted owls present; 1 = single adult present; 2 = adult pair present, no young produced; 3 = adult pair present, one young produced; 4 = adult pair present, two young produced. Three young were rarely produced (four times in 23 years), so we did not include a sixth state with three young. Instead, we categorized these occasions as state 4 (i.e., two young produced). Surveys in which no spotted owls were detected had to be ≥30 min in total duration to be considered adequate for inclusion in the database. We did not include nocturnal detections that were >400 m from the edge of long-term core use areas (Berigan et al., 2012) because these individuals may have been individuals from a neighboring territory or non-territorial "floaters."

We divided each breeding season into 10 bimonthly survey periods (1–15 April, 16–30 April, 1–15 May, 16–31 May, etc.). During each survey period, we recorded the highest occupancy state (0, 1, 2, 3, or 4) observed at each territory; the observed occupancy state may have been less than or equal to the true value. On surveys conducted before 1 June, we constrained the probabilities of detecting reproduction (states 3 and 4) to 0 because young were observed before this date on only 5 occasions during the 23-year study period. If a territory was not surveyed during a bimonthly survey period, we treated it as a missing observation. The primary sampling periods were breeding seasons (i.e., years), and the secondary sampling periods were the bimonthly periods within each breeding season.

We used the model parameterization that contained parameters for initial occupancy, transition probability, and detection probability (MacKenzie et al., 2009). We denoted the probability that a territory was in state m in the initial year as $\varphi^{[m]}$, and defined the initial occupancy vector as follows:

$$\phi_0 = [\,1-\varphi^{[1]}-\varphi^{[2]}-\varphi^{[3]}-\varphi^{[4]} \quad \varphi^{[1]} \quad \varphi^{[2]} \quad \varphi^{[3]} \quad \varphi^{[4]}\,]$$

We denoted the probability of a territory transitioning from state m in year t to state n in year $t+1$ as $\varphi_t^{[m,n]}$, and defined the transition probability matrix as follows:

$$\phi_{t+1} = \begin{bmatrix} 1-\varphi_t^{[0,1]}-\varphi_t^{[0,2]}-\varphi_t^{[0,3]}-\varphi_t^{[0,4]} & \varphi_t^{[0,1]} & \varphi_t^{[0,2]} & \varphi_t^{[0,3]} & \varphi_t^{[0,4]} \\ 1-\varphi_t^{[1,1]}-\varphi_t^{[1,2]}-\varphi_t^{[1,3]}-\varphi_t^{[1,4]} & \varphi_t^{[1,1]} & \varphi_t^{[1,2]} & \varphi_t^{[1,3]} & \varphi_t^{[1,4]} \\ 1-\varphi_t^{[2,1]}-\varphi_t^{[2,2]}-\varphi_t^{[2,3]}-\varphi_t^{[2,4]} & \varphi_t^{[2,1]} & \varphi_t^{[2,2]} & \varphi_t^{[2,3]} & \varphi_t^{[2,4]} \\ 1-\varphi_t^{[3,1]}-\varphi_t^{[3,2]}-\varphi_t^{[3,3]}-\varphi_t^{[3,4]} & \varphi_t^{[3,1]} & \varphi_t^{[3,2]} & \varphi_t^{[3,3]} & \varphi_t^{[3,4]} \\ 1-\varphi_t^{[4,1]}-\varphi_t^{[4,2]}-\varphi_t^{[4,3]}-\varphi_t^{[4,4]} & \varphi_t^{[4,1]} & \varphi_t^{[4,2]} & \varphi_t^{[4,3]} & \varphi_t^{[4,4]} \end{bmatrix}$$

Similarly, we denoted the probability of observing a territory in state l during survey period j of year t when its true state was m as $p_{j,t}^{[l,m]}$, and defined the detection probability matrix as follows (assuming that a territory could not be observed in a state higher than its true state):

$$\begin{array}{c|ccccc} & & & \text{Observed state} & & \\ \text{True state} & 0 & 1 & 2 & 3 & 4 \\ \hline 0 & 1 & 0 & 0 & 0 & 0 \\ 1 & 1-p_{j,t}^{[1,1]} & p_{j,t}^{[1,1]} & 0 & 0 & 0 \\ 2 & 1-p_{j,t}^{[1,2]}-p_{j,t}^{[2,2]} & p_{j,t}^{[1,2]} & p_{j,t}^{[2,2]} & 0 & 0 \\ 3 & 1-p_{j,t}^{[1,3]}-p_{j,t}^{[2,3]}-p_{j,t}^{[3,3]} & p_{j,t}^{[1,3]} & p_{j,t}^{[2,3]} & p_{j,t}^{[3,3]} & 0 \\ 4 & 1-p_{j,t}^{[1,4]}-p_{j,t}^{[2,4]}-p_{j,t}^{[3,4]}-p_{j,t}^{[4,4]} & p_{j,t}^{[1,4]} & p_{j,t}^{[2,4]} & p_{j,t}^{[3,4]} & p_{j,t}^{[4,4]} \end{array}.$$

Related sets of parameters (initial occupancy probabilities, detection and transition probabilities for a specific state) were constrained to sum to 1. For example, the individual probabilities that a territory in state m in year t was in one of the five states in year $t+1$ ($\varphi_t^{[m,0]}$, $\varphi_t^{[m,1]}$, $\varphi_t^{[m,2]}$, $\varphi_t^{[m,3]}$, $\varphi_t^{[m,4]}$) must sum to 1. Similarly, the individual detection probabilities for a territory in state l during a given year and survey period must sum to 1, keeping in mind that a territory cannot be observed in a state higher than its true state. Thus, if a territory was in true state 3 during year t, then $p_{j,t}^{[0,3]}$, $p_{j,t}^{[1,3]}$, $p_{j,t}^{[2,3]}$, and $p_{j,t}^{[3,3]}$ must sum to 1 for each survey period j.

We used Markov chain Monte Carlo (MCMC) methods within a Bayesian framework to estimate the model parameters (Link et al., 2002; MacKenzie et al., 2009). We considered the true state of each territory each year to be a latent (unknown) variable and predicted or imputed its true state from the observed data. As noted by MacKenzie et al. (2009), an advantage of this approach is that relevant summaries of the system (e.g., the number of territories in each state) can be calculated easily. Thus, we estimated the number of fledglings produced each year (J) and the number of adults in the population each year (y) as:

$$J = \text{no. of territories in state } 3 + [2 \times (\text{no. of territories in state } 4)]$$

$$y = \text{no. of territories in state } 1 \\ + [2 \times (\text{no. of territories in states } 2, 3, \text{ or } 4)]$$

For related model parameters that were constrained to sum to 1 (see above), a Dirichlet prior distribution was appropriate. The Dirichlet is a multivariate generalization of the beta distribution and the conjugate prior for multinomial distributions (McCarthy, 2007). However, the parameters of a Dirichlet distribution cannot be stochastic nodes in OpenBUGS software, so we induced a Dirichlet distribution (Spiegelhalter et al., 2003). For each model parameter (i), we specified an associated variable (β_i) with a gamma distribution. Then for a group of related model parameters, we set each parameter, i, equal to $(\beta_i/\sum_{k=1}^{N}\beta_k)$ where N was the total number of parameters within the group; this ensured that their sum was 1 (Spiegelhalter et al., 2003). The gamma distributions were characterized by a shape parameter (r) and a rate parameter (θ) (Spiegelhalter et al., 2003). We incorporated annual random effects for all detection and transition probabilities by specifying uninformative distributions for the parameters of the gamma distribution within a related group of β_i's, where $r \sim$ Uniform (0.5, 10) and $\theta \sim$ Gamma (1, 1). In addition, when a territory's true state was 1, there were only two possible outcomes for the detection probability (0 = no detection, 1 = single owl detected). Therefore, we specified that logit($p_{j,t}^{[1,1]}$) = $\mu + \varepsilon$, where $\mu \sim$ Normal (0, 10,000) and $\varepsilon \sim$ Normal (0, σ). We used a hyperprior ($\sigma \sim$ Uniform[0,10]) in the error term to incorporate annual random effects into the estimation of $p_{j,t}^{[1,1]}$. We held within-year detection probabilities constant to keep the number of estimated parameters at a manageable level, except we constrained the probability of detecting reproduction before 1 June to 0 (see above; MacKenzie et al., 2009).

We conducted the analysis using OpenBUGS (Lunn et al., 2009; see Appendix A for model code). We ran three chains of 20,000 iterations to approximate the posterior distributions of the model parameters after discarding the initial 10,000 iterations of each chain as a burn-in period. After the burn-in period, the chains were well-mixed as the Gelman–Rubin convergence statistic ($\hat{R}$) was <1.1 for all parameters (Gelman and Hill, 2007; see trace history plots for y and J in Appendix C).

2.3.2. *Integrated population model*

The modeled population consisted of three age classes (juvenile, 1 year old, ≥2 years old). We hereafter refer to any owls at least 1 year old as adults. Non-juvenile spotted owls can be distinguished into 3 age classes (1 year old, 2 years old, and ≥3 years old) based on the appearance of their rectrices (Moen et al., 1991). However, prior analyses using Cormack–Jolly–Seber models (Seber, 1982) showed that differences in annual survival among these three age classes were small (<0.10; unpublished data); 1- and 2-year-olds also comprised <10% of the total population on average (unpublished data). Furthermore, we did not use a female-only model because single spotted owls at territories were typically males and a potentially important component of the total population size. We modeled the total population of males and females combined, instead of separate population components for each sex, because another occupancy state would have been required to distinguish between single males and single females, but data were sparse for single females.

As noted above, we used the estimates of y and J provided by the multi-state occupancy model, rather than naïve counts of young and adults, to account for imperfect detection. The mark-recapture data were summarized as m-arrays (Burnham et al., 1987) for juveniles and adults. This format allowed much faster computation but reduced the flexibility of the modeling (i.e., individual covariates could not be used). The data sets were not independent, which is an assumption of the IPM, but Abadi et al. (2010b) demonstrated with simulations that using non-independent data for a structurally identical IPM resulted in minimal bias in the parameter estimates. In addition, they observed increased precision and accuracy in parameter estimation when all three sources of data were analyzed simultaneously, rather than individually.

We again used a state-space approach where the state process was described by the following distributions:

$$N_{1,t+1} \sim Poisson([N_{1,t} + N_{2,t}] \times f_t \times \varphi_{juv,t})$$

$$N_{2,t+1} \sim Binomial([N_{1,t} + N_{2,t}], \varphi_{ad,t}) + Poisson([N_{1,t} + N_{2,t}] \times imm_t)$$

where $N_{1,t}$ was the number of 1-year-old spotted owls at time t; $N_{2,t}$ was the number of spotted owls ≥2 years old at time t; φ_{juv} and φ_{ad} were the apparent survival probabilities of juveniles and adults, respectively, from time t to $t+1$; f_t was the number of young produced per adult at time t; and imm_t was the immigration rate (number of immigrant adult spotted owls into the population at time $t+1$ per adult in the population at time t). Thus, the expected number of 1-year-old spotted owls at time $t+1$ was the product of the number of young produced at time t and juvenile apparent survival from t to $t+1$. The expected number of spotted owls ≥2 years old at time $t+1$ had two components: (i) the number of adults at time t multiplied by adult apparent survival from t to $t+1$, and (ii) the number of adults at time t multiplied by the immigration rate from t to $t+1$. As noted by Abadi et al. (2010a), immigrants were assumed to enter the population as individuals ≥2 years old, but the results would be identical if they were assumed to enter as 1-year-olds. The total population size (N_t) was the sum of $N_{1,t}$ and $N_{2,t}$. We estimated the finite rate of population change (λ_t) as N_{t+1}/N_t and the realized population change (Δ_t) as N_t/N_1.

We specified Poisson distributions for the "count" data (y, J), which allowed the absolute observation error to change proportionally with population size and reproductive output:$y_t \sim Poisson(N_t)$

$$J_t \sim Poisson(R_t \times f_t).$$

Kéry and Schaub (2012) noted for an IPM having the same structure as ours that the Poisson distribution produced faster convergence of the Markov chains and identical parameter estimates when compared to the lognormal or normal distribution. We used a normal distribution to describe the initial population sizes of owls that were 1 year old, ≥2 years old, and immigrants; the priors for each class were ~Normal (100, 10,000). For the mark-recapture data formatted as m-arrays, we used the Cormack–Jolly–Seber (CJS) model with a product multinomial distribution for the estimation of φ_{juv} and φ_{ad} (Kéry and Schaub, 2012). Recapture probabilities (p; not to be confused with detection probability in the occupancy model) were also estimated within the CJS model. We incorporated annual random effects by assuming that the demographic

Table 1
Posterior means (95% credible interval [CRI]) of parameters from a multi-state occupancy model of California spotted owl (*Strix occidentalis occidentalis*) territories in the central Sierra Nevada, 1990–2012. The territory states are: 0 = no spotted owls present; 1 = single adult present; 2 = pair of adults present, no young produced; 3 = pair of adults present, one young produced; 4 = pair of adults present, two young produced.

Parameter	Territory state				
	0	1	2	3	4
Initial occupancy[a]					
$\varphi^{[m]}$	0.02 (0.00–0.15)	0.02 (0.00–0.17)	0.52 (0.22–0.75)	0.03 (0.00–0.30)	0.41 (0.19–0.66)
Detection probabilities[b]					
$p^{l,1}$	0.72 (0.64–0.80)	0.28 (0.20–0.36)	–	–	–
$p^{l,2}$	0.25 (0.21–0.29)	0.25 (0.22–0.29)	0.50 (0.45–0.55)	–	–
$p^{l,3}$ (early)[c]	0.28 (0.23–0.33)	0.29 (0.25–0.34)	0.43 (0.37–0.49)	–	–
$p^{l,3}$ (late)[c]	0.20 (0.16–0.25)	0.22 (0.18–0.27)	0.33 (0.27–0.39)	0.25 (0.20–0.30)	–
$p^{l,4}$ (early)[c]	0.25 (0.21–0.30)	0.24 (0.20–0.28)	0.51 (0.46–0.56)	–	–
$p^{l,4}$ (late)[c]	0.13 (0.10–0.16)	0.16 (0.13–0.20)	0.23 (0.18–0.28)	0.14 (0.11–0.17)	0.34 (0.30–0.38)
Transition probabilities[d]					
$\varphi^{[0,n]}$	0.31 (0.24–0.38)	0.24 (0.19–0.29)	0.16 (0.13–0.20)	0.15 (0.12–0.19)	0.14 (0.11–0.18)
$\varphi^{[1,n]}$	0.25 (0.21–0.30)	0.23 (0.18–0.28)	0.19 (0.15–0.23)	0.17 (0.13–0.21)	0.16 (0.13–0.20)
$\varphi^{[2,n]}$	0.15 (0.12–0.18)	0.16 (0.12–0.19)	0.25 (0.20–0.31)	0.19 (0.15–0.23)	0.25 (0.21–0.30)
$\varphi^{[3,n]}$	0.17 (0.13–0.21)	0.17 (0.14–0.21)	0.24 (0.19–0.29)	0.20 (0.16–0.25)	0.22 (0.17–0.27)
$\varphi^{[4,n]}$	0.14 (0.11–0.17)	0.14 (0.11–0.18)	0.27 (0.22–0.33)	0.21 (0.16–0.26)	0.24 (0.19–0.30)

[a] Probability that a territory was in state *m* in the initial year.

[b] Probability of observing a territory in state *l* given that its true state was 0, 1, 2, 3, or 4. For example, the entry for $p^{l,1}$ and territory state = 0 indicates the value for parameter $p^{0,1}$.

[c] Early = surveys conducted prior to 1 June; late = surveys conducted on and after 1 June.

[d] Probability that a territory in state 0, 1, 2, 3, or 4 in year *t* was in state *n* in year *t* + 1. For example, the entry for $\varphi^{[2,n]}$ and territory state = 0 indicates the value for parameter $\varphi^{[2,0]}$.

parameters (apparent adult survival, apparent juvenile survival, immigration rate, reproductive rate) and recapture probability were realized from normally distributed variables that we transformed to real values using the logit link function for survival and recapture probability and using the log link function for reproductive and immigration rates (Abadi et al., 2010a; Kéry and Schaub, 2012). For each variable that would be transformed into the appropriate demographic parameter or *p*, we estimated the mean (μ) and error (ε) as hyperparameters from normal distributions where $\mu \sim$ Normal (0, 10,000) and $\varepsilon \sim$ Normal (0, σ) with $\sigma \sim$ Uniform (0, 10) (Kéry and Schaub, 2012).

We again used MCMC methods in a Bayesian framework to estimate the model parameters. We conducted the IPM analyses using R2WinBUGS (Sturtz et al., 2005), a package available in program R 2.15 (R Core Team, 2013) that calls WinBUGS (Lunn et al., 2000) for processing the data and model script in batch mode (see Appendix B for model code). We ran three chains of 50,000 iterations to approximate the posterior distributions of the model parameters and discarded the initial 10,000 iterations of each chain as a burn-in period. The chains were well-mixed after the burn-in period ($\hat{R} < 1.1$ for all parameters; see trace history plots in Appendix D). No goodness-of-fit tests are currently available for IPMs (Abadi et al., 2010a; M. Schaub, personal communication). However, we used Program MARK (White and Burnham, 1999) to assess the goodness-of-fit for the mark-recapture data within a CJS model where apparent survival varied by age (juvenile or adult) and year and detection probability varied by year. We found some evidence of overdispersion within the data ($\hat{c} = 1.32$), but Lebreton et al. (1992) suggested that values of $\hat{c} < 3$ indicate adequate fit.

3. Results

3.1. Multi-state occupancy

We identified 45 spotted owl territories on our study area from 1990 to 2012, so the maximum potential population size of territorial spotted owls was 90 individuals (i.e., if all territories were occupied by a pair of owls). Survey coverage increased during the early years of the study, as evidenced by the number of territories that were surveyed at least once each year ($\leq$37 territories from 1990 to 1992, $\geq$41 from 1993 to 1995, $\geq$44 from 1997 to 2012). In the initial year (1990), nearly all surveyed territories were occupied by pairs ($\hat{\varphi}^{[0]} = 0.02$, 95% CRI 0.00–0.15; $\hat{\varphi}^{[1]} = 0.02$, 95% CRI 0.00–0.17; Table 1). The estimated number of territorial adults in the population declined steadily from a maximum of 88 (95% CRI 76–90) in 1990 to a minimum of 42 (95% CRI 39–49) in 2012 (Fig. 2). The estimated number of young produced varied more substantially but also declined over the study, which was expected given the declining number of adults available to breed.

The probability of detecting at least one spotted owl on a survey (i.e., 1 − probability of not detecting any spotted owls) was $\geq$0.72 for all occupancy states except territories with single spotted owls where non-detection rates were high ($\hat{p}^{0,1} = 0.72$, 95% CRI 0.64–0.80). Additionally, the probability of detecting at least one spotted owl increased with the state of a territory (Table 1). The probability of a territory being unoccupied depended upon the territory's state in the previous year, ranging from 0.31 (95% CRI

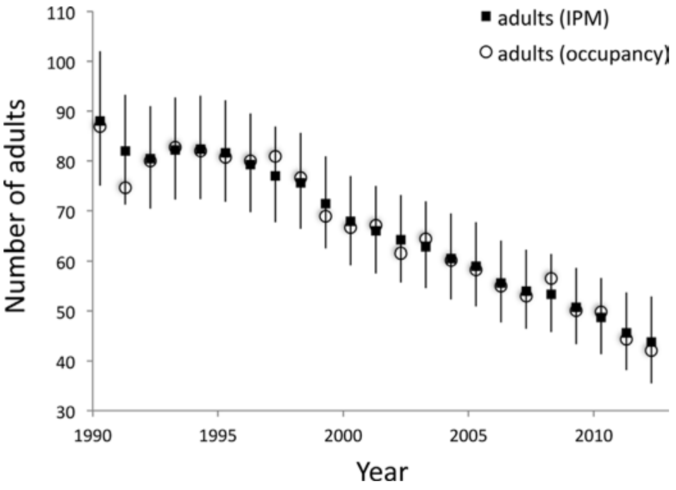

Fig. 2. Posterior means (95% CRI) of the estimated annual number of territorial adults from a Bayesian integrated population model (IPM) for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990–2012. The posterior means of the estimated number of adults from a multi-state occupancy model are also shown; these values were used as "count" data for the IPM.

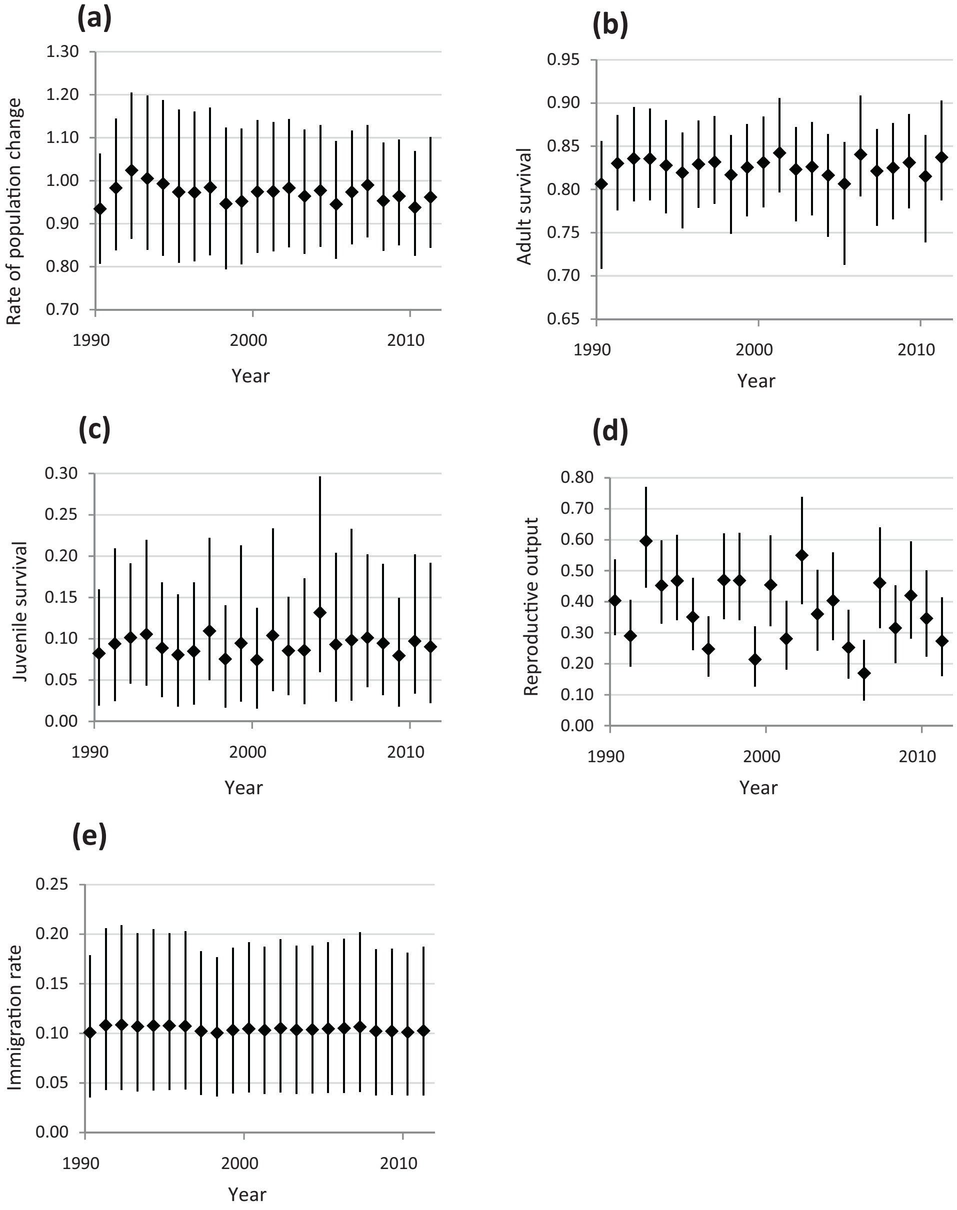

Fig. 3. Posterior means (95% CRI) of estimates for (a) finite rate of population change (λ), (b) apparent adult survival, (c) apparent juvenile survival, (d) reproductive rate, and (e) immigration rate from a Bayesian integrated population model for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990–2011.

0.24–0.38) for a territory that was unoccupied in the previous year to 0.14 (95% CRI 0.11–0.17) for a territory occupied by a pair that produced two young in the previous year (Table 1). Conversely, a territory was more likely to be occupied by a pair (states 2, 3, and 4) if the territory was also occupied by a pair in the previous year (Table 1).

3.2. Integrated population model

The annual estimates of population size were close to the "counts" provided by the occupancy model (Fig. 2). Thus, the observation error was small, which was expected given that the "counts" had already been rigorously modeled to account for imperfect detection. The finite rate of population change ($\hat{\lambda}_t$) was <1.0 in every year except for two years (1992, 1993) early in the study period (Fig. 3), and the geometric mean of $\hat{\lambda}_t$ was clearly <1.0 ($\widehat{\bar{\lambda}}_t = 0.969$, 95% CRI 0.957–0.980). This translated to a population decline of 50% from 1990 to 2012 ($\hat{\Delta}_{2012} = 0.501$, 95% CRI 0.384–0.642; Fig. 4).

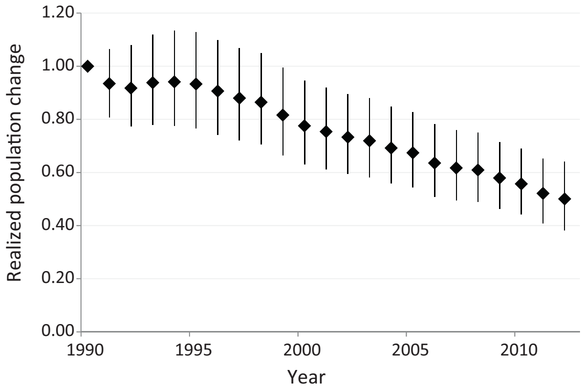

Fig. 4. Posterior means (95% CRI) of realized population change from a Bayesian integrated population model for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990–2012.

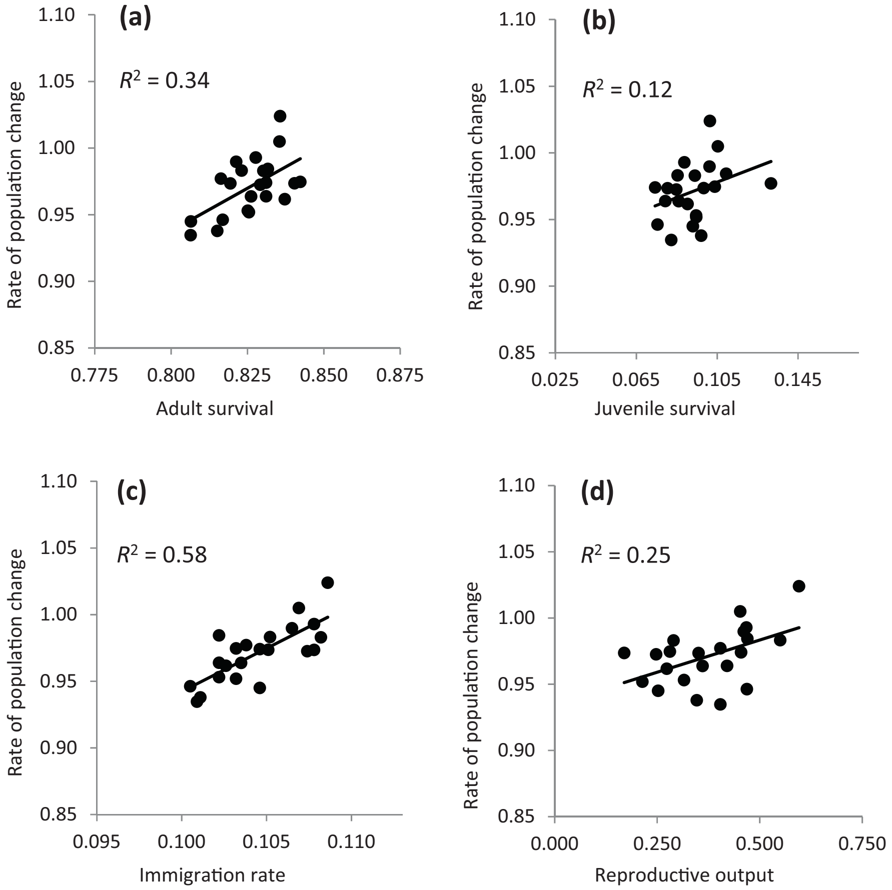

Fig. 5. Posterior means of the estimated finite rate of population change (λ) plotted against the posterior means of the estimates for (a) apparent adult survival, (b) apparent juvenile survival, (c) immigration rate (number of immigrants per adult), and (d) reproductive rate (number of young produced per adult) from a Bayesian integrated population model for California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, 1990–2012. A best-fit regression line is shown on each graph.

We banded 229 non-juvenile owls and 252 juveniles from 1990 to 2012; twenty of the juveniles were later recaptured and banded as one of the 229 non-juvenile owls. Annual estimates of adult apparent survival ($\hat{\varphi}_{ad,t}$) ranged from 0.806 to 0.842 (Fig. 3); mean adult survival over the entire study period was 0.828 (95% CRI 0.801–0.854). In contrast, annual estimates of juvenile apparent survival ($\hat{\varphi}_{juv,t}$) ranged from 0.074 to 0.132 (Fig. 3) with a mean value of 0.087 (95% CRI 0.048–0.129). Immigration rates ($\widehat{imm_t}$) were similar to juvenile survival rates, ranging from 0.100 to 0.109 with a mean value of 0.100 (95% CRI 0.059–0.144; Fig. 3). The reproductive rate (number of young produced per adult) ranged from 0.170 to 0.600 (Fig. 3), and the mean reproductive rate was 0.351 (95% CRI 0.280–0.425). Annual recapture probabilities were high ($\hat{\bar{p}} = 0.868$, 95% CI 0.820, 0.911) and exhibited low temporal variation.

We calculated the correlation coefficients between the population growth rate and each of the demographic rates using the mean values provided by the IPM. All demographic rates were positively correlated with $\hat{\lambda}_t$ (Fig. 5). The correlation was strongest for $\widehat{imm_t}$ ($\beta_{\text{slope}} = 6.49$, 95% CI 4.056, 8.92; $R^2 = 0.58$) and weakest for $\hat{\varphi}_{juv,t}$ ($\beta_{\text{slope}} = 0.58$, 95% CI–0.112, 1.27; $R^2 = 0.12$). The correlations with $\hat{\varphi}_{ad,t}$ ($\beta_{\text{slope}} = 1.28$, 95% CI 0.50, 2.07; $R^2 = 0.34$) and $\hat{f}_t$ ($\beta_{\text{slope}} = 0.10$, 95% CI 0.02, 0.17; $R^2 = 0.25$) were intermediate in strength. The magnitude of the regression slope was also greatest for immigration rate, which further suggested that $\hat{\lambda}_t$ was most sensitive to changes in immigration rate. In addition, we examined correlations between $\hat{f}_t$ and $\widehat{imm_t}$ at 1- to 4-year time lags to assess whether good reproductive years resulted in increased immigration rates in future years. All correlations were weak ($R^2 < 0.07$) except for the 3-year time lag ($\beta_{\text{slope}} = 0.008$, 95% CI–0.001, 0.017; $R^2 = 0.15$).

4. Discussion

We developed an integrated population model to assess population trends of territorial spotted owls in the central Sierra Nevada. Our approach was novel in that we first used a multi-state occupancy model to obtain annual "counts" of the number of adults and young produced, rather than using naïve counts that did not account for imperfect detection. This approach would produce stronger inferences about population trends if detection probabilities exhibited temporal variation (e.g., researchers became more proficient over time at locating individuals on their study area). We found a large decline in owl abundance on our study area from 1990 to 2012 ($\hat{\Delta}_{2012} = 0.501$, 95% CRI 0.384–0.642). Annual rates of population change were generally only slightly below 1.0 (Fig. 3), but the cumulative effect of small annual declines resulted in the loss of almost half of the initial population over the 23-year period. The approximately 50% decline in abundance was considerably greater than declines estimated for our study population based on separate analyses of mark-recapture ($\hat{\Delta}_{2011} = 0.725$, 95% CI 0.445–1.004) and occupancy ($\hat{\Delta}_{2011} = 0.702$, 95% CI 0.552–0.852) data collected from 1993 to 2011 (Tempel and Gutiérrez, 2013). We suspect that declines were greater when population growth was estimated with the IPM than with previous approaches for at least two reasons. First, the IPM allowed for the inclusion of an additional three years (1990–1992) of data at the beginning

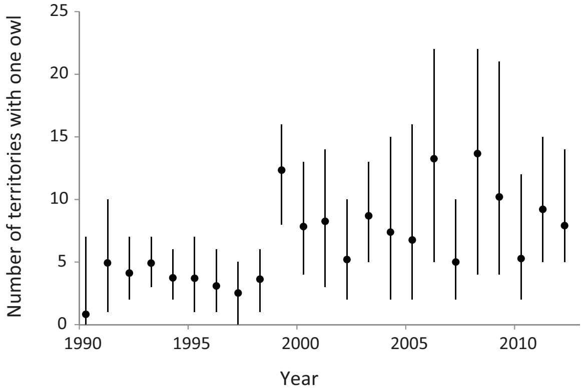

Fig. 6. Posterior means (95% CRI) of the number of California spotted owl (*Strix occidentalis occidentalis*) territories occupied by a single adult from a Bayesian multi-state occupancy model for a population in the central Sierra Nevada, 1990–2012.

of the study when funding constraints prevented us from surveying the entire study area; population growth was negative during these years as well. A basic assumption of the mark-recapture model was that the size of the study area remained constant over time (Pradel, 1996), but the effective size of the study area increased in 1993. In contrast, the multi-state occupancy model that we used to obtain annual "counts" for the IPM imputed the true state of unsurveyed territories during each Markov chain iteration (MacKenzie et al., 2009), and the IPM utilized the mark-recapture data solely to estimate adult survival. Second, the larger decline estimated with the IPM, as least compared to the occupancy-based estimate, can also be attributed to an increasing number of territories that were occupied by single owls during the study (Fig. 6). The loss of one member of a territorial pair without replacement does not affect occupancy status (as defined in Tempel and Gutiérrez, 2013), but clearly reduces population growth rates. An additional advantage of the IPM was that it provided a much more precise estimate of the total change in population size than the mark-recapture analysis and a somewhat more precise estimate of change than the occupancy analysis. Although the gain in precision over the occupancy analysis was not large, even modest improvements in the precision of trend estimates can facilitate conservation decisions about endangered species when there are contentious issues. Moreover, as discussed above, IPMs can provide more direct measures of population growth than analogous occupancy-based metrics and should register the signal associated with changes in the number of territories occupied by a single individual.

Adult spotted owl apparent survival was high 0.828 (95% CRI 0.801–0.854) and had low temporal variation, which was consistent with prior results for both California and northern (*S. o. caurina*) spotted owls (LaHaye et al., 2004; Blakesley et al., 2010; Forsman et al., 2011). In contrast, juvenile apparent survival was only 0.087 (95% CRI 0.048–0.129), which was markedly lower than the estimate reported by LaHaye et al. (2004) ($\bar{\varphi}_{juv} = 0.368$, SE 0.038). The primary reason for this difference was that LaHaye et al. (2004) studied an insular population of spotted owls, so their estimates of juvenile apparent survival were unaffected by juvenile emigration. Thus, we suspected that the true survival rate of juveniles born on our study area was substantially higher than apparent survival, but the difference was unknown because we did not have information on emigration rates of juveniles (see Burnham et al., 1996). However, juvenile apparent survival was the appropriate parameter for the IPM because we studied an open population in which immigration and emigration were components of population change (i.e., emigration is equivalent to death when estimating the rate of population change within study area boundaries). Although adult spotted owl apparent survival varied less than the reproductive rate, the two parameters made similar contributions to variation in population change. This finding was consistent with the results of Seamans and Gutiérrez (2007b), who found that adult apparent survival exhibited low temporal variation relative to reproduction but had a similar influence on λ, which was more sensitive to changes in adult survival. Our results supported the hypothesis that spotted owls have evolved a life-history strategy that favors longevity to increase the likelihood of experiencing favorable years for reproduction, which can be strongly influenced by annual climatic conditions (Franklin et al., 2000; Seamans and Gutiérrez, 2007b).

While our findings of the relative importance of survival and reproduction were similar to previous studies, the IPM provided novel insights into the spatial population dynamics of spotted owls. The mean annual immigration rate indicated that immigration was fairly high (almost 10% of individuals present in a given year were immigrants) and immigration contributed more to annual variation in population growth than survival or reproduction. One potential explanation was that our study area contained sink habitat and the population was maintained by immigration of individuals from the larger regional population. If habitat quality declined on our study area, some territories may have become unsuitable over the past 20 years. For example, Seamans and Gutiérrez (2007a) found that loss of spotted owl habitat was negatively correlated with territory colonization and positively correlated with dispersal of breeding individuals to other territories. An alternative explanation was that conditions on our study area were similar to those in the greater region and that the observed importance of immigration was largely an artifact of juvenile dispersal distances being large relative to the size of our study area. In other words, spotted owl emigration rates from our study area may have been equivalent to, or even exceeded, immigration rates onto the study area. If this were the case, then the observed population decline would have been indicative of overall trends in the larger regional population. Furthermore, if reproduction on our study area was indicative of reproduction adjacent to our study area, then years of high reproductive output should have been resulted in years of higher immigration at some future point in time. Indeed, we found some evidence that immigration was positively correlated with the reproductive rate three years prior (see Section 3.2). Regardless, the estimate of almost 10% annual immigration, as well as the tight correlation between immigration and population growth, suggested that factors impacting owls in one region could impact other regions by affecting immigration rates. Our inability to distinguish between these alternatives underscored the need for additional research that assesses the directionality of owl movements on the landscape.

The literature on IPMs thus far has been mainly concerned with model development and evaluation (Schaub and Abadi, 2011), but our results illustrated the value of using IPMs to assess the status of species of conservation concern. In conjunction with recent estimates of population decline within two other regions of the Sierra Nevada (Conner et al., 2013), our finding of a large, long-term decline in a spotted owl population has potential important ramifications for forest management in the Sierra Nevada, where a primary goal of U.S. Forest Service management is to maintain viable spotted owl populations (U.S.D.A. Forest Service, 2004). Thus, it becomes imperative to understand the causes of population decline and to determine whether current management actions are sufficient to maintain spotted owls or even if they are partially responsible for the decline. For example, we recently found that the amount of high-canopy-cover (≥70%) forest within owl territories was highly correlated with population growth rate and site occupancy and that the amount of this vegetation type on our study area declined by 7.4% from 1993 to 2012 (Tempel et al., in press).

Finally, our results suggest that rigorous monitoring of this species should continue.

Integrated population models offer important advantages over the traditional approach of conducting separate analyses for each available data source. First, IPMs can improve the precision of population estimates, and achieving sufficient statistical power is critical for the implementation of successful monitoring programs (Lindenmayer et al., 2013). Annual population declines in previous spotted owl studies had been difficult to detect (Blakesley et al., 2010), but we demonstrated the utility of IPMs for detecting population change in the spotted owl. Although we analyzed a long-term and relatively large dataset, the improved precision afforded by IPMs should be even more important in situations where data are sparse (Schaub et al., 2007). Second, IPMs provide a unified framework for estimating immigration rates, as opposed to ad hoc approaches that rely on comparing vital rates obtained from separate analyses (Peery et al., 2006). IPMs, however, do not enable one to determine whether a population is a sink or source population (Pulliam, 1988) unless one also has information on emigration derived from radio- or GPS-marked individuals. Nevertheless, knowing the extent to which a local population is open and thus affected by regional processes will be useful for making appropriate conservation decisions. Finally, the IPM accommodates the use of data from years of reduced survey effort, a situation that often occurs because of limited budgets, unexpected budget reductions, and other logistical limitations. The use of IPMs does require multiple data sources, which can require greater field effort, but occupancy data are often collected incidentally during mark-recapture studies of territorial species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2014.07.005.

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Effects of forest management on California Spotted Owls: implications for reducing wildfire risk in fire-prone forests

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Abstract. Management of many North American forests is challenged by the need to balance the potentially competing objectives of reducing risks posed by high-severity wildfires and protecting threatened species. In the Sierra Nevada, California, concern about high-severity fires has increased in recent decades but uncertainty exists over the effects of fuel-reduction treatments on species associated with older forests, such as the California Spotted Owl (*Strix occidentalis occidentalis*). Here, we assessed the effects of forest conditions, fuel reductions, and wildfire on a declining population of Spotted Owls in the central Sierra Nevada using 20 years of demographic data collected at 74 Spotted Owl territories. Adult survival and territory colonization probabilities were relatively high, while territory extinction probability was relatively low, especially in territories that had relatively large amounts of high canopy cover ($\geq$70%) forest. Reproduction was negatively associated with the area of medium-intensity timber harvests characteristic of proposed fuel treatments. Our results also suggested that the amount of edge between older forests and shrub/sapling vegetation and increased habitat heterogeneity may positively influence demographic rates of Spotted Owls. Finally, high-severity fire negatively influenced the probability of territory colonization. Despite correlations between owl demographic rates and several habitat variables, life stage simulation (sensitivity) analyses indicated that the amount of forest with high canopy cover was the primary driver of population growth and equilibrium occupancy at the scale of individual territories. Greater than 90% of medium-intensity harvests converted high-canopy-cover forests into lower-canopy-cover vegetation classes, suggesting that landscape-scale fuel treatments in such stands could have short-term negative impacts on populations of California Spotted Owls. Moreover, high-canopy-cover forests declined by an average of 7.4% across territories during our study, suggesting that habitat loss could have contributed to declines in abundance and territory occupancy. We recommend that managers consider the existing amount and spatial distribution of high-canopy forest before implementing fuel treatments within an owl territory, and that treatments be accompanied by a rigorous monitoring program.

Key words: California Spotted Owl; fire severity; forest management; fuels reduction; high-canopy-cover forest; Sierra Nevada, California, USA; Strix occidentalis occidentalis; *timber harvest; wildfire.*

INTRODUCTION

Forest managers in North America are challenged by the need to balance the potentially competing objectives of reducing wildfire risk and protecting threatened species. For millennia, low- to moderate-severity wildfires occurred at frequent (often less than 20-year) intervals in many western forests. These fires naturally removed fuels such as woody debris, shrubs, and small trees, and shaped the ecology of these forests (Agee 1993, Noss et al. 2006). However, decades of wildfire suppression have disrupted historic fire regimes, increased the amount of surface and ladder fuels, and have led to more frequent high-severity wildfires that now threaten ecological and human communities (Westerling et al. 2006). In addition, warmer and drier conditions associated with climate change may lead to further increases in fire activity over the next century (Westerling and Bryant 2008, Liu et al. 2013). As a result, policy makers and forest managers have proposed landscape-scale forest treatments to remove surface and ladder fuels and reduce the risk of high-severity fires in many western forests (e.g., USFS 2004).

Proposed fuel-reduction measures pose a potential risk to wildlife species associated with older forests because they change forest structure in ways that may negatively affect the species' ability to survive and

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reproduce. Species such as the Spotted Owl (*Strix occidentalis*), fisher (*Pekania pennanti*), and American marten (*Martes americana*) have already declined because of habitat loss and fragmentation resulting from more than a century of timber harvest (Gutiérrez 1994, Zielinski et al. 2005). Although fuels management may provide long-term benefits to such species by reducing future habitat loss from high-severity fires (Finney 2001, Ager et al. 2007, Finney et al. 2007, Collins et al. 2011), regulations protecting sensitive species often constrain the placement and number of potential fuel treatments (Collins et al. 2010). Thus, there is an urgent need to understand the effects of fuel-reduction treatments on old-forest-associated species so that fire risk can be managed while maintaining viable populations of these species (Zielinski et al. 2013). Doing so, however, is challenging because many of these species are rare and long-lived such that impacts may not be immediately apparent. Thus, long-term studies are needed to provide sufficient statistical power to discriminate between the effects of forest management and other sources of variation in demographic rates.

A high-profile example of the attempt to balance wildfire risk and species conservation is the management of public forests and Spotted Owls in the Sierra Nevada, California, USA. As with other western forests, the area burned by high-severity fires in the Sierra Nevada has increased over the past several decades (Miller et al. 2009). However, the implementation of landscape-scale fuel treatments in the Sierra Nevada (USFS 2004) has been contentious because of the potential for these fuel treatments to negatively affect the Spotted Owl and other sensitive species. For example, site occupancy of California Spotted Owls declined following the alteration of >20 ha of habitat within territories (Seamans and Gutiérrez 2007*a*). However, Seamans and Gutiérrez (2007*a*) did not attribute habitat changes to specific causes (e.g., fire, different types of logging) or assess the relationship between these events and reproduction, survival, or fitness. Thus, considerable uncertainty remains about the impact of forest management on California Spotted Owls.

We assessed the effects of timber harvest, wildfire, and vegetation conditions on a declining population of California Spotted Owls in the central Sierra Nevada, California, from 1993 to 2012. Specifically, we assessed the effects of forest treatments and vegetation conditions on reproduction, survival, and territory occupancy of California Spotted Owls and used these vital rates to determine the sensitivity of population growth and occupancy to changes in vegetation conditions due to wildfire or timber harvest. Our objectives were to understand the potential direct, short-term impacts of management actions intended to reduce wildfire risk on Spotted Owls, and to gain insight into the causes of an approximate 30% decline in abundance on our study area over the past two decades (Tempel and Gutiérrez 2013). Moreover, our study is particularly timely because of heightened public concern following the 2013 fire season in the Sierra Nevada, which included one of the largest wildfires in California history (Rim Fire) and a wildfire that burned part of our study area (American Fire).

MATERIAL AND METHODS

Study area

Our study area was located in the central Sierra Nevada, California, between the North and South Forks of the American River. Within this area, we had a 345-km^2 Density Study Area (DSA) that we completely surveyed for Spotted Owls each year from 1993 to 2012, regardless of land ownership or past occupancy by owls. About 60% of the DSA was National Forest, and the remainder was privately owned land. In 1997 we established a Regional Study Area (RSA) surrounding the DSA. The RSA consisted of historical (previously known) owl territories and territories that we began surveying during 1997–1999. We then conducted annual surveys within owl territories on the RSA from 1997 to 2012, but we did not completely survey the landscape between these territories. In 2007, we established the 248-km^2 Last Chance Study Area (LCSA) as part of the Sierra Nevada Adaptive Management Project, 2013 (SNAMP).[5] The LCSA was adjacent to the northern boundary of the DSA and was also completely surveyed for Spotted Owls each year from 2007 to 2012, regardless of land ownership or past occupancy by owls. We detected no Barred Owls (*Strix varia*) during our study, although we did detect two Barred × Spotted Owl hybrids that were not included in our assessment.

The study area consisted of mountainous terrain bisected by steep river canyons with elevations ranging from 300 to 2500 m. The study area had a mediterranean climate with cool, wet winters and hot, dry summers. Sierran mixed-conifer forest was the principal vegetation type and had a canopy dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), and Douglas-fir (*Pseudotsuga menziesii*). California black oak (*Quercus keloggii*), tanoak (*Lithocarpus densiflora*), and big-leaf maple (*Acer macrophyllum*) were common understory species. Forests dominated by red fir (*A. magnifica*) and lodgepole pine (*P. contorta*) occurred at the highest elevations. Montane chaparral and black oak woodlands were vegetation types that were locally distributed at lower and middle elevations. The area has experienced a complex history of timber harvests over the past century, which added to the spatial complexity of vegetation conditions.

Spotted Owl surveys

Each year we conducted nighttime surveys from April through August to locate individuals by imitating vocalizations of Spotted Owls for a minimum of 10

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[5] http://snamp.cnr.berkeley.edu

TABLE 1. Description of vegetation classes used to characterize forest conditions used by Spotted Owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, California, USA.

Class	Description	dbh (cm)	Canopy cover (%)
1	Hardwood forest		>10 hardwood; <10 conifer
2	Shrubs and/or saplings	<15.2	
3	Pole conifer forest	15.2–30.4	
4	Medium-sized conifer forest with low canopy cover	30.5–60.9	30–69
5	Medium-sized conifer forest with high canopy cover	30.5–60.9	≥70
6	Large-sized conifer forest with low canopy cover	≥61.0	30–69
7	Large-sized conifer forest with high canopy cover	≥61.0	≥70
8	Water or barren rock		
9	Medium/large-sized, conifer forest with very low canopy cover	≥30.5	<30

minutes at call stations spaced ~0.8 km apart, or while walking routes that connected multiple call stations. If owls were detected, we conducted walk-in surveys at dawn or dusk in an attempt to identify owls and locate nests and roosts. We attempted to capture and band all Spotted Owls following the methods of Franklin et al. (1996). We fitted captured owls with a U.S. Geologic Survey (USGS) locking aluminum band on one leg and a unique color band and tab combination on the other leg. We determined sex of individuals by the pitch of calls and behavior (Forsman et al. 1984). We identified four age classes based on plumage characteristics: juvenile, first-year subadult, second-year subadult, and adult (≥3 years old) (Moen et al. 1991).

We estimated reproduction of Spotted Owls (i.e., the number of young produced per pair per year) by feeding live mice to owls (Franklin et al. 1996). Reproducing owls usually take offered prey to their nest or young, whereas nonreproducing owls usually eat or cache the mice. We inferred that owl pairs were nonreproductive if: (1) an owl took two or more mice and cached the last mouse without bringing a mouse to a nest or young; (2) an owl ate or cached four or more mice without bringing a mouse to a nest or young; (3) an owl ate two mice and ignored a third mouse for >1 hour; (4) a female owl was captured prior to 1 June and did not have a brood patch; or (5) a female owl was observed roosting for ≥60 minutes before 1 June, which suggested that the female was not incubating eggs or brooding. The number of young fledged from successful nests was determined by observing the delivery of offered mice from parents to young and by counting young during visual searches of the nest stand.

We determined site occupancy following the protocol of Tempel and Gutiérrez (2013). We divided the survey season each year into 10 bimonthly sampling periods (i.e., 1–15 April, 16–30 April, 1–15 May, 16–31 May, and so forth). We identified 74 owl territories using the criterion that reproduction must have been observed at least once at that location during our study. We considered the detection of at least one owl at a territory to indicate site occupancy. We eliminated nocturnal detections >400 m from the territory core area (i.e., areas frequently used by nesting and roosting owls at a territory; Berigan et al. 2012) to minimize the inclusion of false positive detections of non-territorial floaters or residents straying from nearby territories.

Vegetation and forest treatment mapping

We interpreted aerial photographs to map vegetation cover types and changes in cover type that resulted from forest management, succession, and wildfire within all 74 owl territories during 1993–2012. Our vegetation map represented a spatial and temporal expansion of a similar map developed for our study area that also relied upon aerial photo interpretation, but was limited to a subset of territories and years (Chatfield 2005, Seamans and Gutiérrez 2007*a*). We mapped cover types within a 1128 m radius (400-ha) circle around each owl territory center; this radius was equal to half of the mean nearest neighbor distance during our study. We did not know if territorial owls used the entire 400 ha, but owls responded to our vocal surveys within these areas, and these areas encompassed all known nest locations on our study area (Seamans and Gutiérrez 2007*a*). We estimated a single center for each owl territory as the geometric mean of the most informative owl location(s) from each year that the territory was occupied. We used a nest location if one was located that year, but if we did not find a nest, we used the mean location of all roost trees located that year.

Vegetation cover was assigned to one of nine possible classes based on species composition, canopy cover, and the size class of dominant trees (Table 1; Appendix A). We used vegetation classes based upon the California Wildlife Habitat Relationships system (CWHR; Mayer and Laudenslayer 1988). As noted, we used a cover map developed by Chatfield (2005) as our base map, which had an overall accuracy (i.e., correct classification of cover types) of 83% based on randomly sampled vegetation plots. We updated this map for each year of our study using National Agriculture Imagery Program images, USGS 1-m digital orthophoto quarter quads (DOQQs), and geo-rectified aerial photographs (1:15 840 scale) obtained for the following years: 1993, 1996–1998, 2000, 2005, 2009, and 2010–2012. We drew polygons around relatively homogenous vegetation classes visible on the images using a minimum polygon size of ~1 ha. When we could not reliably assign a year to a visible change in cover type between available images, we assumed that the change occurred at the midpoint between image years (see Fig. 1 as an example of the vegetation cover map for a single owl territory).

We identified the timing, location, and type of timber harvests from the U.S. Forest Service (USFS) Activity and Tracking System (FACTS; database *available online*),[6] the California Department of Forestry and Fire Protection (CDFFP) Timber Harvest Plans (database *available online*),[7] and information provided by private landowners. These databases contained 16 different timber harvest practices that we pooled into three broad categories for analytical purposes: low-intensity, medium-intensity, and high-intensity timber harvest (Appendix B). The classification scheme was based on the expected change in forest structure and was developed after consultation with three local forest managers who were naïve to the objectives of our study. We confirmed or modified the year and boundary of all treatments in the databases by visually examining the imagery and obtaining supplementary information from field visits, the USFS, and private landowners. We acquired fire perimeter data from the CDFFP Fire and Resource Assessment Program (*available online*).[8]

We did not specifically test for effects on Spotted Owls of Forest Service-implemented fuel-reduction treatments as proposed in USFS (2004) because implementation of these treatments was relatively recent (only 11 owl territories were affected by these treatments after 2007). However, these recent fuel-reduction treatments had effects on forest structure similar to those of other treatments in the medium-intensity category, most of which also occurred on USFS land. Prior to 2004, USFS timber harvests were governed by an "interim" management plan designed to maintain viable Spotted Owl populations (USFS 1993). Similar to the 2004 plan, the 1993 interim plan was designed to protect known owl nest stands from any significant modification, to protect large trees ($\geq$76.2 cm dbh), to retain at least 40% canopy cover, and to reduce the threat of stand-destroying fires. The primary change implemented by the 2004 plan was a greater emphasis placed on the removal of understory fuels. Thus, we identified the occurrence of understory treatments through conversations with USFS and private timber company personnel and visual interpretation of aerial photos, and further categorized these treatments as "medium-intensity with understory removal."

We extracted spatial data relevant to Spotted Owl ecology (see *Methods: A priori model development and selection*) from the cover maps with ArcGIS 10.0 (ESRI, Redlands, California, USA) using Patch Analyst 5.1.0.0 (Rempel et al. 2012) for subsequent use in demographic analysis. To calculate the amount of edge between vegetation classes, we used Patch Grid after first converting vector data to raster data at a 30-m scale (Rempel et al. 2012). All other spatial variables were calculated directly from the vector maps. All habitat and timber harvest variables that we extracted from our vegetation maps were time-varying and could change annually because of natural disturbance, timber harvest, or regrowth. We expected that reproduction, survival, and occupancy at a territory would be impacted by timber harvest and wildfire in previous years, as well as the current year. Thus, we calculated harvest and wildfire covariates over three temporal scales: 3 years, 6 years, and 9 years. For example, at the 6-year time scale, the area of a specific disturbance type was the sum of those disturbances that occurred in the previous five years and the current year.

A priori model development and selection

We modeled putative relationships between vegetation classes and four vital rates (reproduction, survival, territory colonization, and territory extinction) by evaluating the level of support for competing, a priori models. We used Akaike's information criterion (AIC) values to rank competing models (Burnham and Anderson 2002). When evaluating support for covariate effects within a given model, we assessed whether the 95% confidence interval of the associated parameter estimate overlapped zero. We conducted the modeling in three steps to reduce the number of candidate models and thus reduce the likelihood of finding spurious relationships (Table 2). In the first step, we evaluated covariates that represented the amount of potential owl nesting and roosting habitat within territories. In the second step, we used the covariates from the top-ranked model from the first step and included additional covariates for potential owl foraging habitat, amount of private land, and the spatial distribution of forest cover types. In the third step, we used the covariates from the top-ranked model in the second step and included additional covariates that represented different types of forest disturbance. By using this hierarchical approach, we were able to control for existing habitat conditions within each territory when assessing the impacts of forest disturbance. For steps 1 and 2 of our modeling, we used the entire 20-year data set. For step 3, we used the covariates from the most parsimonious models from step 2, but then used reduced data sets for the three temporal scales because we lacked timber harvest data for years prior to 1993. None of the covariates that we used were highly correlated with each other ($r > 0.60$).

Previous studies of our study population revealed that high canopy cover and large trees were important components of nesting and roosting conditions used by Spotted Owls (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997). Therefore, in step 1 of our analysis we evaluated support for the combined areas of vegetation classes 5 and 7 (57; model 1.1) and the combined areas of vegetation classes 6 and 7 (67; model 1.4). Vegetation

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[6] www.fs.usda.gov/main/r5/landmanagement/gis

[7] ftp.fire.ca.gov/forest/

[8] http://frap.fire.ca.gov/data/frapgisdata-subset.php

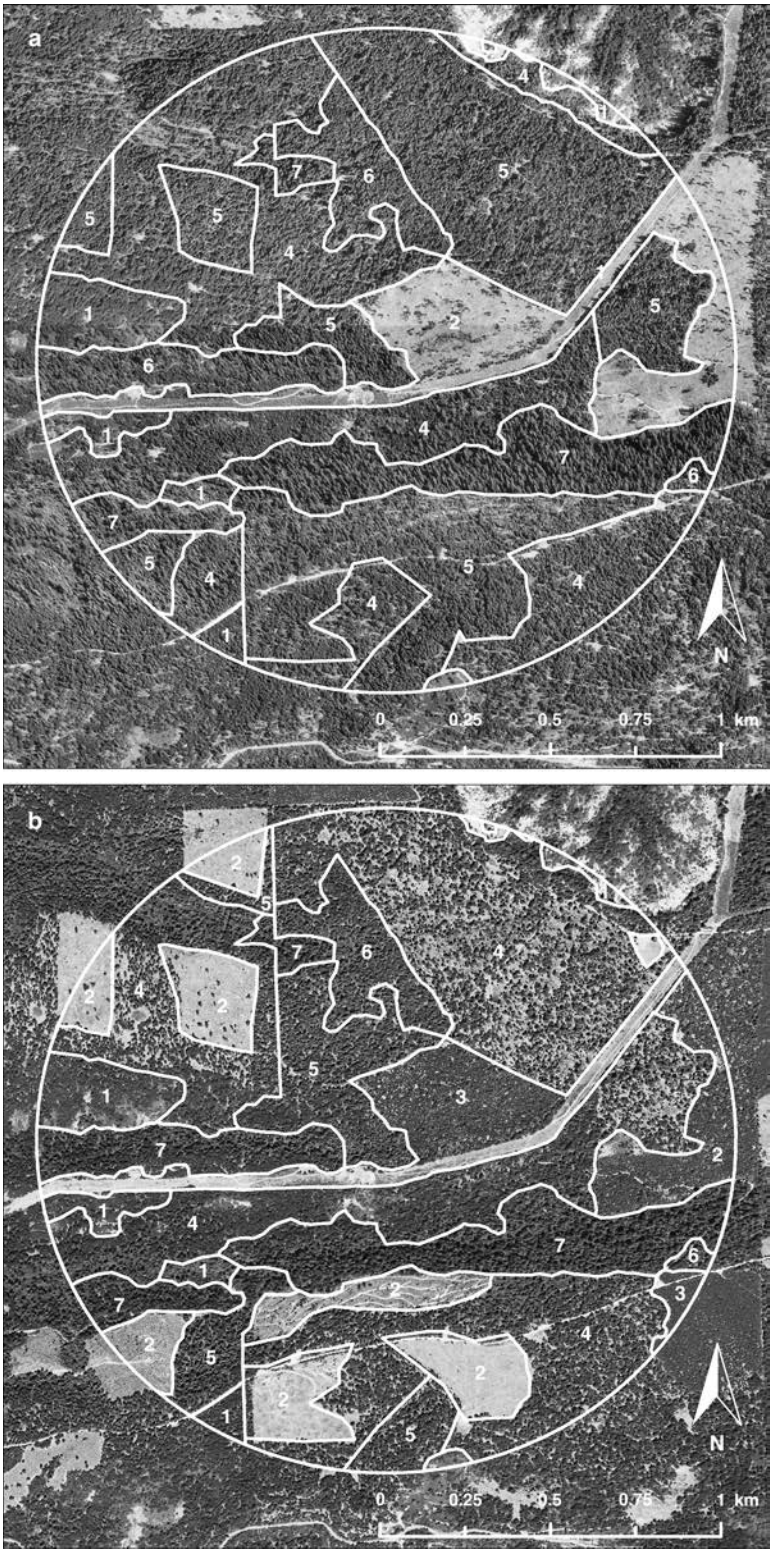

FIG. 1. Example of a vegetation cover map based on aerial photographs taken in 1993 (a) and 2012 (b) for a California Spotted Owl (*Strix occidentalis occidentalis*) territory on our study area in the central Sierra Nevada, California, USA. The territory is delineated by a circular boundary that encompasses 400 ha. See Table 1 for definitions of the numbered vegetation classes.

TABLE 2. List of a priori models for three-step modeling of reproduction, survival, and territory occupancy of Spotted Owls in the central Sierra Nevada, California, USA.

Model	Covariates	Description
Step 1		
1.1	57	linear relationship with area (ha) of classes 5 + 7
1.2	log(57)	log-linear relationship with area (ha) of classes 5 + 7
1.3	$57 + (57)^2$	quadratic relationship with area (ha) of classes 5 + 7
1.4	67	linear relationship with area (ha) of classes 6 + 7
1.5	log(67)	log-linear relationship with area (ha) of classes 6 + 7
1.6	$67 + (67)^2$	quadratic relationship with area (ha) of classes 6 + 7
Step 2		
2.1	[step 1]† + hardwoods	[step 1] + area (ha) of hardwoods
2.2	[step 1] + edge	[step 1] + edge (km) between vegetation class 2 and classes 4, 5, 6, and 7
2.3	[step 1] + private	[step 1] + area (ha) of private land
2.4	[step 1] + habitat diversity	[step 1] + habitat diversity (Shannon-Wiener)‡
2.5	[step 1] + mean patch size	[step 1] + mean habitat patch size (ha)‡
Step 3		
3.1	[step 2]§ + high	[step 2] + area (ha) of high-intensity harvests
3.2	[step 2] + fire	[step 2] + area (ha) of wildfire
3.3	[step 2] + understory	[step 2] + area (ha) of medium-intensity harvests with understory removal
3.4	[step 2] + medium	[step 2] + area (ha) of all medium-intensity harvests
3.5	[step 2] + low	[step 2] + area (ha) of low-intensity harvests
3.6	[step 2] + [treatment] + interaction between habitat and treatment	[step 2] + variables from best model among 3.1–3.6 + interaction with step 1 habitat

Note: We used the same models for all three time scales that we considered (3, 6, and 9 years); vegetation classes are defined in Table 1.

† The variables from the top model in step 1.

‡ Habitat diversity and mean patch size were calculated using either 57 or 67, depending on which habitat variable (if any) was in the best step 1 model. Combined area of vegetation classes 5 and 7 includes the amount of forest with high ($\geq$70%) canopy cover and a dominant tree size of $\geq$30.5 cm dbh; combined area of vegetation classes 6 and 7 includes the amount of forest dominated by large trees $\geq$ 61.0 cm dbh with a lower threshold ($\geq$30%) for canopy cover.

§ Variables from the top model in step 2.

classes 5 and 7 represented the amount of forest with high ($\geq$70%) canopy cover and a dominant tree size of $\geq$30.5 cm diameter at breast height (dbh). In addition to providing nesting and roosting conditions, this forest type provides habitat for northern flying squirrels (*Glaucomys sabrinus*; Waters and Zabel 1995), which were the primary prey item of Spotted Owls on our study area (R. J. Gutiérrez, *unpublished data*). Vegetation classes 6 and 7 represented the amount of forest dominated by large trees ($\geq$61.0 cm dbh) with a lower threshold ($\geq$30%) for canopy cover. The current management plan for national forests in the Sierra Nevada (USFS 2004) contains harvest limits on both canopy cover (minimum 40–50% postharvest) and tree size (<76.2 cm dbh). Although these two covariates (57, 67) were correlated ($r = 0.60$), we chose to retain both covariates in our analyses to test whether high canopy cover or large trees were more important components of owl habitat. We also considered log-linear (models 1.2, 1.5) and quadratic (models 1.3, 1.6) relationships because such relationships between habitat and Spotted Owl vital rates have been detected in other regions (Franklin et al. 2000, Dugger et al. 2005, Forsman et al. 2011). We included a covariate for age (a subadult is 1 or 2 years old, an adult is at least 3 years old) when modeling survival and reproduction, and a covariate for sex when modeling survival, because age and sex have been shown to be important predictors of these vital rates for Spotted Owls (Blakesley et al. 2010). Finally, we included a null model without explanatory covariates in which each vital rate had a constant value over time.

In step 2 of our analysis, we hypothesized that hardwood forests (vegetation class 1; model 2.1) may support greater densities of dusky-footed woodrats (*Neotoma fuscipes*) than other forest types (Sakai and Noon 1993, Innes et al. 2007); woodrats are an important prey item for Spotted Owls on our study area, especially at lower elevations (*unpublished data*). We posited that the amount of edge between shrubs or saplings (vegetation class 2) and forests dominated by trees $\geq$30.5 cm (vegetation classes 4, 5, 6, and 7; model 2.2) may have positively affected Spotted Owl vital rates because the presence of brush fields adjacent to older forest may increase the availability of woodrats to owls (Sakai and Noon 1997). We hypothesized that the area of private land (model 2.3) may negatively affect Spotted Owl vital rates because data from a radiotelemetry study conducted in our study area during 2006–2007 suggested that owls use private lands less than expected, possibly owing to a history of more intensive timber harvests on private land (Williams et al. 2014). Finally, we hypothesized that the spatial arrangement of owl habitat may affect owl vital rates (Franklin et al. 2000). For example, high interspersion of different forest cover types within a territory may allow owls to more easily meet all of their life history requirements (nesting, roosting, foraging). We first examined the correlation between several potential territory spatial metrics (mean distance between patches, mean patch size, number of patches, diversity) and found that most were correlated with each other or with habitat covariates from step 1 ($r > 0.60$). Thus, we chose to use two metrics that were not highly correlated with each other or with the step 1 covariates: the Shannon-Wiener diversity index (model 2.4) and the mean size of owl habitat patches (model 2.5). We calculated these metrics for the owl habitat type (57 or 67) found in the best model from step 1. We log-transformed all step 2 covariates (except for the Shannon-Wiener diversity index) for our analyses because their distributions were right-skewed.

In step 3 of our analysis, we introduced covariates that represented the potential effects of forest disturbances. Disturbances generally consisted of timber harvest, but also included wildfires that occurred within 12 owl territories during our study. We expected all types of disturbance to negatively impact vital rates of Spotted Owls, and ranked them in order of the expected magnitude of their effects as follows: high-intensity harvests, wildfire, medium-intensity harvests with understory removal, all medium-intensity harvests, and low-intensity harvests (models 3.1–3.5). We ranked wildfire second because most of the acreage burned on our study area was the result of a single fire in 2001 that was predominantly a stand-replacing fire and impacted eight territories to varying degrees. We then sequentially added the disturbance covariates to the best model from step 2 in order of their expected impact and retained the covariate in the model if it reduced the model's AIC value. Finally, we considered a model (model 3.6) in which the amount of habitat (57 or 67) interacted with the disturbance covariate(s) from the best model among models 3.1–3.5. We considered this a test of the hypothesis that territories containing relatively large amounts of Spotted Owl habitat would be more resilient to disturbance (Seamans and Gutiérrez 2007*a*). All step 3 covariates were right-skewed, so we added 1 to their values and log-transformed them for our analyses.

Statistical modeling

Reproduction.—We used mixed-model analysis of variance (PROC MIXED in SAS 9.3; Littell et al. 2006) to test the a priori hypotheses described previously with respect to reproduction. In these analyses, we treated reproduction (i.e.; the number of young fledged per territory per year) as the dependent variable, habitat covariates and female age (subadult or adult) as fixed effects, and territory identity and year (1993–2012) as random effects. We considered territory to be a random blocking factor because reproduction within a territory may not be independent among years. We treated reproduction as a normally distributed variable because McDonald and White (2010) found that analysis of variance procedures based on a normal distribution performed well for small count data similar to ours. Moreover, before examining a priori habitat models, we used restricted maximum likelihood estimation to model the following potential variance–covariance structures within territories across years: compound symmetric, first-order autoregressive, heterogeneous first-order autoregressive, and log-linear (Littell et al. 2006). Once we identified the best variance–covariance structure (i.e., lowest AIC value), we used full maximum likelihood estimation to model the influence of the fixed effects on reproduction according to the framework just described. We considered female age a factor in all models, based on differences in reproduction between subadults and adults in previous studies (Blakesley et al. 2010).

Survival.—We used the Cormack-Jolly-Seber open-population model (CJS; Cormack 1964, Jolly 1965, Seber 1965) implemented in the R package *marked* (Laake et al. 2013) to test the a priori hypotheses previously described with respect to apparent survival of Spotted Owls. Apparent survival refers to the inability to differentiate between true mortality and permanent emigration from the study area. Although capture histories were developed based on the capture and resighting of individual Spotted Owls, our goal was to make inferences based on the habitat occupied by an owl, which varied by territory. Thus, we modified the capture histories used for the temporal analyses to reflect movement among territories (sensu Franklin et al. 2000). If an individual was not resighted for one or more years and was then resighted on a new territory, we removed the portion of its capture history pertaining to the original territory. We did this to avoid making assumptions about the owl's location during the intervening period. As a result, we used partial capture histories for 14 of the 350 individuals in our data set.

No methods exist for estimating overdispersion ($\hat{c}$) in CJS models containing individual covariates (Jeff Laake, *personal communication*), so instead we used Program MARK to estimate $\hat{c}$ for our most highly parameterized model without covariates, $\varphi(\text{age} \times \text{sex} \times \text{year})$ and $p(\text{age} \times \text{sex} \times \text{year})$. We found no evidence for a lack of model fit ($\hat{c} = 0.998$). Prior to modeling survival rates, we first examined a priori model structures for the probability of recapture (p). We examined three covariates that may influence recapture probabilities: age (subadult or adult), sex, and survey effort (the amount of time spent conducting walk-in surveys each year) (Blakesley et al. 2010). Using the best model structure for p, we then followed the framework described previously to model the influence of habitat and forest disturbance on apparent survival.

Occupancy.—We used a multi-season occupancy model with parameters for local extinction (ε_t) and local colonization (γ_t) of Spotted Owl territories (MacKenzie et al. 2003). We separately modeled the extinction and colonization processes using Program PRESENCE v. 5.9 (Hines 2006). When modeling extinction, we specified a full time structure for colonization (i.e., different parameter estimates for each year), and vice versa when modeling colonization. The primary sampling periods were each year of the study, and the secondary sampling periods were the 10 bimonthly intervals within each year. Two critical assumptions of this model were: (1) occupancy status at each territory did not change during the survey season (i.e., no permanent emigration); and (2) detections at each territory were independent (MacKenzie et al. 2006). Because nearly all of the owls on our study area were marked, we could determine when individuals moved among territories during the survey season. Such movements only occurred on 10 occasions during our study, and we only considered one of the territories to be occupied in these situations (i.e., where the individual was most frequently detected). In addition, we excluded nocturnal detections >400 m from a territorial core area to help ensure independence of detections at territories. Finally, we interpreted occupancy as the proportion of territories used by owls during a breeding season because some territories may not have been continuously occupied throughout the entire season (MacKenzie et al. 2006).

We first examined a priori model structures for detection probabilities (*p*). For the occupancy analyses, *p* represented the probability of detecting an owl during a survey when the territory was occupied. Note that for the mark–recapture analyses, *p* represented the probability of recapturing an individual during a given year. We modeled within-year *p* using two covariates, *initial* and *repro* (Tempel and Gutiérrez 2013). *Initial* specified a different *p* for all survey occasions subsequent to the first detection at a territory each year, and *repro* indicated whether owls attempted to nest at a territory that year. We then modeled annual *p* with the following temporal effects: linear, log-linear, quadratic, different for each year, and constant. We selected the model with the best-fitting time structure and then introduced covariates for vegetation class (57 and 67) relative to *p* and initial occupancy probability (ψ_1). Using the best model structure, we then followed the framework described previously to model the relationships between vegetation class and forest disturbance on territory extinction and colonization.

Sensitivity analyses

Life stage simulation.—We conducted life stage simulation analyses (LSA) to assess which covariates had the greatest influence on annual population growth rate (λ) of Spotted Owls by estimating the amount of variation in λ explained by each covariate that appeared in the top-ranked models of reproduction and survival (Wisdom et al. 2000). We used a stage-based, post-breeding census Lefkovitch matrix model parameterized with reproductive and survival rates to represent changes in female population size:

$$\begin{bmatrix} N_{\mathrm{J},t+1} \\ N_{\mathrm{S1},t+1} \\ N_{\mathrm{S2},t+1} \\ N_{\mathrm{A},t+1} \end{bmatrix} = \begin{bmatrix} 0 & \varphi_{\mathrm{S},t}b_{\mathrm{S},t} & \varphi_{\mathrm{S},t}b_{\mathrm{A},t} & \varphi_{\mathrm{A},t}b_{\mathrm{A},t} \\ \varphi_{J,t} & 0 & 0 & 0 \\ 0 & \varphi_{\mathrm{S},t} & 0 & 0 \\ 0 & 0 & \varphi_{\mathrm{S},t} & \varphi_{\mathrm{A},t} \end{bmatrix} \begin{bmatrix} N_{\mathrm{J},t} \\ N_{\mathrm{S1},t} \\ N_{\mathrm{S2},t} \\ N_{\mathrm{A},t} \end{bmatrix} \quad (1)$$

where $N_{\mathrm{J},t}$, $N_{\mathrm{S1},t}$, $N_{\mathrm{S2},t}$, and $N_{\mathrm{A},t}$ were the number of juvenile, first-year subadult, second-year subadult, and adult females at time *t*, respectively; $\varphi_{\mathrm{J},t}$, $\varphi_{\mathrm{S},t}$, and $\varphi_{\mathrm{A},t}$ were the apparent survival rates of juvenile, subadult, and adult females from time *t* to $t+1$, respectively; and $b_{\mathrm{S},t}$ and $b_{\mathrm{A},t}$ were the fecundity rates for subadult and adult females at time *t*, respectively. Fecundity was the number of female offspring produced per female in the population. We assumed a 1:1 sex ratio of offspring and divided the reproductive rate from our reproduction model by two. We estimated λ as the dominant eigenvalue of the matrix.

We expressed apparent survival and fecundity as functions of covariates and set the beta coefficients for all covariate effects equal to their estimated values from the top-ranked models for apparent survival and fecundity (Table 3). As an example, apparent survival was estimated as

$$\mathrm{logit}(\varphi) = \beta_0 + \beta_1 \times \mathrm{sex} + \beta_2 \times \mathrm{age} + \beta_3 \times \log(57) + \beta_4 \times \mathrm{edge} \quad (2)$$

where sex is 0 for females and 1 for males, and age is 0 for subadults and 1 for adults. Thus, apparent survival for non-juvenile females was estimated as

$$\mathrm{logit}(\varphi) = -1.010 + 0.452 \times \mathrm{age} + 1.004 \times \log(57) + 0.763 \times \mathrm{edge}. \quad (3)$$

We allowed the vegetation covariates to vary between the minimum and maximum values observed within any territory during the 20-year study period (range for area of 57 is 0–332.8 ha; range for edge is 0–28.5 km). In addition, we lacked reliable estimates of juvenile survival for our study area, so we used the reported estimate from an insular population of California Spotted Owls ($\varphi_{\mathrm{J},t} = 0.368$; LaHaye et al. 2004). We ran additional simulations in which we allowed juvenile survival to range from 0.318 to 0.418, and the results were nearly identical. We used SAS 9.3 (SAS Institute, Cary, North Carolina, USA) to conduct 1000 simulations in which we randomly generated sets of vegetation class covariate values from uniform probability distributions, estimated λ for each simulation, and regressed λ against each vegetation covariate for all 1000 simulations. The percentage of variation in λ that was explained by each vegetation covariate was a measure of the sensitivity of λ to changes in the vegetation covariate (Wisdom et al. 2000).

Occupancy.—Analogous to the LSA, we assessed which vegetation covariates had the greatest influence on the equilibrium territory occupancy (ψ_{Eq}) by estimating the variation in ψ_{Eq} explained by each covariate that appeared in our best-fitting dynamic

TABLE 3. Model results for analyses of California Spotted Owl reproduction (number of young fledged), apparent survival, territory extinction, and territory colonization at a 6-year time scale in the central Sierra Nevada, 1993–2012.

Model covariates	k	AIC	ΔAIC	w_i
Reproduction				
Female age + hardwoods + medium	8	1205.1	0.00	0.29
Female age + hardwoods	7	1205.6	0.50	0.23
Female age + hardwoods + high	8	1206.0	0.90	0.19
Female age + hardwoods + fire	8	1207.1	2.00	0.11
Female age + hardwoods + low	8	1207.4	2.30	0.09
Female age + hardwoods + understory	8	1207.5	2.40	0.09
Adult survival				
Sex + age + log(57) + edge	9	1311.11	0.00	0.32
Sex + age + log(57) + edge + medium	10	1312.82	1.71	0.14
Sex + age + log(57) + edge + understory	10	1313.07	1.96	0.12
Sex + age + log(57) + edge + high	10	1313.07	1.96	0.12
Sex + age + log(57) + edge + low	10	1313.10	1.99	0.12
Sex + age + log(57) + edge + fire	10	1313.11	2.00	0.12
Sex + age + log(57) + edge + medium + medium × log(57)	11	1314.39	3.28	0.06
Territory extinction				
57 + diversity(57) + high	39	3808.93	0.00	0.30
57 + diversity(57) + high + medium	40	3809.63	0.70	0.21
57 + diversity(57) + high + fire	40	3810.34	1.41	0.15
57 + diversity(57) + high + understory	40	3810.80	1.87	0.12
57 + diversity(57) + high + low	40	3810.85	1.92	0.11
57 + diversity(57) + high + high × 57	40	3810.92	1.99	0.11
57 + diversity(57)	38	3815.70	6.77	0.01
Territory colonization				
log(57) + diversity(57) + fire	39	3800.63	0.00	0.32
log(57) + diversity(57) + fire + medium	40	3802.25	1.62	0.14
log(57) + diversity(57) + fire + understory	40	3802.28	1.65	0.14
log(57) + diversity(57) + fire + low	40	3802.38	1.75	0.14
log(57) + diversity(57) + fire + fire × log(57)	40	3802.63	2.00	0.12
log(57) + diversity(57)	38	3803.02	2.39	0.10
log(57) + diversity(57) + high	39	3804.94	4.31	0.04

Notes: Shown are values for k, the number of model parameters; AIC, Akaike's information criterion; ΔAIC, the difference in AIC value from the top-ranked model; and w_i, AIC weight. See Table 2 for covariate definitions. Combined vegetation classes 5 and 7 (57) and classes 6 and 7 (67) are as defined in Table 2.

occupancy models. If local extinction (ε) and local colonization (γ) rates are constant, ψ_{Eq} can be calculated as $\gamma/(\gamma + \varepsilon)$ (MacKenzie et al. 2006). This equation was equivalent to a mainland–island metapopulation model with no rescue effect (Hanski 1999), where each territory was a "subpopulation" within a larger population of Spotted Owl territories. Although owl territories were not strictly subpopulations, they represented breeding units within our study area because we defined them as locations where reproduction was observed at least once. The proportion of occupied territories probably never reached equilibrium during our study, so the actual values of ψ_{Eq} should be interpreted with caution. Nevertheless, we believe that our approach provided general insight into the importance of habitat and forest disturbance to occupancy dynamics of Spotted Owls.

We again set the beta coefficients for all covariate effects equal to their estimated values from the top-ranked models and allowed the vegetation covariates (except for the amount of wildfire, which we will discuss) to vary between their minimum and maximum observed values. As with the LSA, we used SAS 9.3 to conduct 1000 simulations, determined ψ_{Eq} for each simulation, and regressed ψ_{Eq} against each vegetation covariate for all 1000 simulations.

We handled the wildfire covariate, which appeared in the territory colonization model, in a more spatially explicit manner. The effect of wildfire on territory colonization was strongly negative due to a high-severity fire that occurred on our study area in 2001 and completely burned two territories, which subsequently were never colonized by owls. However, most owl territories were unaffected by wildfire because fire occurred within only 12 territories during our study. Therefore, we defined two types of territories, burned and unburned. For each simulation, we randomly varied the number of territories that burned from 1 to 12. For burned territories, we then randomly varied the amount of wildfire from 0 to 400 ha. We separately calculated γ and ψ_{Eq} for burned and unburned territories and calculated an overall ψ_{Eq} for the 74 territories as a weighted average of ψ_{Eq}. We regressed ψ_{Eq} against the average amount of wildfire in all 74 territories; for example, if 100 ha of wildfire occurred in six territories during a simulation, then the average amount of wildfire per territory was 8.1 ha (600/74). In addition, we conducted 1000 additional simulations in which we varied the number of burned territories from 1 to 24 to represent a scenario of increased wildfire activity.

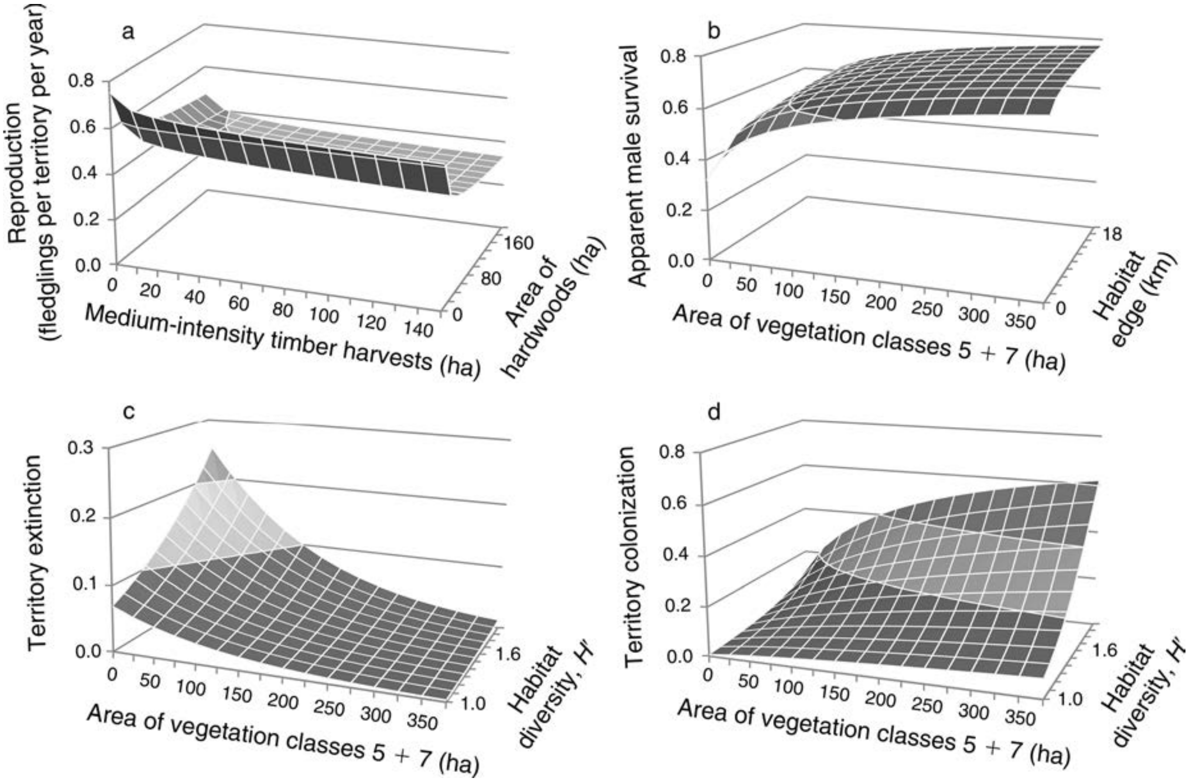

FIG. 2. Vital rates of California Spotted Owls in the central Sierra Nevada, California, 1993–2012, as a function of habitat, timber harvest, and wildfire covariates. We show (a) reproduction for adult females (number of young fledged per territory per year) vs. the total area of medium-intensity timber harvests in the previous 6 years and the area of hardwood forests within owl territories; (b) apparent survival for adult males vs. the total area of vegetation classes 5 and 7 and the amount of habitat edge within owl territories; (c) territory extinction (the probability that a territory occupied in year t becomes unoccupied in year $t+1$); and (d) territory colonization (the probability that a territory not occupied in year t becomes occupied in year $t+1$) as a function of the total area of classes 5 and 7 and habitat diversity (Shannon-Wiener index).

RESULTS

The results from the reproduction, survival, and occupancy analyses were similar for the three temporal scales (3, 6, and 9 years) used to calculate the timber harvest and wildfire covariates. Thus, we only present results for models containing timber harvest and wildfire covariates using the 6-year time frame, and we used this time frame for the sensitivity analyses as well. We present results for the 3- and 9-year time frames in Appendix C.

Reproduction

We assessed reproduction on 676 occasions at 70 territories, excluding territories with fewer than three reproductive observations and cases in which territories were occupied by a single owl. There were, on average, 0.612 ± 0.032 young fledged per territory per year (mean ± SE), and we detected 0, 1, 2, and 3 young on 62.1%, 14.8%, 22.8%, and 0.30% of the sampling occasions, respectively. The autoregressive variance–covariance structure was supported over the compound-symmetric (ΔAIC = 7.6) or default (ΔAIC = 13.9) variance–covariance structures. This structure indicated that reproduction in consecutive years was negatively correlated (ARH1 = −0.148, SE = 0.048) and was used in all subsequent modeling of fixed effects. The random year and territory effects were either statistically significant or nearly statistically significant (for year, $Z = 2.74$, $P = 0.003$; for territory, $Z = 1.28$, $P = 0.100$), so we retained both random effects when modeling fixed effects.

None of the vegetation covariates considered in step 1 (linear and nonlinear forms of 57 and 67) lowered the AIC value when added to a model containing only female age (Appendix C). The top-ranked model from step 2 included covariates for the area of hardwood forest within a territory and female age, and was 2.90 AIC units lower than the second-ranked model (Appendix C). The best overall model from step 3 contained a covariate for the area of medium-intensity timber harvests, but this model was only 0.50 AIC units lower than the best model from step 2 (Table 3). This model suggested a negative influence of medium-intensity (subscript "med") timber harvests on reproduction of Spotted Owls, but we found only weak support for this effect based on the degree to which the 95% CI of the beta coefficient overlapped zero ($\beta_{\text{med}} = -0.065$, 95% CI = −0.145 to 0.016; Fig. 2a). In addition, adult females (subscript "ad") had higher reproduction than subadults (β_{ad} = 0.335, 95% CI = 0.136–0.533), and reproduction was negatively related to the area of hardwood ("hw") forests ($\beta_{hw} = -0.123$, 95% CI = –0.219 to –0.027) (Fig. 2a).

Survival

We estimated apparent survival using 350 individual capture histories. The best structure for recapture probability contained covariates for age, sex, and survey effort. Recapture probability was higher for adults (β_{ad} = 1.320, 95% CI = 0.522–2.119) and males (β_{male} = 0.571, 95% CI = 0.121–1.022) and was positively correlated with annual survey effort ("eff") (β_{eff} = 1.607, 95% CI = 0.342–2.872). We used this structure for recapture probability in all subsequent modeling of survival. Real values of recapture probability estimates were high. When annual survey effort was set equal to its mean value, recapture probability was estimated to be 0.92, 0.87, 0.75, and 0.63 for adult males, adult females, subadult males, and subadult females, respectively.

The top-ranked survival model in step 1 (Appendix C) contained covariates for sex, age, and the logarithm of the combined area of vegetation classes 5 and 7. The top-ranked model from step 2 also contained a covariate for the amount of habitat edge within a territory, and was 7.14 AIC units lower than the second-ranked model (Appendix C). None of the step 3 covariates (timber harvest, wildfire) lowered the AIC value when added to the best model from step 2. The second-ranked overall model (ΔAIC = 1.71) contained a covariate for the area of medium-intensity timber harvests (Table 3), but this model was poorly supported, given that the maximum possible ΔAIC is 2 when an uninformative parameter is added (Arnold 2010). In the top-ranked model, adults (β_{ad} = 0.452, 95% CI = 0.016–0.889) and males (β_{male} = 0.304, 95% CI = 0.034–0.575) had higher survival rates than subadults and females, respectively. Survival was positively correlated with the area of 57 ($\beta_{\log(57)}$ = 1.004, 95% CI = –0.337 to 2.345) (Fig. 2b) and the amount of edge (β_{edge} = 0.763, 95% CI = –0.104 to 1.629) (Fig. 2b), but the 95% CI for the beta coefficients overlapped zero. If we set the habitat covariates equal to their mean value for all territories, apparent survival was estimated to be 0.73, 0.66, 0.63, and 0.56 for adult males, adult females, subadult males, and subadult females, respectively.

Occupancy

We estimated territory extinction and colonization probabilities using 4907 survey occasions. The best model for detection probability (p) indicated that p was different for each year. Within years, p was higher at territories with reproducing owls (β_{repr} = 1.566, 95% CI = 1.339–1.794), at territories containing more forest dominated by large trees (β_{67} = 0.017, 95% CI = 0.000–0.033), and on surveys subsequent to the initial ("init") detection of owls at a territory (β_{init} = 1.185, 95% CI = 1.011–1.359). The probability of initial occupancy (ψ_1) was not dependent on the amount of vegetation classes 57 or 67 within a territory (i.e., ψ_1 was constant). We used this structure for detection and initial occupancy probabilities for all subsequent modeling of territory extinction and colonization. Real values of detection probability estimates were high. When the area of forest with large trees was set equal to its mean value for all territories, detection probability was estimated to be 0.94, 0.83, 0.77, and 0.50 at territories with reproducing owls after the initial detection, territories with reproducing owls before the initial detection, territories with nonreproducing owls after the initial detection, and territories with nonreproducing owls before the initial detection, respectively.

Territory extinction.—The top-ranked model from step 1 (Appendix C) contained a covariate for the combined area of vegetation classes 5 and 7. The top-ranked model from step 2 included a covariate for habitat diversity in addition to the area of 57 and was 4.28 AIC units lower than the second-ranked model (Appendix C). The best overall model from step 3 also included the area of high-intensity timber harvests. In this model, territory extinction was negatively correlated with the area of 57 ($\beta_{57} = -0.117$, 95% CI = –0.189 to –0.044), such that occupied territories with greater amounts of 57 were less likely to become extinct (Fig. 2c). Surprisingly, territory extinction was also negatively correlated with the area of high-intensity timber harvests ($\beta_{high} = -0.776$, 95% CI = –1.327 to –0.224). Finally, territory extinction was positively correlated with habitat diversity (β_{div} = 1.509, 95% CI = 0.148–2.871) (Fig. 2c).

Territory colonization.—The top-ranked model from step 1 (Appendix C) contained a covariate for the logarithm of the combined area of vegetation classes 5 and 7. The top-ranked model from step 2 contained an additional covariate for habitat diversity and was 1.57 AIC units lower than the second-ranked model (Appendix C). The best overall model from step 3 included the area of wildfire that occurred within a territory. In this model, wildfire had a strong negative effect on territory colonization ($\beta_{fire} = -24.057$), but the standard error was unestimable because of the small number of territories that experienced fire. However, the value for β_{fire} was consistent across all of the models. Territory colonization was positively correlated with the area of 57 ($\beta_{\log(57)}$ = 1.299, 95% CI = –0.857 to 3.456) (Fig. 2d) and habitat diversity (β_{div} = 2.985, 95% CI = –0.222 to 6.191) (Fig. 2d), but the beta coefficients had 95% CI's that overlapped zero, suggesting that these effects were relatively weak.

Sensitivity analyses

Life stage simulation.—Estimates of apparent survival from our simulations ($\bar{\hat{\varphi}}_A$ = 0.68, 95% CI = 0.54–0.76; $\bar{\hat{\varphi}}_S$ = 0.58, 95% CI = 0.42–0.67) were lower than those previously reported for this population (Blakesley et al. 2010) because we removed part of the capture histories for 14 individuals that relocated to different

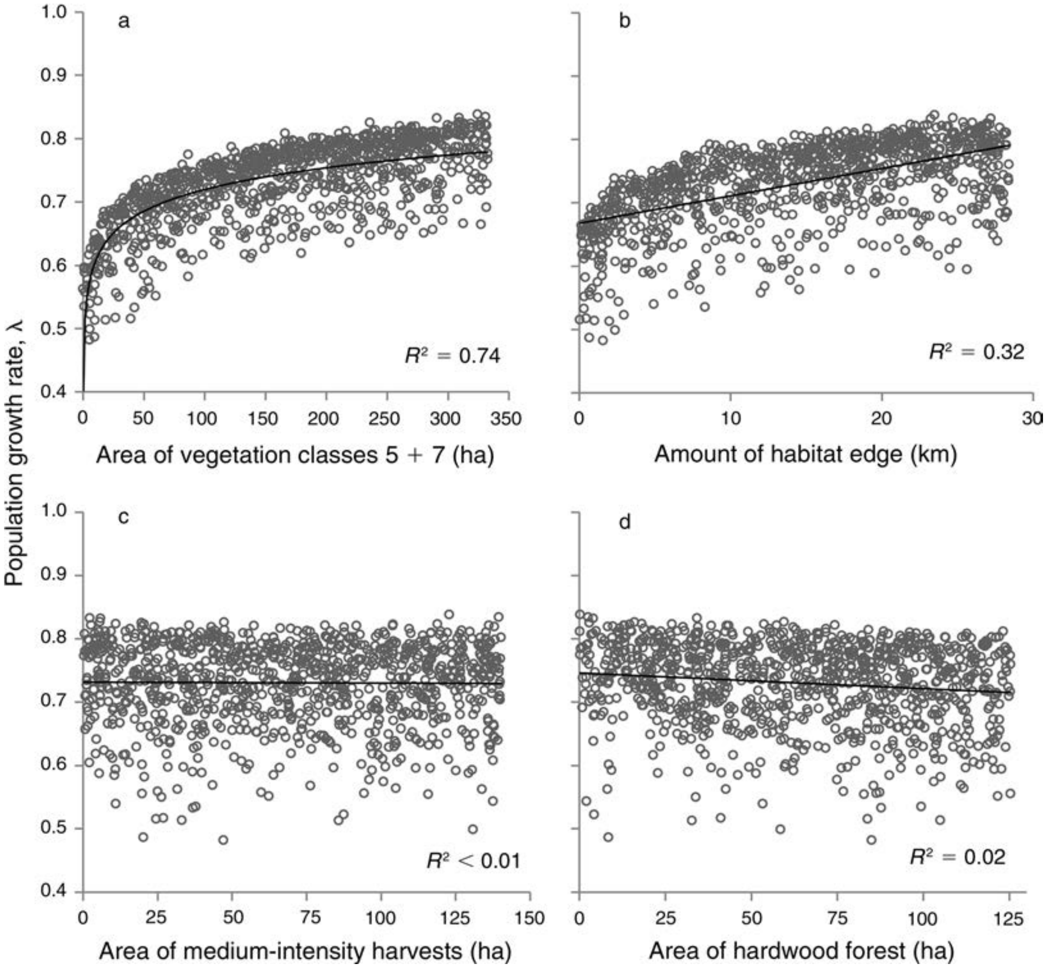

FIG. 3. Results of a life stage simulation analysis that we used to assess the sensitivity of annual population growth rate (λ) of California Spotted Owls to changes in forest vegetation conditions within owl territories. We generated 1000 λ values by randomly drawing (a) area of vegetation classes 5 and 7; (b) amount of habitat edge; (c) area of medium-intensity timber harvests; and (d) area of hardwood forest from a uniform distribution. Panel (a) is a best-fit logarithmic regression, and all other panels are best-fit linear regressions.

territories after a "missing" interval of one or more years (see *Methods: Sensitivity analyses*). Estimates of fecundity from our simulations were higher for adults ($\bar{\hat{b}}_{\text{A}} = 0.22$ female offspring per female, 95% CI = 0.18–0.28) than for subadults ($\bar{\hat{b}}_{\text{S}} = 0.05$ female offspring per female, 95% CI = 0.02–0.11), a pattern that has been previously reported for this study population (Blakesley et al. 2010).

Population growth rate was most sensitive (positive correlations) to the area of 57 and habitat edge, the two covariates that also best explained variation in apparent survival. We noted that population growth rate and the area of 57 were clearly related in a nonlinear fashion, so we calculated R^2 using a logarithmic relationship for this covariate; we specified a linear relationship for all other covariates. Population growth rate was positively correlated with the area of 57 ($R^2 = 0.74$; Fig. 3a) and habitat edge ($R^2 = 0.32$; Fig. 3b). In contrast, population growth rate was not sensitive to either of the covariates used to model reproduction (for area of medium-intensity harvests, $R^2 < 0.01$; for area of hardwood forests, $R^2 = 0.02$; Fig. 3c, d). Population growth rate was always less than 1.0 ($\bar{\hat{\lambda}} = 0.73$, 95% CI = 0.57–0.82), but we expected our matrix model to underestimate λ in the presence of immigration (Peery et al. 2006). Additionally, as we have noted, our apparent survival estimates were biased low. Nonetheless, changes in population growth rate allowed us to evaluate the relative importance of each covariate.

Occupancy.—Estimates of territory colonization from our simulations were strongly dependent upon the occurrence of wildfire during the previous six years ($\bar{\hat{\gamma}}$ without fire = 0.21, 95% CI = 0.04–0.52; $\bar{\hat{\gamma}}$ with fire = 0.00, 95% CI = 0.00–0.00) because we only observed three postfire colonization events at burned territories in the following six years. However, fire did not negatively affect territory occupancy in all cases. For example, the largest and most intense fire occurred on our study area in 2001 and impacted nine owl territories. Five of these territories remained occupied every year after the fire, and thus, postfire colonization could not occur at these sites. Estimates of territory extinction were low ($\bar{\hat{\varepsilon}} = 0.03$, 95% CI = 0.00–0.12), which reflected the strong site fidelity displayed by Spotted Owls (e.g., Blakesley et al. 2005, Seamans and Gutiérrez 2007*a*).

Equilibrium occupancy was most sensitive (positive correlation) to the area of 57 within a territory. We again noted a nonlinear relationship between equilibrium occupancy and the area of 57 and calculated R^2 using a logarithmic relationship for this covariate ($R^2 = 0.87$; Fig. 4a). Equilibrium occupancy was not sensitive to changes in habitat diversity ($R^2 = 0.02$; Fig. 4b) or high-intensity timber harvests ($R^2 = 0.01$; Fig. 4c). Equilibrium occupancy was weakly negatively correlated with wildfire when it occurred at the same frequency as during our study ($R^2 = 0.02$; Fig. 4d). However, when we doubled the frequency of wildfire to represent a future scenario of increased fire activity, we found a stronger negative association between the area burned and equilibrium occupancy ($R^2 = 0.11$; Fig. 4e). As a result, equilibrium occupancy was higher under the scenario with fewer fires ($\bar{\hat{\psi}} = 0.78$, 95% CI = 0.37–0.96) than the scenario with more fires ($\bar{\hat{\psi}} = 0.72$, 95% CI = 0.36–0.94).

Discussion

We characterized associations between territory-scale changes in forest conditions and demographic rates in a declining population of California Spotted Owls to assess the potential consequences of implementing landscape-scale fuel treatments in the Sierra Nevada. Although the correlative nature of our study posed constraints on inferences, we used 20 years of data on owl demography, forest treatments, and detailed changes in forest conditions. Our study differed from most previous, long-term Spotted Owl studies in that we quantified habitat within owl territories on an annual basis, rather than assuming that habitat was static over time. Thus, we believe that the relationships that we detected can help to guide forest management intended to balance reductions in high-severity fires with the needs of a key old-forest-associated species in the Sierra Nevada, as well as provide insight into mechanisms responsible for observed declines in California Spotted Owls in this region.

The amount of forest with high (>70%) canopy cover dominated by medium- or large-sized trees was the most important predictor of variation in demographic rates; this variable occurred in the top-ranked models for survival, territory extinction, and territory colonization rates, and explained far more variation in population growth rate and equilibrium occupancy than other covariates based on our simulations. This result is consistent with previous studies of Northern and California Spotted Owls that found a strong correlation between the area of high-canopy-cover forest and adult survival, and in some cases, reproduction and occupancy of territories (Franklin et al. 2000, Blakesley et al. 2005, Dugger et al. 2005, Seamans and Gutiérrez 2007*a*). We also found that forests with large trees and a lower threshold of canopy cover (>30%) were not a significant predictor of owl vital rates. This finding suggested that high canopy cover was a more important habitat component than large trees, although forests containing both were probably the highest quality habitat. The specific reasons for why high-canopy-cover forests are important for California Spotted Owls are unknown, but prey availability, predator avoidance, or microclimate may all be important factors (Verner et al. 1992). Nevertheless, consistent positive associations between demographic rates of Spotted Owls and forest with high canopy cover across studies and subspecies indicate the importance of these forest conditions for Spotted Owl populations.

The positive association between owl demographic rates and high-canopy-cover forest, coupled with the average loss of 10.6 ha (7.4%) of high-canopy-cover forest within territories on the DSA from 1993–2012 (Fig. 5a), suggests that habitat loss may have been at least partially responsible for the observed ~30% decline in abundance and territory occupancy in our study population (Tempel and Gutiérrez 2013). We were unable to assess the potential lag effects associated with habitat change prior to 1993, when more stringent harvesting guidelines were implemented on public land (USFS 1993); thus, observed declines could also reflect the historic legacy of timber harvesting. Nevertheless, many factors not considered here such as predation, prey availability, and disease, also could have contributed to population declines. Associations between high-canopy-cover forest and both population growth and equilibrium occupancy were nonlinear such that further loss of habitat could lead to relatively rapid declines in abundance and occupancy (Figs. 3a and 4a). For example, 26 owl territories currently contain between 100 and 150 ha of high-canopy-cover forest (Fig. 5b). If the average amount of high-canopy-cover forest within territories were reduced from 150 to 100 ha, the estimated decrease in population growth rate ($\lambda_{150\mathrm{ha}} = 0.740$, $\lambda_{100\mathrm{ha}} = 0.720$) would lead to a significant difference in realized population change when extrapolated over long time periods. We expected our estimates of population growth rate to be biased low, but the importance of forest with high canopy cover nevertheless can be assessed by relative changes in population growth rate.

As predicted, medium-intensity timber harvests characteristic of proposed fuel treatments were negatively related to reproduction of Spotted Owls in our study. Reproduction appeared sensitive to modest amounts of medium-intensity harvests, and was predicted to decline from 0.54 to 0.45 when 20 ha were treated (assuming the mean area of hardwoods in territories, 60 ha). Greater areas harvested in this manner only resulted in slightly

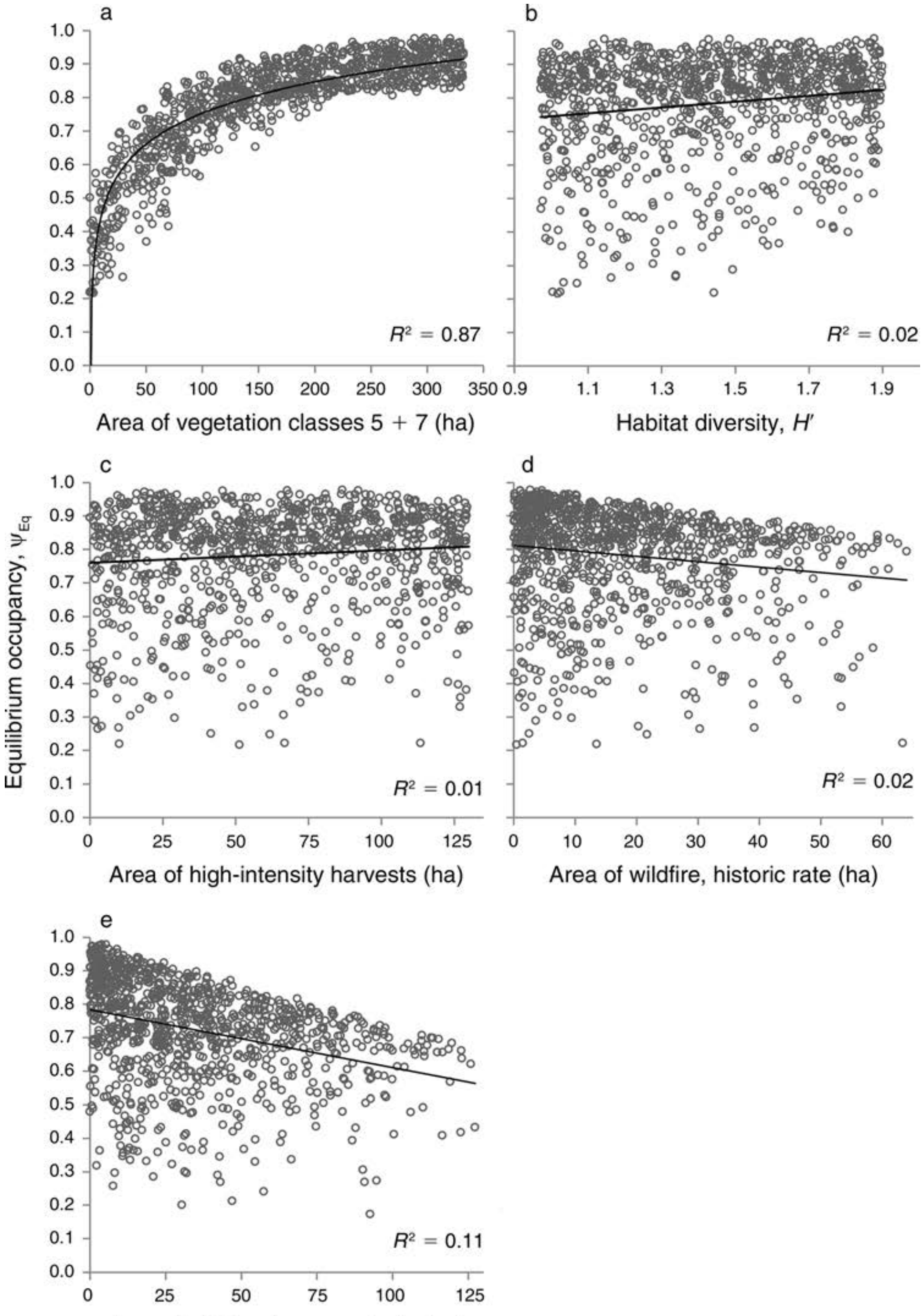

FIG. 4. Assessment of the sensitivity of equilibrium occupancy (ψ_{Eq}) of California Spotted Owl territories to changes in forest vegetation conditions within owl territories. We generated 1000 ψ_{Eq} values by randomly drawing: (a) area of vegetation classes 5 and 7; (b) habitat diversity (Shannon-Wiener index); and (c) area of high-intensity timber harvests from a uniform distribution. Panels (d) and (e) were generated under two different wildfire scenarios: a maximum of 12 territories burned (the observed number during our study) and a maximum of 24 territories burned (representing the potential for increased fire frequency in the future), respectively. Panel (a) is a best-fit logarithmic regression, and all other panels are best-fit linear regressions.

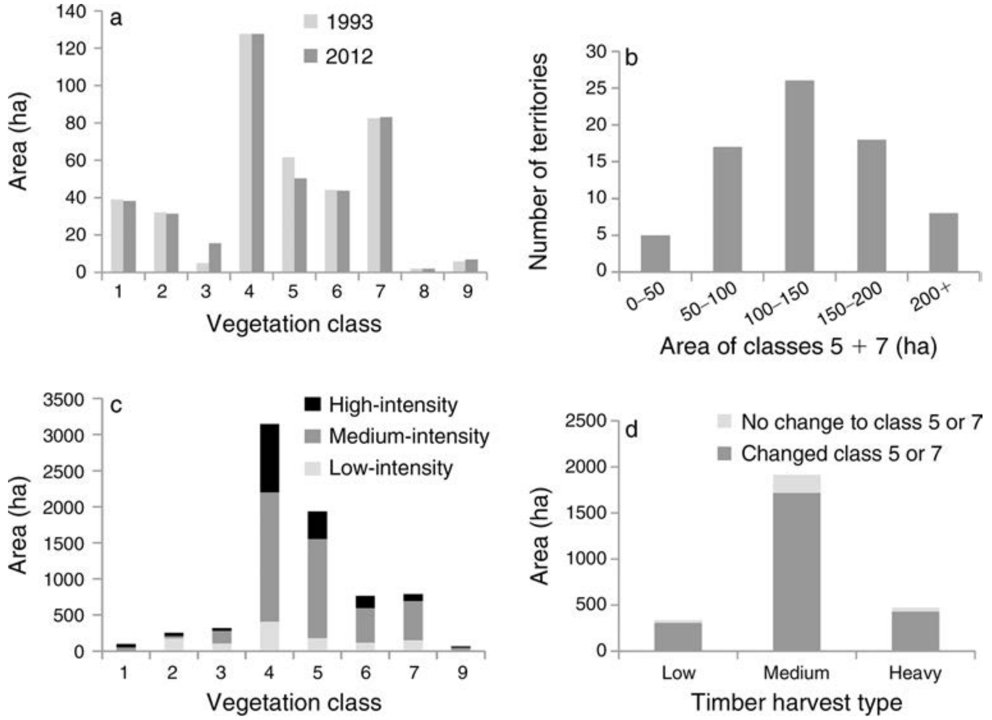

FIG. 5. Vegetation conditions within California Spotted Owl territories on our study area in the central Sierra Nevada, California, as represented by (a) the area of each vegetation class in owl territories on the Density Study Area in 1993 and 2012; (b) the number of owl territories containing different areas of vegetation classes 5 and 7 in 2012; (c) the area of low-, medium-, and high-intensity timber harvests that occurred in each vegetation class from 1993–2012 (class 8, water or barren rock, was omitted here as no timber harvest was possible); and (d) the area of low-, medium-, and high-intensity timber harvests occurring in vegetation classes 5 and 7 that did or did not result in a change in vegetation class from 1993 to 2012.

larger declines in reproduction (Fig. 2a). The mechanism linking medium-intensity timber harvests to declines in reproduction is not entirely clear, but the thinning practices characteristic of medium-intensity harvests typically reduce the vertical forest structure and understory complexity that are believed to be important characteristics of foraging conditions used by Spotted Owls (Verner et al. 1992). Although we detected an overall effect of medium-intensity timber harvests on reproduction, we did not detect an effect of understory removal independent of modifications to the overstory for medium-intensity harvests. Understory removal is generally an important component of fuel-reduction strategies, but we caution that medium-intensity harvesting with understory treatments occurred on only 5.2% of the total area within owl territories, which could have limited our power to detect effects.

Unlike reproduction, we did not detect a relationship between the area of medium-intensity harvests and apparent survival or territory occupancy. The absence of an association is perhaps not surprising, given the Spotted Owl's "bet-hedging" life history strategy in which individuals have evolved long life spans and forgo reproduction when environmental conditions are unfavorable without compromising lifetime reproductive success (Seamans and Gutiérrez 2007*b*). In addition, only 42.8% of medium-intensity harvests occurred in forests with high canopy cover; thus, over half of these harvests occurred in habitats that might be less important to Spotted Owls (Fig. 5c). When medium-intensity harvests were implemented within high-canopy-cover forests, they reduced the canopy sufficiently for mapped polygons to be reclassified into a lower-canopy-cover vegetation class in 90.1% of these treated areas (Fig. 5d). As we described previously, such changes were associated with reductions in survival and territory colonization rates, as well as increases in territory extinction rates. As a result, we believe that the most appropriate inference about the influence of medium-intensity harvesting practices is that they appear to reduce reproductive potential, and when implemented in forests with high canopy cover, are likely to reduce survival and territory occupancy as well.

Contrary to our prediction, the probability of a territory going extinct was reduced in proportion to the area harvested with high-intensity practices such as clear-cutting and shelterwood harvest. In principle, harvesting prescriptions creating small gaps might promote brushy habitat suitable for prey species such as woodrats and increase prey availability for Spotted Owls along the edges of forested habitats (Sakai and Noon 1997). Similarly, we found that owl survival and population growth were positively associated with the amount of habitat edge between shrubs/saplings and forests dominated by trees ≥30.5 cm dbh, so the juxtaposition of owl and prey habitat could be important, as suggested by Franklin et al. (2000). Nevertheless, these associations are largely speculative without direct evidence of foraging by owls and elevated prey availability along ecotones. Moreover, high-intensity treatments occurred on only 5.4% of the total area within our owl territories and larger scale implementation of heavy harvesting could have adverse impacts on Spotted Owls. Finally, flying squirrels are the most important prey by biomass within our study area (R. J. Gutiérrez, *unpublished data*), and intensive harvesting practices are believed to negatively impact this species (Waters and Zabel 1995, Manning et al. 2012). Thus, while detailed studies of prey availability and Spotted Owl foraging near brush habitat are merited, we believe it would be premature to implement such timber-harvesting practices as a tool for managing prey availability for California Spotted Owls.

Although our results suggested that fuel treatments can have negative and direct impacts on Spotted Owl habitat quality in the short term, comprehensive assessments must consider the potential long-term benefits of reduced wildfire risk. Long-term benefits will depend on both the risk that fire poses to Spotted Owls and the extent to which fuel treatments reduce high-severity fires. We detected a large decline in territory colonization following wildfire, but not all burned territories were negatively affected by fire. Several burned territories remained occupied in all years after a fire (see *Results: Sensitivity analyses*); as a result, colonization could not occur, by definition. Thus, while our results were somewhat consistent with other studies that detected adverse impacts of high-severity fires on Spotted Owls, particularly when coupled with salvage logging (Clark et al. 2013, Lee et al. 2013), the effect of wildfire on Spotted Owls and their habitat is undoubtedly complex (Bond et al. 2009, 2013). Nonetheless, because equilibrium occupancy declined more under a scenario of increased fire activity (Fig. 4e), which is projected under some climate change scenarios (Liu et al. 2013), we believe a valid need exists to reduce the risk of wildfire to Spotted Owls. Previous modeling efforts indicated that the benefits of reducing habitat loss from high-severity fires outweighed the impacts of fuel treatments on forest conditions used by Spotted Owls (Lee and Irwin 2005, Ager et al. 2007). However, these studies were either conducted for Northern Spotted Owls in another physiographic province (Ager et al. 2007) or did not assess the immediate effects of fuel treatments on California Spotted Owl demographic rates using empirical data (Lee and Irwin 2005). Thus, additional research is needed to determine the long-term trade-offs between direct reductions in owl habitat from fuel treatments vs. habitat loss from increased fire frequency or severity.

We suggest the following caveats from our study when considering the impact to Spotted Owls from forest fuel treatments and wildfire. First, our study was observational, not experimental, and thus observed relationships between covariates and owl demographic rates were correlative and not directly attributable to cause and effect. Second, a broad range of timber harvests occurred within owl territories during our study, which may have confounded our ability to assess specific management practices (e.g., fuel-reduction treatments following current management prescriptions; USFS 2004). Nevertheless, proposed fuel-reduction treatments have effects on forest structure similar to those in our medium-intensity timber harvest category (Appendix B). Third, we used aerial photos to compile our vegetation map, which required us to subjectively categorize vegetation classes into relatively coarse bins. Thus, we were unable to assess the potential effects of small (e.g., 10%) reductions in canopy cover that did not result in changes in vegetation class. Our mapping approach also precluded the inclusion of potentially important habitat elements such as large, residual trees and understory structure. Large trees are known to be important components of nesting and roosting conditions used by Spotted Owls (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997), and the high-canopy-cover forest that we found to be highly correlated with owl demographic rates included vegetation class 7 (trees with dbh ≥ 76.2 cm). Finally, the potential effects of habitat, forest treatments, and wildfire within owl territories were probably confounded with differences in individual quality, which can be an important source of variation in avian demographic rates (e.g., Goodburn 1991, Espie et al. 2004, Sergio et al. 2009). Despite these caveats, we identified several reasonable predictors of Spotted Owl demographic parameters supported by prior knowledge of Spotted Owl environmental requirements that we believe can contribute to forest management.

Conclusions

Our results suggest that reductions in the area of high-canopy-cover forest resulting from either logging or high-severity wildfire could reduce the viability of California Spotted Owl populations and may be contributing to ongoing declines in abundance and territory occupancy (Conner et al. 2013, Tempel and Gutiérrez 2013). Nevertheless, our results also suggest that fuel treatments that occur in forests with lower canopy cover (<70%) or do not significantly reduce canopy in high-canopy-cover forests are less likely to have adverse impacts on Spotted Owls. While such a constraint may seem restrictive because fuel-reduction treatments necessarily target dense, fire-prone stands, we note that 50.7% of all medium-intensity harvests implemented from 1993 to 2012 occurred in medium-sized forest with low canopy cover (vegetation class 4 = 40.1%) or large-sized forest with low canopy cover (vegetation class 6 = 10.6%; Fig. 5c). Moreover, fuel treatments in dense stands can emphasize thinning from below while maintaining sufficient canopy cover and some vertical stand structure (Verner et al. 1992).

Zielinski et al. (2013) recently concluded that it may be possible to implement fuel-reduction treatments that achieve fire-reduction goals without affecting occupancy by fishers, another species associated with older forests in the Sierra Nevada. However, they did not distinguish among different types of timber harvest, nor did they assess where timber harvests occurred with respect to preexisting vegetation types. We recommend that landscape-scale fuel treatments intended to reduce fire risk in the Sierra Nevada proceed with caution to reduce the chance of impacting old-forest-associated species, particularly in high-canopy-cover forests. Specifically, we recommend that fuel treatments focus on ladder fuels and reduction in tree density while maintaining relatively high canopy cover. Given the uncertain relationship between timber harvest and demography of Spotted Owls, we suggest that landscape-scale fuel treatments be accompanied by a rigorous monitoring program.

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Supplemental Material

Ecological Archives

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Meta-analysis of California Spotted Owl (*Strix occidentalis occidentalis*) territory occupancy in the Sierra Nevada: Habitat associations and their implications for forest management

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RESEARCH ARTICLE

Meta-analysis of California Spotted Owl (*Strix occidentalis occidentalis*) territory occupancy in the Sierra Nevada: Habitat associations and their implications for forest management

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ABSTRACT

We assessed the occupancy dynamics of 275 California Spotted Owl (*Strix occidentalis occidentalis*) territories in 4 study areas in the Sierra Nevada, California, USA, from 1993 to 2011. We used Landsat data to develop maps of canopy cover for each study area, which we then used to quantify annual territory-specific habitat covariates. We modeled the relationships between territory extinction and colonization using predictor variables of habitat, disturbance (logging, fire), climate, and elevation. We found that forests with medium (40–69%) and high ($\geq$70%) canopy cover were the most important predictors of territory occupancy in all study areas, and that both canopy cover categories were positively correlated with occupancy. We used analysis of deviance to estimate the amount of variation explained by the habitat covariates (primarily medium and high canopy cover) and found that these covariates explained from 35% to 67% of the variation in occupancy. Climatic covariates were not correlated with occupancy dynamics and explained little of the variation in occupancy. We also conducted a post hoc analysis in which we partitioned canopy cover into 10% classes, because our original partitioning into 3 classes may have lacked sufficient resolution to identify canopy cover levels where occupancy changed abruptly. In this post hoc analysis, occupancy declined sharply when territories contained more area with $<$40% canopy cover, and the amount of 50–59% and 60–69% canopy cover had a more positive association with occupancy than did 40–49% canopy cover. Our results suggest that some fuels treatments intended to reduce fire risk and improve forest resilience could be located within Spotted Owl territories without adversely impacting territory occupancy if such treatments do not consistently reduce canopy cover below 50%. We suggest that future work quantify components of forest structure (e.g., large tree density, vertical complexity) known to be selected by owls and relate these characteristics to occupancy and fitness metrics.

Keywords: California Spotted Owl, canopy cover, forest management, occupancy, Sierra Nevada, *Strix occidentalis occidentalis*

Meta análisis de la ocupación de territorios de *Strix occidentalis occidentalis* en la Sierra Nevada: asociaciones de hábitat y sus implicaciones para el manejo forestal

RESUMEN

Determinamos la dinámica de ocupación de 275 territorios de *Strix occidentalis occidentalis* en 4 áreas de estudio en la Sierra Nevada, California, entre 1993 y 2011. Usamos datos de Landsat para desarrollar mapas de cobertura del dosel para cada área de estudio, que usamos luego para cuantificar covariables de hábitat anuales específicas de cada territorio. Modelamos la relación entre la extinción y la colonización de los territorios usando variables predictoras de hábitat, disturbio (tala, incendios), clima y elevación. Encontramos que los bosques con cobertura de dosel media (40–69%) y alta ($\geq$70%) fueron los predictores más importantes de la ocupación de los territorios en todas las áreas de estudio, y ambas categorías de cobertura de dosel se correlacionaron positivamente con la ocupación. Usamos análisis de desviación para estimar la cantidad de variación explicada por las covariables del hábitat (principalmente cobertura de dosel media y alta) y encontramos que estas covariables explican entre 35.1% y 67.1% de la variación en la ocupación. La covariables del clima no se correlacionaron con la dinámica de ocupación y explicaron poco de la variación en ocupación. También hicimos un análisis post-hoc en el que hicimos particiones de la cobertura del dosel en clases de 10% porque nuestra partición original en 3 clases podría no tener suficiente resolución para identificar los niveles de cobertura del dosel en los que la ocupación cambia abruptamente. En este análisis post-hoc, la ocupación disminuyó fuertemente cuando los territorios contenían menos de 40% de cobertura de dosel, y las clases de cobertura entre 50–59% y 60–69% presentaron una asociación más positiva con la ocupación de lo que la tuvo la clase de cobertura entre 40–49%. Nuestros resultados sugieren que algunos tratamientos con la intención de reducir el riesgo de incendios y mejorar la resiliencia de los bosques podrían ser ubicados dentro de los territorios de *S. o. occidentalis* sin afectar seriamente la ocupación de los territorios si tales tratamientos no reducen la cobertura del dosel por debajo del 50%. Sugerimos que trabajos futuros cuantifiquen los componentes de la estructura del bosque (e.g. densidad de árboles grandes, complejidad vertical) que se sabe son seleccionados por los búhos y relacionen estas características con la ocupación y medidas de aptitud.

Palabras clave: cobertura del dosel, manejo forestal, ocupación, Sierra Nevada, *Strix occidentalis occidentalis*

INTRODUCTION

The range of the California Spotted Owl (*Strix occidentalis occidentalis*) extends from the southern Cascade Range, USA, to northern Baja California, Mexico, but most of its population is found in the Sierra Nevada, California, USA (Verner et al. 1992, Gutiérrez et al. 1995). For nesting and roosting, it selectively uses economically valuable, older forests that have been affected by timber harvesting for more than a century (Gutiérrez et al. 1995). Although it is the only Spotted Owl subspecies not protected under the U.S. Endangered Species Act, management guidelines developed to retain important Spotted Owl habitat in Sierra Nevada forests have been in place for >20 yr (Verner et al. 1992, USDA Forest Service 2004), and Spotted Owl habitat remains a central component of forest management in the Sierra Nevada (USDA Forest Service 2016).

Management of Spotted Owl habitat in the Sierra Nevada is complicated by changing fire regimes that are largely the result of decades of fire suppression, which has allowed uncharacteristic accumulation of fuel loads on the landscape (Stephens et al. 2015). Whereas historical fire regimes were typified by relatively frequent fires that burned mainly at low and moderate severity (Skinner and Chang 1996), the relative proportion and patch sizes of high-severity fires have increased within the past 30 yr (Miller et al. 2009, Miller and Safford 2012). High-severity fire is often characterized by ≥75% mortality of overstory trees and can result in habitat loss for species associated with older forests. In fact, large patches of high-severity fire have been shown to negatively affect occupancy of Spotted Owl territories after controlling for postfire timber harvest (Lee et al. 2013, Jones et al. 2016a). In addition, climate change is expected to increase the incidence of extreme fire behavior in California (Westerling and Bryant 2008, Liu et al. 2013).

As a result, forest managers in the Sierra Nevada modify forest vegetation structure (i.e. implement "forest treatments"), primarily by removing surface and ladder fuels (Finney 2001, USDA Forest Service 2004), in attempts to reduce wildfire intensity, size, and rate of spread. Although concern exists that these treatments may adversely impact Spotted Owl habitat in the short term (5–10 yr), it is possible that they may provide long-term benefits by reducing future habitat loss as a result of high-severity fire (Tempel et al. 2015). Thus, reconciling forest restoration and Spotted Owl habitat conservation is important because owl populations in the Sierra Nevada have declined by up to 50% in the past 20 yr (Conner et al. 2013, Tempel et al. 2014a). Furthermore, managers are now considering recommendations to modify forest treatments to emphasize forest heterogeneity at the spatial scales of the forest stand and the landscape (North et al. 2009, North 2012). Under these recommendations, forest treatments would be less uniform and tailored to local conditions (e.g., topography, soil, aspect), resulting in a range of stand conditions (tree density, canopy cover) on the landscape (North et al. 2009). This approach also is believed to increase forest resilience to ecological stressors such as high-severity fire, warming temperatures, or extended drought (e.g., Asner et al. 2016).

To assess the potential effects of forest management on Spotted Owls, we related territory occupancy dynamics to canopy cover using presence–absence data collected from 1993 to 2011 in 4 long-term demographic study areas in the Sierra Nevada. We also evaluated the relationship between annual climatic variables and territory occupancy dynamics because changing climatic conditions could affect occupancy dynamics (Jones et al. 2016b). To quantify forest structure within owl territories, we used Landsat imagery to develop raster-based maps of forest canopy cover for each study area and assigned canopy cover into categories. We hypothesized that high (≥70%), medium (40–69%), and low (<40%) canopy cover would be biologically meaningful for Spotted Owls in different ways, because forests with ≥70% canopy cover are selected by owls for nesting and roosting (Moen and Gutiérrez 1997), whereas forests with 40–69% canopy cover may be used for foraging, and forests with <40% canopy cover are often

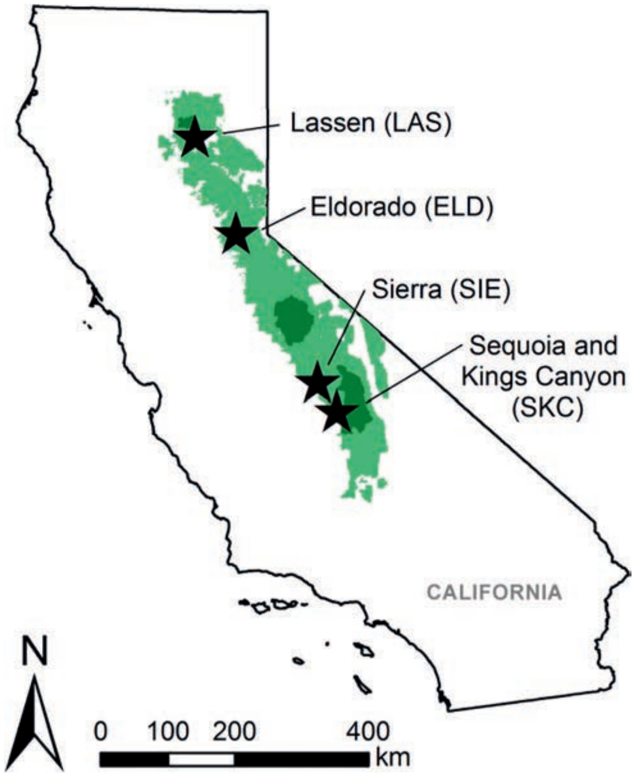

FIGURE 1. Locations of 4 study areas for California Spotted Owls, 1993–2011. Light shading indicates national forests; dark shading indicates national parks.

avoided (Call et al. 1992). We were unable to accurately estimate other important Spotted Owl habitat features (e.g., large trees, snags, vertical structure) with Landsat, and these variables were omitted from our analyses. We also tested whether spatially explicit metrics of forest structure, such as the spatial dispersion of high-canopy-cover forest and heterogeneity in canopy-cover conditions, were related to territory occupancy dynamics.

METHODS

Study Areas

Our long-term demographic study areas were situated on a north–south axis from the southern Cascades to the southern Sierra Nevada, California, USA (Figure 1). The Lassen study area (LAS) was in the southern Cascades, but was managed by the USDA Forest Service as part of the Sierra Nevada province, and the owls here are more likely to be California Spotted Owls than Northern Spotted Owls (*Strix occidentalis caurina*; USDA Forest Service 2004, Barrowclough et al. 2011). The Lassen, Eldorado (ELD), and Sierra (SIE) study areas consisted mainly of public land managed by the Forest Service, but also contained some privately owned land. Most private land within the Lassen study area was not surveyed for owls, but some owl territories on private land adjacent to the Lassen National Forest were included. The Eldorado and Sierra study areas contained 37% and 8% private land, respectively. The Sequoia–Kings Canyon (SKC) study area was entirely within 2 national parks of the same name. Barred Owls (*Strix varia*) were not present in any of the study areas until the last several years of our study, and they were either uncommon (Lassen) or extremely rare ($\leq$3 individuals each in the Eldorado, Sierra, and Sequoia–Kings Canyon sites). Most precipitation in each study area fell as rain or snow during winter and early spring. Summers in all study areas were hot and dry. Additional detailed climatic information is described in Franklin et al. (2004).

The Lassen study area was located in the Lassen National Forest between Mineral and Susanville, California, at 1,200 m to 2,100 m elevation, and encompassed 2,200 km^2. The primary vegetation type in this study area was mixed-conifer forest dominated by sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and incense cedar (*Calocedrus decurrens*). California black oak (*Quercus kelloggii*) and Pacific dogwood (*Cornus nuttallii*) occurred in the understory, and red fir (*A. magnifica*) was present at higher elevations as pure stands or mixed with white fir.

The Eldorado site was located in the Eldorado and Tahoe national forests east of Georgetown, California, between 300 and 2,500 m elevation, and encompassed 818 km^2. Mixed-conifer forest was the primary vegetation type in this study area, and was dominated by sugar pine, ponderosa pine, white fir, Douglas-fir, and incense cedar. California black oak, canyon live oak (*Q. chrysolepis*), tanoak (*Notholithocarpus densiflorus*), and bigleaf maple (*Acer macrophyllum*) were common understory species. Red fir and lodgepole pine (*Pinus contorta*) occurred at the higher elevations.

The Sierra study site was located in the Sierra National Forest east of Fresno, California, between 300 and 2,900 m elevation, and encompassed 693 km^2. This study area contained 3 major vegetation types. Oak woodland (26% of the study area) dominated by blue oak (*Q. douglasii*), interior live oak (*Q. wislizeni*), canyon live oak, and California foothill pine (*Pinus sabiniana*) occurred at lower elevations. Mixed-conifer forest (61%) dominated by sugar pine, ponderosa pine, white fir, incense cedar, black oak, red fir, and Jeffrey pine (*P. jeffreyi*) occurred at middle elevations. Conifer forest (13%) dominated by red fir, lodgepole pine, and western white pine (*P. monticola*) occurred at higher elevations.

The Sequoia–Kings Canyon study area was located in Sequoia and Kings Canyon national parks northeast of Visalia, California, at elevations ranging from 425 to 3,050 m and encompassed 343 km^2. This study area consisted of 3 major vegetation types. Oak woodlands (24% of the study area) containing blue oak, interior live oak, canyon live oak, and California foothill pine were present at lower elevations. Mixed-conifer forest (67%) dominated by sugar pine, ponderosa pine, white fir, and incense cedar occurred at middle elevations. Ten giant sequoia (*Sequoiadendron giganteum*) groves (7%) were found within the mixed-conifer zone. Conifer forests dominated by red fir, lodgepole pine, and western white pine occurred at higher elevations.

Spotted Owl Surveys

We conducted Spotted Owl surveys annually across each study area from 1993 to 2011 during the breeding season. All study areas consisted of a core study area that we surveyed completely in each year of the study (i.e. both the areas containing owl territories and all areas not containing owls within the core area were surveyed every year). In addition, we added some owl territories over time, either as an expansion of the core area (Lassen) or as individual satellite territories to increase owl sample sizes for demographic analysis (Lassen and Eldorado), and we deleted a portion of the Sequoia–Kings Canyon site in 2006. We accounted for these changes in our analyses. We surveyed all satellite sites used in our occupancy analyses for a minimum of 3 yr; most territories in the core areas were surveyed for $\geq$15 yr. We conducted surveys from April 1 to August 31 in the Lassen and Eldorado study areas and from March 1 to September 30 in the Sierra and Sequoia–Kings Canyon sites. However, no surveys were conducted in the Sequoia–Kings Canyon study site in 2005 because of a temporary suspension of funding.

We imitated Spotted Owl vocalizations at designated survey stations or while walking survey routes through historical owl territories or between survey stations. We determined a responding owl's sex by the pitch of its 4-note territorial call; males have a lower-pitched call than females (Forsman et al. 1984). If owls were detected during nocturnal surveys, we conducted diurnal surveys to band unmarked owls, resight marked owls, assess reproduction, locate roosting areas, and band fledglings (Franklin et al. 1996). We included both nocturnal and diurnal surveys in our occupancy analyses.

Canopy Cover Map Development

We developed annual, raster-based canopy cover maps at 30 × 30 m spatial resolution using Landsat 5 Thematic Mapper satellite images from 1990 to 2011 acquired during July or August of each year. In each of these images, we estimated the fractional tree cover (in 1% increments) in a pixel using the Mixed Stratified Spectral Mixture Analysis method (MixSSMA; Koltunov et al. 2014, Koltunov and Ramirez 2015; see Supplemental Material Appendix A for complete details). To test the accuracy of the canopy cover maps, we compared them to 2 independent sets of canopy cover data obtained from airborne LiDAR (Light Detection and Ranging) and by double-blind visual interpretation of multitemporal high-resolution imagery from Google Earth (Google, Mountain View, California, USA) and the National Agriculture Imagery Program (NAIP; USDA Farm Service Agency, Salt Lake City, Utah, USA). The LiDAR data were acquired at a density of ~8–10 points m^{-2} during 2009–2012, but were available only for parts of 2 study areas, Lassen and Sierra. We selected a stratified random sample of 3 × 3 pixel (90 × 90 m) polygons with no overlap (550 polygons for the Lassen study site, 376 for Sierra; Supplemental Material Figure S1) and compared the Landsat-derived canopy cover for 2010 with the fraction of LiDAR returns above 3 m. The mean (± SD) absolute differences in canopy cover were 8.4 (± 8.8) for Lassen and 9.5 (± 9.5) for Sierra, and the pseudo r^2 values were 0.83 for Lassen and 0.71 for Sierra (Supplemental Material Figure S2). The test set based on high-resolution imagery was developed for all 4 study areas in 2005 and 2010. We selected 3 × 3 pixel (90 × 90 m) polygons with no overlap (195 to 600+ polygons per study area; Supplemental Material Figure S1), and again compared the Landsat-derived canopy cover with the values based on high-resolution imagery. The mean absolute differences in canopy cover ranged between 9.7 and 15.5, and the pseudo r^2 values ranged between 0.33 and 0.80 (Supplemental Material Table S1).

Canopy cover at the pixel scale was grouped into one of 3 classes (<40%, 40–69%, $\geq$70%) to minimize the effect of map error on inference. Although our classes were relatively coarse, they were less subject to mapping error than classes with a narrower range of values, and thus more likely to yield robust relationships between canopy cover and territory occupancy. Furthermore, previous Spotted Owl occupancy studies have used similar or identical canopy cover classes to these 3 classes (Blakesley et al. 2005, Seamans and Gutiérrez 2007b, Tempel et al. 2014b). However, forest managers could benefit from finer resolution as to how occupancy is related to canopy cover levels within these classes (e.g., the difference that might be expected if forest treatments reduce canopy cover from 70% to 40% vs. 70% to 60%). Thus, we performed a post hoc analysis using 10% canopy cover classes (see Statistical Analysis—Model selection). It is important, however, to recognize that canopy cover conditions are mapped with lower accuracy in this analysis and that inferences are more likely influenced by map uncertainty. As such, we did not make explicit predictions, for example, of how much forest with 70–80% canopy cover would be needed to achieve a specific target goal of territory occupancy. Rather, we searched for broad patterns across study areas in the directionality of relationships between the area of forest within 10% canopy cover classes and Spotted Owl territory occupancy metrics.

Statistical Analysis

We used the annual survey data to identify Spotted Owl territories and construct occupancy histories for our analyses. We identified owl territories as sites where at least 1 owl was detected during diurnal hours in $\geq$3 yr, where diurnal hours occurred between dawn and dusk based on civil twilight times (http://aa.usno.navy.mil/data/docs/RS_OneYear.php). For the purpose of quantifying habitat covariates within Spotted Owl territories, we first calculated the geometric center of each territory as the average spatial coordinates of all nest and roost locations in the territory. We then calculated the mean nearest-neighbor distance among territory centers for each study area as the average distance between each territory center and the center of its nearest neighboring territory, and we defined the spatial extent of a "territory" as a circle around each territory center with a radius of half of the mean nearest-neighbor distance. The resulting territory size for each study area decreased along a north–south gradient: Lassen = 639.4 ha (1,427-m radius), Eldorado = 399.5 ha (1,128-m radius), Sierra = 301.6 ha (980-m radius), and Sequoia–Kings Canyon = 254.3 ha (900-m radius). This process nearly eliminated spatial overlap among adjacent territory circles. We did not include nocturnal detections outside a territory circle when compiling occupancy histories to eliminate potential spurious detections of owls from nearby territories or nonterritorial, floater owls. A survey in which no owls were detected needed a total duration of $\geq$30 min to be included in the occupancy history.

We used a multiple-season, robust-design occupancy model to assess territory occupancy dynamics in each study area separately, in which the statistical model contained parameters for initial occupancy (ψ_1), territory extinction (ε_t), territory colonization (γ_t), and detection probability ($p_{t,j}$; MacKenzie et al. 2003). Our primary sampling periods (t) were breeding seasons (i.e. years), and our secondary sampling periods (j) were bimonthly periods within each breeding season (March 1–15, March 16–31, April 1–15, April 16–30, etc.). Thus, the Lassen and Eldorado study areas had 10 secondary periods each year, and the Sierra and Sequoia–Kings Canyon study areas had 14 secondary periods each year. If multiple surveys were conducted within the same secondary period, we assigned a "0" to the survey history if no owls were detected during any survey and a "1" if at least 1 owl was detected during any survey. When fitting the models for Sequoia–Kings Canyon, we fixed all 2005 detection probabilities and ε and γ from 2004 to 2005 at 0 because no surveys were conducted in 2005. We used program PRESENCE 10.2 (USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA) to fit models and estimate parameters for individual models that contained covariates (Table 1) that we hypothesized would affect detection probability, initial occupancy, territory colonization, and territory extinction.

Model covariates. We hypothesized that within-year detection probability would be higher on survey occasions subsequent to the survey when owl(s) were initially detected at a territory (*initial*) because surveyors might intensify their efforts to relocate detected birds in order to resight or capture them and to assess reproduction (Riddle et al. 2010, Tempel and Gutiérrez 2013). We expected nesting owls (*repro*; value equal to 1 for all surveys in a territory in a given year if reproduction was detected during any survey) to be more easily detected than nonnesting owls because nesting owls defend their territories more aggressively or spend more time near the territory center (MacKenzie et al. 2009, Tempel and Gutiérrez 2013). We also considered linear (*T*), logarithmic (*lnT*), and quadratic (*TT*) time trends for within-year detection probability, and that $p_{t,j}$ could be different during each bimonthly sampling period (*survey*). We hypothesized that among-year detection probability would vary in a linear (*T*), logarithmic (*lnT*), or quadratic (*TT*) time trend, or that $p_{t,j}$ would be different for each year of the study (*year*; Tempel and Gutiérrez 2013).

We used the raster-based canopy cover maps to quantify annual, territory-specific vegetation covariates that could have affected occupancy. We first used ArcMap 10.1 (ESRI, Redlands, California, USA) to calculate the proportion of each owl territory that contained forest (i.e. pixels) with $\geq$70% canopy cover (*highCC*) and forest with canopy cover between 40% and 69% (*mediumCC*). Previous studies have shown that California Spotted Owls select high-canopy-cover forest for nesting and roosting (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997) and that territory occupancy is positively correlated with the amount of high-canopy-cover forest (Blakesley et al. 2005, Tempel et al. 2014b). Forests with intermediate amounts of canopy cover may function as Spotted Owl nesting or roosting habitat if large, residual trees are present (Moen and Gutiérrez 1997, Hunter and Bond 2001), or might be used by foraging owls (Call et al. 1992).

We then used FRAGSTATS 4.2 (McGarigal et al. 2012) to calculate 3 annual covariates that represented the spatial arrangement or distribution of *highCC* and/or *mediumCC* within a territory. We hypothesized that the density of edge (*edge*) between *highCC* and any vegetation type with <40% canopy cover would be positively correlated with occupancy because these edges could increase the availability of prey such as dusky-footed woodrats (*Neotoma fuscipes*) and other rodents (Sakai and Noon 1997). Similarly, we hypothesized that owls would experience improved foraging conditions if *highCC* was spatially dispersed throughout the territory, rather than being aggregated into large patches. Therefore, we calculated the area-weighted clumpiness index for *highCC* within a territory

TABLE 1. Covariates used to model detection probability ($p_{t,j}$), initial occupancy (ψ_1), territory extinction (ε_t), and territory colonization (γ_t) for California Spotted Owls in 4 study areas in the Sierra Nevada, California, USA, 1993–2011. The predicted effects were: positive correlation between covariate and parameter (+), negative correlation (–), and no specific prediction (x). The covariate was not modeled for a parameter if the predicted effect is blank.

		Predicted effect on parameter			
Covariate	Definition	$p_{t,j}$	ψ_1	ε_t	γ_t
initial	Different *p* in surveys after initial detection of owls.	+			
repro	Reproductive status of owls (0 = not nesting, 1 = nesting).	+			
survey	Different *p* for each survey within a year.	x			
year	Year-specific variation in parameter value.	x		x	x
T	Linear temporal trend.	x			
lnT	Logarithmic temporal trend.	x			
TT	Quadratic temporal trend.	x			
highCC	Proportion of owl territory containing forest with $\geq$70% canopy cover.	x	+	−	+
mediumCC	Proportion of owl territory containing forest with canopy cover between 40% and 69%.	x	+	−	+
edge	Edge density (m m^{-2}) between *highCC* and any vegetation type with $<$40% canopy cover.			−	+
clump	Clumpiness index for *highCC*, a measure of its spatial aggregation.			+	−
even	Shannon's evenness index for *highCC*, *mediumCC*, and $<$40% canopy cover.			−	+
logging	Proportion of owl territory within which canopy cover was reduced by at least 10% in the previous 3 yr from logging (or other causes in SKC [a]).			+	−
fire	Proportion of owl territory within which canopy cover was reduced by at least 10% in the previous 3 yr due to fire.			+	−
Rxfire	Proportion of owl territory affected by prescribed fire in the previous 3 yr.			−	+
Pwinter	Total precipitation (cm) from November to March averaged across all territories in each study area.			+	−
Twinter	Mean of daily minimum temperatures (°C) from November to March averaged across all territories in each study area.			−	+
Pnest	Total precipitation (cm) from April to May averaged across all territories in each study area.			+	−
Tnest	Mean of daily minimum temperatures (°C) from April to May averaged across all territories in each study area.			−	+
Tsummer	Mean of daily maximum temperatures (°C) from July to August averaged across all territories in each study area.			+	−
elev	Average elevation (m) of owl territory.			x	x

[a] SKC = Sequoia–Kings Canyon study area.

(*clump*), which provided an index of fragmentation of *highCC* (McGarigal et al. 2012). Finally, we hypothesized that owls would benefit when *highCC*, *mediumCC*, and any vegetation type with $<$40% canopy cover were present in equal proportions within a territory because each class may fulfill different requirements of the owl's life history. For example, *highCC* may provide optimal nesting and roosting sites, as well as habitat for northern flying squirrels (*Glaucomys sabrinus*; Waters and Zabel 1995), which can be an important prey item for Spotted Owls. Conversely, areas containing shrubs and pole-sized timber ($<$40% canopy cover) may be source habitat for woodrats (Sakai and Noon 1993). Thus, we calculated Shannon's evenness index (*even*) for these 3 classes within each territory.

We also quantified annual habitat disturbance covariates that we attributed either to fire or to timber harvest. First, we used ArcMap 10.1 to identify each pixel on our annual canopy cover maps where canopy cover declined by at least 10% during the previous 3 yr. We then obtained shapefiles from the California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (http://frap.cdf.ca.gov/) of the perimeters of all California fires, including prescribed burns, that occurred during 1990–2011. We overlaid the fire perimeters on the annual canopy cover maps and attributed $>$10% canopy cover loss to fire if the pixel was located where a fire had occurred during the previous 3 yr. For pixels located where fire had not occurred during the previous 3 yr, we attributed $>$10% canopy cover loss to timber harvest (except in the

Sequoia–Kings Canyon study area, where no timber harvest occurred) because no large-scale tree mortality from sources other than fire (e.g., disease, insect outbreaks) occurred in the Lassen, Eldorado, and Sierra study sites. Thus, we calculated annual habitat disturbance covariates for fire (*fire*) or timber harvest (*logging*) within territory circles during the previous 3 yr. We chose a 3-yr timeframe because most logging projects were implemented over a period of 2 to 3 yr and postfire tree mortality often occurred for several years after wildfire. We acknowledge that canopy cover loss from fire and postfire salvage logging were confounded in the *fire* covariate for Lassen, Eldorado, and Sierra, and that the *logging* covariate for Sequoia–Kings Canyon represented canopy cover loss that was the result of disease or insect outbreaks, not timber harvest. Although prescribed fire was essentially nonexistent in the Lassen and Eldorado study areas, prescribed burns were frequently conducted in the Sierra and Sequoia–Kings Canyon study areas. We hypothesized that Spotted Owls may have benefited from managed fires that mimicked historical fires (Roberts et al. 2011). Thus, in the Sierra and Sequoia–Kings Canyon study areas, we included a covariate for the proportion of an owl territory that was affected by prescribed fire in the previous 3 yr (*Rxfire*).

Finally, we calculated annual climate covariates for each study area that may have affected Spotted Owl survival rates and thus indirectly affected occupancy. We hypothesized that cold, wet conditions during winter (November–March) would be energetically stressful for owls and hinder their ability to hunt for prey (Seamans et al. 2002, Seamans and Gutiérrez 2007a). Thus, we predicted that winters with greater precipitation (*Pwinter*) and colder temperatures (*Twinter*) than average would negatively affect occupancy in the following breeding season; for example, that precipitation from November 2003 to March 2004 would affect territory colonization and extinction rates between the 2003 and 2004 breeding seasons. Similarly, we hypothesized that cold, wet conditions during the nesting season (April–May) would be energetically stressful for both female and male owls (Seamans et al. 2002, LaHaye et al. 2004). Once nesting has been initiated, males bring food to incubating females, and after young fledge both males and females hunt for prey to feed their offspring. In this case, we hypothesized that greater precipitation (*Pnest*) and colder temperatures (*Tnest*) would negatively affect occupancy in the following year; for example, that precipitation during April and May 2004 would affect territory colonization and extinction rates between the 2004 and 2005 breeding seasons. We hypothesized that high summer temperatures (July–August; *Tsummer*) would negatively affect owls through heat stress because Spotted Owls appear to be cold-adapted (Weathers et al. 2001). Therefore, we predicted that hot summer temperatures during July and August 2004 would affect territory colonization and extinction rates between the 2004 and 2005 breeding seasons. We extracted all climatic data (1992–2011) from PRISM (PRISM Climate Group, Oregon State University, Corvallis, Oregon, USA) at 4-km spatial resolution using ArcMap 10.1. We first extracted the climate covariate values for each territory (see Jones et al. 2016b), and then calculated annual values for each study area as the average of all territory values. We used annual climatic means rather than territory-specific values because temperature and precipitation were highly correlated with elevation at the territory level ($r > 0.8$; Jones et al. 2016b). We felt that it was more important to treat elevation as a territory-specific covariate given that managers can employ different management practices at different elevations. Despite variation among territories in climatic variables, mean study area values are often correlated with Spotted Owl demographic rates and capture broad-scale variation in weather conditions (e.g., wet vs. dry years). We estimated average elevation at each territory (*elev*; m) using 30-m resolution digital-elevation models in ArcMap 10.1.

Model selection. We used a hierarchical, multistage framework to evaluate our occupancy models because we had many covariates and wished to avoid fitting an excessive number of models, which could result in spurious relationships by chance. We examined correlations between covariates appearing in the same models, and none of these covariates were highly correlated ($r < 0.65$). At each stage, we compared candidate models using Akaike's Information Criterion (AIC; Burnham and Anderson 2002), and then used the best model (i.e. lowest AIC value) from a given stage as the base model for the next stage (see Supplementary Material Tables S2–S5 for all modeling results). The stages in our modeling framework were:

(1) We assessed within-year, survey-specific variation in detection probability using the following covariates: *repro*, *initial*, *survey*, *T*, *lnT*, *TT*, and constant value (i.e. the null model and indicated by '.'). In this stage, we included general year effects for the other model parameters including among-year variation in detection probability: $\psi_1(.)$, ε(*year*), γ(*year*), *p*(*year*).

(2) We assessed among-year variation in detection probability using the following covariates: *year*, *T*, *lnT*, *TT*, constant, *highCC*, and *mediumCC*. We included *highCC* and *mediumCC* to ensure that any correlation between these habitat covariates and ε or γ was not simply the result of their effect on detection probabilities. We used the best structure for within-year variation in detection probability from stage 1 and included general year effects for the other model parameters: $\psi_1(.)$, ε(*year*), γ(*year*).

(3) We examined potential covariate effects on initial occupancy probability at a territory using the following covariates: *highCC*, *mediumCC*, and constant. Furthermore, we considered linear, logarithmic, and quadratic relationships between the habitat covariates (*highCC*, *mediumCC*) and ψ_1. We used the best structure for within-year and among-year variation in *p* from the previous modeling stages and included general year effects for territory extinction and colonization rates: ε(*year*), γ(*year*).

(4) We examined the potential effects of our primary habitat covariates (*highCC*, *mediumCC*) on territory extinction and colonization because we expected these covariates to have the strongest association with occupancy dynamics (e.g., Tempel et al. 2014b). We again considered linear, logarithmic, and quadratic relationships between these covariates and ε and γ because previous Spotted Owl studies have found evidence for nonlinear relationships (Dugger et al. 2005, Forsman et al. 2011, Tempel et al. 2014b). We also included a model with an interaction term between *highCC* and *mediumCC*. We modeled habitat effects on ε and γ separately. When we modeled extinction probability, we included a general year effect for colonization (γ[*year*]). When we modeled colonization probability, we included a general year effect for extinction (ε[*year*]).

(5) We next assessed the potential effects of covariates related to the spatial arrangement of habitat and habitat disturbance from logging or fire: *edge*, *clump*, *even*, *logging*, *fire*, and *Rxfire* (the latter for Sierra and Sequoia–Kings Canyon study areas only). We modeled ε and γ separately. We also included a model with interaction terms between *highCC* and/or *mediumCC* (if either covariate was still in the model) and any covariates from this stage that appeared in the top-ranked model.

(6) Then we assessed 10 models that represented different combinations of our climate covariates (*Pwinter*, *Twinter*, *Pnest*, *Tnest*, and *Tsummer*). We again modeled ε and γ separately. We also included a model with interaction terms between *highCC* and/or *mediumCC* (if either covariate was still in the model) and any covariates from this stage that appeared in the top-ranked model.

(7) Finally, we modeled the potential effects of *elev* on ε and γ separately. We also included a model with interaction terms between *highCC* and/or *mediumCC* (if either covariate was still in the model) and *elev*, as well as a model with interaction terms between climate covariates (if any were still in the model) and *elev.*

Furthermore, we included interactions between *highCC*, *mediumCC*, and other covariates under the hypothesis that territories containing more Spotted Owl habitat would be more resilient to disturbance (Seamans and Gutiérrez 2007b) or adverse climatic conditions (Jones et al. 2016b). We included interactions between *elev* and climate because territories located at higher elevations were expected to have colder temperatures and more precipitation than territories at lower elevations. We did not retain a model if the standard errors for any beta coefficients were inestimable, which frequently occurred for models with interaction terms.

We assessed the importance of covariates in the top-ranked occupancy model for each study area in 2 ways. First, we calculated equilibrium occupancy (ψ_{eq}) from the territory colonization and extinction rates as $\gamma/(\gamma + \varepsilon)$ (MacKenzie et al. 2006). When using this equation, one assumes that γ and ε are stable over time, which was not likely to be true for some of our study areas. Therefore, we did not interpret ψ_{eq} as an expected long-term proportion of occupied territories within each study area, but rather we used ψ_{eq} to assess the relative importance of covariates in the top model by examining how occupancy varied over a range of typical values for these covariates. Second, we used the analysis of deviance (ANODEV) test in Program MARK (White and Burnham 1999) to estimate how much variation in occupancy was explained by the habitat and climate covariates in the top-ranked models. The ANODEV test compares the amount of deviance explained by the covariates in a model with the amount of deviance not explained by these covariates and thus provides an estimate of r^2 for the model (Skalski et al. 1993). The global model for each study area that we used for the ANODEV test consisted of the top-ranked model with additional annual effects for γ and ε, and the constant model consisted of the best structure for detection probability with constant values for γ and ε.

Finally, because *mediumCC* and *highCC* encompassed a relatively large range in canopy cover, we performed a post hoc analysis in which we grouped canopy cover into 10% classes and evaluated whether occupancy changed abruptly between levels of canopy cover. For each study area, we successively replaced any habitat covariates for extinction and colonization in the top-ranked model with a covariate for the proportion of a territory containing 0–9% canopy cover, a covariate for 10–19% canopy cover, etc., up to 90–100% canopy cover. For example, the top-ranked model for Lassen was ψ_1(.), ε(*highCC* + *mediumCC* + *Tsummer*), γ(*highCC* + *Twinter* + *elev*), *p*(*year*, *repro* + *initial*), so we fit the model ψ_1(.), ε(*0–9% canopy cover* + *Tsummer*), γ(*0–9% canopy cover* + *Twinter* + *elev*), *p*(*year*, *repro* + *initial*), then fit the model ψ_1(.), ε(*10–19% canopy cover* + *Tsummer*), γ(*10–19% canopy cover* + *Twinter* + *elev*), *p*(*year*, *repro* + *initial*), etc. We then used the beta coefficients for extinction and colonization from each model to iteratively compute ψ_{eq} for each 10% canopy

TABLE 2. Mean values (SD) for the habitat, climate, and elevation covariates used to assess California Spotted Owl territory occupancy dynamics in 4 study areas in the Sierra Nevada, California, USA, 1993–2011. Study site abbreviations: LAS = Lassen, ELD = Eldorado, SIE = Sierra, and SKC = Sequoia–Kings Canyon. Covariate definitions are provided in Table 1.

	Study area			
Covariate	LAS	ELD	SIE	SKC
highCC [a]	0.26 (0.12)	0.37 (0.19)	0.24 (0.12)	0.29 (0.18)
mediumCC [a]	0.33 (0.05)	0.24 (0.06)	0.40 (0.08)	0.37 (0.08)
edge (m m^{-2})	43.6 (13.1)	50.6 (16.6)	41.5 (19.4)	26.8 (16.2)
clump [b]	0.33 (0.08)	0.41 (0.15)	0.23 (0.08)	0.33 (0.09)
even [b]	0.94 (0.06)	0.88 (0.14)	0.92 (0.07)	0.90 (0.09)
logging [a]	0.008 (0.020)	0.008 (0.015)	0.010 (0.016)	0.007 (0.024)
fire [a]	0.004 (0.032)	0.006 (0.053)	0.011 (0.055)	0.012 (0.040)
Rxfire [a]	—	—	0.011 (0.055)	0.030 (0.098)
Pwinter (cm)	91.5 (31.1)	118.3 (37.7)	73.4 (27.2)	78.4 (26.7)
Pnest (cm)	18.7 (10.1)	24.5 (12.6)	14.5 (9.4)	14.9 (9.4)
Twinter (°C)	−3.4 (0.7)	0.4 (0.5)	−0.5 (0.6)	−1.7 (0.7)
Tnest (°C)	0.4 (1.1)	3.7 (1.3)	3.1 (1.6)	1.8 (1.4)
Tsummer (°C)	26.9 (1.2)	29.0 (1.1)	28.1 (0.9)	26.8 (0.9)
elev (m)	1732.7 (160.0)	1441.0 (205.3)	1643.5 (562.0)	1783.4 (385.2)

[a] Covariate values are the proportion of an owl territory.

[b] Unitless index.

cover class when the covariate value for the class was equal to 0.25 (i.e. 25% of the territory consisted of vegetation in that 10% canopy cover class).

RESULTS

Survey Results and Environmental Conditions during the Study Period

We identified 90, 74, 66, and 45 owl territories in the Lassen, Eldorado, Sierra, and Sequoia–Kings Canyon study areas, respectively. Eldorado was the only study area in which the mean proportion of *highCC* within owl territories was greater than *mediumCC* (0.37 vs. 0.24), but *highCC* varied more than *mediumCC* in all 4 study areas (Table 2). Logging (tree disease in Sequoia–Kings Canyon) or fire generally affected <1% of any given owl territory annually, regardless of study area (Table 2). Wildfires that occurred from 1990 to 2011 affected a small number of territories in each study area (12 in Lassen, 14 in Eldorado, 3 in Sierra, and 14 in Sequoia–Kings Canyon), although some of these territories were greatly affected by high-severity fire (>50% of the territory). In contrast, prescribed fire was more common than wildfire in the 2 southern study areas, as 20 territories were affected by prescribed burns in Sierra and 22 in Sequoia–Kings Canyon. The Sierra and Sequoia–Kings Canyon study areas were drier than the 2 northern study areas; Eldorado was the wettest and warmest study area (Table 2).

The covariate *highCC* exhibited more spatial variation (spatial CV ranged from 0.47 to 0.61) than *mediumCC* (spatial CV ranged from 0.13 to 0.24). Temporal variation was much lower than spatial variation for both *highCC* (temporal CV ranged from 0.01 to 0.03) and *mediumCC* (temporal CV ranged from 0.02 to 0.05). The variation in climate covariates shown in Table 2 was due solely to temporal variation because we calculated a single value for these covariates within a study area during each year of our study (see Statistical Analysis—Model covariates).

Estimates of Parameters

Within each study area we estimated annual extinction and colonization probabilities and bimonthly detection probabilities using the model ψ_1(.), ε(*year*), γ(*year*), and the most parsimonious structure for $p_{j,t}$ within a given study area. Additionally, we derived annual estimates of territory occupancy probability from ψ_1, ε, and γ. Territory occupancy declined over time in the Lassen, Eldorado, and Sierra study areas as the result of declining colonization and increasing extinction rates, but increased over time in the Sequoia–Kings Canyon study site (Figure 2). Initial territory occupancy probabilities were high for all study areas (Lassen = 1.00, Eldorado = 1.00, Sierra = 0.96, Sequoia–Kings Canyon = 0.91), and these rates were not due to a sampling artifact (i.e. pseudo-increase in early years of sampling associated with a learning curve) because all territories within the core study areas were surveyed in 1993. Territory occupancy probabilities in 2011 (Lassen = 0.85, Eldorado = 0.73, Sierra = 0.71, Sequoia–Kings Canyon = 1.00) were lower than at the beginning of the study in all study areas except Sequoia–Kings Canyon. Owl densities (i.e. number of occupied territories) in Lassen, Eldorado, and Sierra appeared to be at or near their maximum values in 1993 and slowly declined over time as some territories became unoccupied and were not

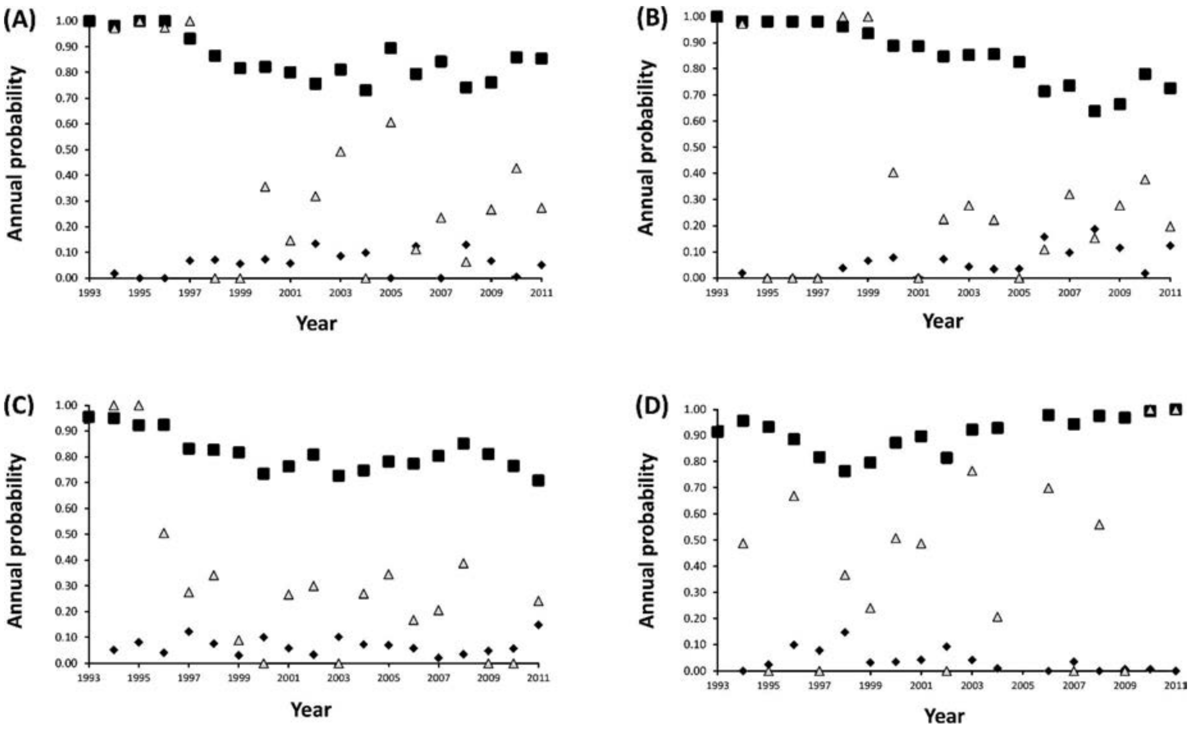

FIGURE 2. Annual estimates of occupancy (■), extinction (◆), and colonization (Δ) probabilities for California Spotted Owl territories in 4 study areas in the Sierra Nevada, California, USA, 1993–2011, calculated using the dynamic occupancy model with annual variation in extinction and colonization probabilities and the best detection probability structure for each study area. Annual occupancy estimates were derived from the extinction and colonization estimates. The study areas are: (**A**) Lassen, (**B**) Eldorado, (**C**) Sierra, and (**D**) Sequoia–Kings Canyon. Note that no surveys were conducted in the Sequoia–Kings Canyon site in 2005.

recolonized, a pattern which has previously been reported for Eldorado (Tempel and Gutiérrez 2013). Detection probabilities during bimonthly sampling periods were higher for Eldorado (average = 0.68, range = 0.51–0.91), Sierra (average = 0.70, range = 0.35–0.90), and Sequoia–Kings Canyon (average = 0.71, range = 0.49–0.82) than for Lassen (average = 0.56, range = 0.39–0.70).

Model Selection Results

Detection probability. The reproductive status of birds at a territory, *repro*, was positively correlated with p in all 4 study areas (i.e. nesting owls were more likely to be detected than nonnesting owls; Table 3; see also complete model-selection results [stages 1–7] for each study area in Supplemental Material Appendix B). For within-year variation in detection probability, *initial* was positively correlated with p in the Lassen and Eldorado study sites; thus, owls were more likely to be detected during surveys subsequent to the initial detection at a territory in a given year (Table 3). For Sierra and Sequoia–Kings Canyon, within-year detection probability followed a quadratic relationship (*TT*), so that p increased gradually during the survey season before dropping off sharply in August and September (Table 3). In Lassen, Eldorado, and Sierra, the best model for annual variation in detection probability contained year-specific parameter estimates (*year*). However, the best model for annual variation in p in Sequoia–Kings Canyon suggested that p was positively correlated with forest conditions (*highCC*, *mediumCC*) within a territory (Table 3).

Occupancy. We have provided the complete model-selection results (stages 1–7) for each study area in Supplemental Material Appendix B. In the Lassen study area, the top-ranked occupancy model was ψ_1(.), ε(*highCC* + *mediumCC* + *Tsummer*), γ(*highCC* + *Twinter* + *elev*). As predicted, territory extinction was negatively correlated with both *highCC* and *mediumCC*, and colonization was positively correlated with *highCC*. With respect to climate covariates, *Tsummer* had a positive relationship with ε, and *Twinter* was positively related to γ (i.e. territories were more likely to be colonized following warmer winters). In addition, colonization was positively related to *elev*. Although the covariates in the top-ranked occupancy model were supported in model selection, the 95% confidence intervals for the beta coefficients overlapped zero for all terms except ε(*highCC*) and γ(*elev*).

In the Eldorado study area, the top-ranked model was ψ_1(.), ε(ln[*highCC*] + ln[*mediumCC*] + *logging* + *edge*),

TABLE 3. Beta coefficients (SE) for covariate effects on model parameters in the top-ranked California Spotted Owl territory occupancy models for 4 study areas in the Sierra Nevada, California, USA, 1993–2011. Covariate definitions are provided in Table 1. Blank cells denote that a covariate did not affect a given parameter, and + indicates that there are separate beta coefficients for each year that we do not list to save space. Bold font indicates that the 95% confidence interval did not overlap zero.

	Beta coefficients		
Covariate	Detection ($p_{t,j}$)	Extinction (ε_t)	Colonization (γ_t)
Lassen:			
year	+		
repro	**1.49 (0.09)**		
initial	**0.85 (0.07)**		
highCC		**−9.94 (2.58)**	2.98 (2.98)
mediumCC		−5.27 (3.74)	
Tsummer		0.26 (0.15)	
Twinter			0.83 (0.45)
elev			**4.78 (2.36)**
Eldorado:			
year	+		
repro	**1.53 (0.12)**		
initial	**1.23 (0.09)**		
ln(*highCC*)		**−6.48 (1.86)**	
ln(*mediumCC*)		−7.07 (5.34)	**8.24 (3.35)**
logging		−42.28 (21.61)	
edge		**4.22 (1.80)**	
Sierra:			
year	+		
repro	**1.42 (0.12)**		
T	**1.81 (0.71)**		
TT	**−3.09 (0.59)**		
highCC		−2.39 (1.56)	0.94 (1.94)
mediumCC		**−5.25 (1.99)**	**9.96 (3.15)**
edge		**3.63 (0.90)**	**−2.61 (1.04)**
Pwinter		0.41 (0.26)	
Sequoia–Kings Canyon:			
repro	**1.29 (0.11)**		
highCC	**0.78 (0.25)**	−16.13 (10.64)	**−33.05 (11.85)**
$(highCC)^2$			**61.06 (21.38)**
mediumCC	**2.26 (0.58)**	−16.09 (8.68)	
*highCC*mediumCC*		44.88 (30.67)	
T	0.66 (0.80)		
TT	**−1.60 (0.68)**		
fire		−40.57 (34.40)	
Rxfire			−8.68 (6.77)
Twinter			0.01 (0.65)
elev			**−2.10 (1.00)**
*elev*Twinter*			**5.26 (2.06)**

γ(ln[*mediumCC*]). Again, territory extinction was negatively related to both *highCC* and *mediumCC*, but colonization was positively correlated only with *mediumCC*. Contrary to our expectations, *logging* was negatively correlated with ε, whereas *edge* was positively related to ε. No climate covariates or *elev* were found in the best model. The 95% confidence intervals for the beta coefficients did not include zero for ε(ln[*highCC*]), ε(*edge*), and γ(ln[*mediumCC*]).

In the Sierra study area, the top-ranked model was ψ_1(.), ε(*highCC* + *mediumCC* + *edge* + *Pwinter*), γ(*highCC* + *mediumCC* + *edge*). Territory extinction was negatively correlated with both *highCC* and *mediumCC*, and territory colonization was positively related to both *highCC* and *mediumCC*. In contrast, *edge* was positively related to extinction and negatively related to colonization, so it had a negative association with territory occupancy. Territory extinction was also positively correlated with *Pwinter* (i.e. territories were more likely to become unoccupied following wetter winters). The 95% confidence intervals for the beta coefficients of ε(*mediumCC*), ε(*edge*), γ(*mediumCC*), and γ(*edge*) did not overlap zero.

In the Sequoia–Kings Canyon study area, the top-ranked model was ψ_1(.), ε(*highCC* + *mediumCC* + *highCC*mediumCC* + *fire*), γ(*highCC* + $[highCC]^2$ + *Rxfire* + *Twinter* + *elev* + *elev*Twinter*); thus, Sequoia–Kings

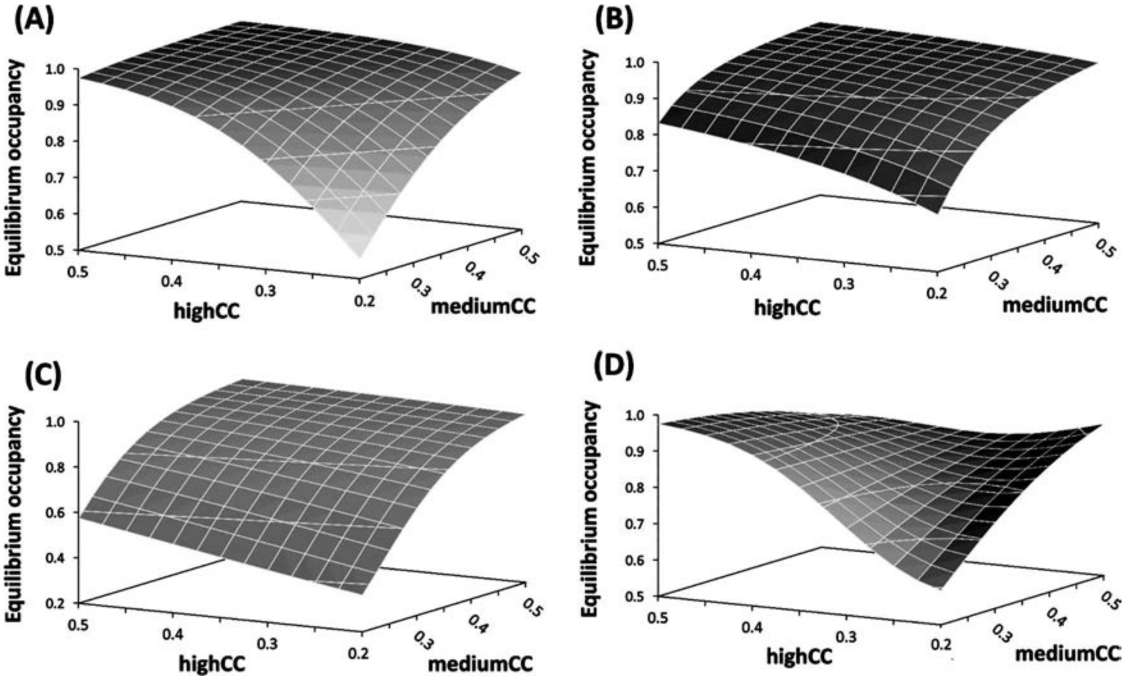

FIGURE 3. Equilibrium occupancy for California Spotted Owl territories in 4 study areas in the Sierra Nevada, California, USA, 1993–2011. Occupancy is plotted against the proportion of owl territories containing forest with $\geq$70% canopy cover (highCC) and forest with 40–69% canopy cover (mediumCC). We used the beta coefficients from the top-ranked extinction and colonization models in each study area: (**A**) Lassen, (**B**) Eldorado, (**C**) Sierra, and (**D**) Sequoia–Kings Canyon.

Canyon was the only study area for which interaction terms appeared in the best model. The extinction beta coefficients for *highCC* and *mediumCC* were both negative, but their interaction was positive. Furthermore, the colonization coefficient was negative for *highCC* and positive for $(highCC)^2$, so that colonization was lowest at intermediate amounts of *highCC*. Territory extinction was negatively related to *fire*, and colonization was negatively related to *Rxfire*. Although *Twinter* had a weak association with colonization, *elev* had a negative association, and their interaction was positive. This suggested that territories at higher elevations were less likely to be colonized except after warmer winters. All of the 95% confidence intervals for the extinction beta coefficients overlapped zero, but they did not do so for $\gamma(highCC)$, $\gamma([highCC]^2)$, $\gamma(elev)$, and $\gamma(elev{*}Twinter)$.

The only covariates that were consistently important for all 4 study areas were *highCC* and *mediumCC*, so we calculated equilibrium occupancy for each study area while varying these 2 covariates from 0.2 to 0.5, which encompassed the typical range of values in the study areas (Table 2). When doing so, we included all covariates and their corresponding beta coefficients that appeared in the top-ranked model for a study area. For covariates other than *highCC* and *mediumCC*, we either used their average value across the study area (all climate covariates, *elev*, and *edge*) or set their value to zero (*logging*, *fire*, *Rxfire*). For all 4 study areas, equilibrium occupancy reached its lowest value when both *highCC* and *mediumCC* were minimized at 0.2 and reached its highest value (or near it in the case of Sequoia–Kings Canyon) when both were maximized at 0.5 (Figure 3). Furthermore, in Eldorado and Sierra, *mediumCC* was more positively correlated with occupancy than *highCC* (Figure 3). The amounts of *highCC* and *mediumCC* within owl territories were clearly important because the analyses of deviance showed that the habitat covariates explained much of the variation in occupancy in all of the study areas—41% in Lassen, 47% in Eldorado, 67% in Sierra, and 35% in Sequoia–Kings Canyon. In contrast, the climate covariates explained much less variation in occupancy—7% in Lassen, 4% in Sierra, and 4% in Sequoia–Kings Canyon (no climate covariates were included in the top-ranked model for Eldorado).

The post hoc analysis in which we categorized canopy cover into 10% classes suggested that thresholds existed at 30% or 40%, depending on the study area; equilibrium occupancy declined sharply when below these thresholds (Figure 4). In addition, we observed that occupancy for the 40–49% canopy cover class was always lower than occupancy for the 50–59% and 60–69% canopy cover classes, and that occupancy was lower for the 90–100% class in 2 study areas (Figure 4).

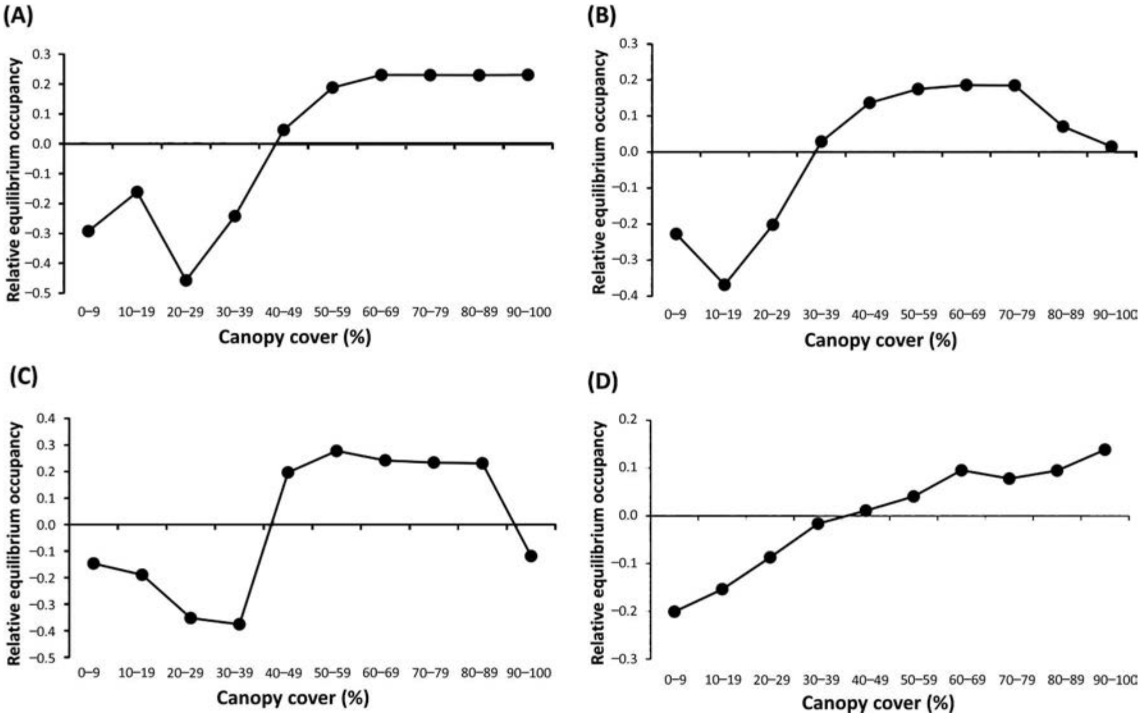

FIGURE 4. Equilibrium occupancy (relative to the mean value) for California Spotted Owl territories in 4 study areas in the Sierra Nevada, California, USA, 1993–2011. Relative occupancy is plotted against the proportion of owl territories containing canopy cover in 10% classes. We used the beta coefficients from the extinction and colonization models to estimate equilibrium occupancy for each canopy cover class, then calculated the "relative" occupancy by subtracting the mean equilibrium occupancy of all 10 canopy cover classes. The study areas are: (**A**) Lassen, (**B**) Eldorado, (**C**) Sierra, and (**D**) Sequoia–Kings Canyon.

DISCUSSION

We modeled the territory occupancy dynamics of California Spotted Owl populations in 4 study areas which were large in spatial extent and spanned the length of the Sierra Nevada. As such, we believe that our results have implications for forest management throughout this region. One of our key findings was the consistently positive association between both medium (40–69%) and high ($\geq$70%) canopy cover forests and territory occupancy metrics (i.e. increased colonization and decreased extinction) and that these vegetation variables explained a high proportion of variance in occupancy. By extension, and as suggested by our post hoc analysis, forests having $<$40% canopy cover were not Spotted Owl habitat, which supports a long history of such findings from habitat studies of California Spotted Owls (see below). In contrast, we did not consistently find strong support for associations between occupancy and fire, logging, habitat configuration, or climate.

The positive association that we detected between Spotted Owl territory occupancy and the amount of forest with $\geq$70% canopy cover for each study area is consistent with a previous occupancy–habitat study using Eldorado data only (Tempel et al. 2014b). Notably, the 2 studies used different and independent vegetation data sources (Landsat with verification based on other remote sensing techniques vs. aerial-photo interpretation with ground verification); collectively, they strengthen the inference that high-canopy-cover forests promote territory occupancy by Spotted Owls. Furthermore, other studies have shown that forest with $\geq$70% canopy cover serves as important nesting and roosting habitat for owls (Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Bond et al. 2004). In contrast, the positive association between California Spotted Owl occupancy and forest with medium (40–69%) canopy cover is a novel finding.

The proportion of area within owl territories having $<$40% canopy cover was negatively related to territory occupancy in 3 study areas and nearly so in the fourth (Figure 4), and such forests thus do not appear to constitute suitable Spotted Owl habitat. It has been suggested that much of the Sierra Nevada historically consisted of forests having low tree density with $<$40% canopy cover (Collins et al. 2015) and, by extension, that such forests were suitable for owls in the past. A possible explanation for this dichotomy is that existing areas of $<$40% canopy cover that have resulted from forest management or disturbance may not be ecologically equivalent to historical areas of low canopy cover, particularly if they lack larger trees. However, the negative relationship between occupancy and forests with <40% canopy cover in the Sequoia–Kings Canyon study area, where the vegetation presumably more closely reflected historical conditions under which Spotted Owls evolved (Lydersen and North 2012), suggests that forests with <40% canopy cover may not have constituted suitable Spotted Owl habitat in the Sierra Nevada historically either. Moreover, the relationship with occupancy continued to strengthen as canopy cover increased in Sequoia–Kings Canyon, suggesting that forests with ≥70% canopy cover may have been important to the owls prior to the recent period of fire suppression. However, owl territories in Sequoia–Kings Canyon did not contain appreciably less high-canopy-cover forest than the other study areas (Table 2) and may not have fully reflected "reference conditions" prior to changes associated with fire suppression. Thus, additional work is needed to understand how closely forest characteristics at owl sites in Sequoia–Kings Canyon reflect or do not reflect conditions prior to fire suppression.

We had expected the amount of edge between high-canopy-cover forest and areas with <40% canopy cover to have positive associations with Spotted Owl occupancy via increased prey availability (Franklin et al. 2000), but edge was negatively related to occupancy in 2 of the study areas (Eldorado, Sierra). In addition, our other measures of spatial heterogeneity (evenness, clumpiness) were not supported in the occupancy models for any of the study areas. These spatial metrics may have been relatively unimportant for territory occupancy, although prior research has suggested that habitat heterogeneity and fire history have important effects on Spotted Owl prey abundance and diversity (Roberts et al. 2015). However, we measured habitat heterogeneity at a different spatial scale than Franklin et al. (2000), who mapped forest stands with a minimum size of 2 ha (as opposed to 0.09-ha pixels) and found an edge relationship between old forest and "other" cover types (i.e. not specifically <40% canopy cover as we hypothesized). In addition, habitat configuration may influence Spotted Owl fitness, as demonstrated by Franklin et al. (2000), but not necessarily occupancy, as in our present study. Finally, other aspects of habitat heterogeneity that we did not quantify may have more biological significance for Spotted Owls.

Logging was associated with occupancy in only one study area (Eldorado), where it unexpectedly had a positive association with territory colonization. However, we may have underestimated the amount of logging in the Lassen, Eldorado, and Sierra study areas as evidenced by the low values of our *logging* covariate within these study areas (Table 2). We used the criterion of a 10% reduction in canopy cover to infer logging activity and, therefore, omitted potential logging activities that reduced canopy cover by <10%, which can occur. Furthermore, we examined logging events within a relatively short time-frame, and the cumulative effects of logging activities over decades could still adversely impact Spotted Owl territories. Three of the study areas had a history of timber harvest in the 20th century, which undoubtedly left a historical legacy in terms of the distribution of forest with high canopy cover and large trees within the individual study areas. The Sequoia–Kings Canyon study site did not have this logging history and it had the only study population that did not show a decline in occupancy. This spatial variation in forest conditions among territories was important in these study areas, as evidenced by the strong positive correlation between territory occupancy and forest with medium or high canopy cover.

The relationship between Spotted Owls and fire is complex and likely depends upon the overall severity of the specific fire and the proportion and patch sizes affected by high-severity fire. Some studies have found that fire had no discernible negative impact on Spotted Owl territory occupancy (Roberts et al. 2011, Lee et al. 2012, Lee and Bond 2015). However, other studies of large, contiguous areas affected by high-severity fire have reported negative effects on Spotted Owl territory occupancy after controlling for postfire salvage logging (Lee et al. 2013, Jones et al. 2016a). In our study, fire effects were included in the top-ranked model for only 1 study area (Sequoia–Kings Canyon); few territories were affected by fire in the other 3 study areas, which reduced our statistical power to detect any potential effects. Although Tempel et al. (2014b) reported that fire was negatively related to territory colonization in the Eldorado study area over a similar time period (1993–2012), their model failed to estimate a standard error for the beta coefficient of the fire covariate. We also were unable to estimate a standard error for the fire effect on territory colonization within Eldorado, so we chose to exclude the fire covariate from further modeling stages (see Statistical Analysis—Model selection). In the Sequoia–Kings Canyon study area our results were mixed, in that fire (either wildfire or prescribed fire) that reduced canopy cover by >10% reduced the probability of territory extinction, but the amount of prescribed fire within a territory reduced colonization (Table 3). The mixed results for Sequoia–Kings Canyon suggest that fire may affect owl occupancy in different ways. For example, Southern and Lowe (1968; see also Hirons 1985) suggested that Tawny Owls (*Strix aluco*) could survive poor years because they could mitigate bad years owing to their accumulated experience and intimate knowledge of territories. Under this hypothesis, if fire creates prey habitat by opening canopy and allowing shrubs to grow, it might increase foraging opportunities for established owls that have acquired knowledge of their territory. Alternatively, if fire has negative effects, resident owls might simply shift foraging areas because they have experience with other potential foraging areas within their territory (i.e. they might mitigate the negative impact). On the other hand, new owls attempting to colonize an area that had experienced some fire (e.g., controlled burns in Sequoia–Kings Canyon in our case) would not have the accumulated territory knowledge (i.e. experience) to avoid areas affected by fire, and thus fire would reduce their incentive to colonize an unoccupied, but available, area.

Our climate covariates were not strongly correlated with Spotted Owl territory occupancy dynamics, but we modeled annual climate covariates to control for potential sources of variation in occupancy dynamics separately from habitat change. Associations between climate and occupancy, however, may be reflected over longer time periods or after time lags (Jones et al. 2016b). For example, if favorable weather conditions result in a year with high reproduction, the effects of these conditions on territory occupancy may not become apparent for several years, until the birds of that cohort have had the opportunity to colonize vacant territories. In addition, bad weather may lead to individual mortality, but no territory extinction will be observed if at least one member of an owl pair survives or if a new individual colonizes the territory before the next breeding season. Thus, occupancy may be relatively insensitive to weather conditions.

Although territory occupancy dynamics were clearly influenced by canopy cover conditions within Spotted Owl territories, we observed declining occupancy rates in 3 study areas as the result of increased extinction and decreased colonization rates in individual territories (Figure 2). These declines occurred despite relatively constant canopy cover conditions over the duration of our study. Additional components of forest structure (e.g., density of large old trees and snags, vertical complexity) undoubtedly make important contributions to owl habitat selection, territory occupancy, and fitness. We did not have the data to accurately quantify these elements at the required large spatial scales over nearly 2 decades or to determine changes in these elements that occurred prior to our study but that could have had lasting effects on owls, but the development of such datasets could significantly advance our understanding of habitat effects on Spotted Owl demography. Interestingly, the one study area (Sequoia–Kings Canyon) in which territory occupancy did not decline was located within a national park, rather than a national forest interspersed with varying amounts of private land. The different occupancy trajectory in Sequoia–Kings Canyon may have been related to different forest management practices, the presence of giant sequoia groves in this study area, a different proportion of oak woodlands, or some combination of these factors (Blakesley et al. 2010).

Management Implications

Recent proposals to revise forest management practices in the Sierra Nevada emphasize increasing forest resilience to fire, climate change, and drought (i.e. the capacity of the forest to return to its predisturbance state while maintaining characteristic ecosystem processes; Allen et al. 2002) by promoting within-stand and landscape heterogeneity (North et al. 2009, North 2012). Fuels and restoration treatments that reduce tree density and canopy cover are considered important tools in this effort (Stephens and Moghaddas 2005, Stephens et al. 2009, Stevens et al. 2014). Thus, a key management consideration involves the degree to which canopy cover can be reduced without causing significant impacts on old-forest species such as Spotted Owls that depend on forests characterized by high canopy cover. When considering the implications of our results, we stress that our study relied on Landsat imagery to quantify canopy cover, whereas forest managers typically use the Forest Vegetation Simulator (FVS; Dixon 2002) to produce canopy cover estimates when planning management activities. Because FVS generally underestimates canopy cover, especially at higher values (Fiala et al. 2006), our canopy cover data should be calibrated against the source data used during planning. We also reiterate that we estimated equilibrium occupancy under the assumption of stable extinction and colonization rates, a condition that was not true for 3 of our study areas (Figure 2), and thus that the values of ψ_{eq} in Figure 3 should not be construed as the expected long-term proportion of occupied territories under different habitat conditions. Nonetheless, we believe that these values can be used to assess the relative importance of the canopy cover covariates on occupancy dynamics, particularly because these covariates exhibited low temporal variation in all study areas.

Collectively, our study suggests that fuels and restoration treatments could be used to reduce canopy cover below 70% in some high-canopy-cover forest within Spotted Owl territories without having a significant impact on expected occupancy rates. Specifically, treatments within a territory comprised of 50% high- and 50% mid-canopy-cover forest (i.e. the peaks in Figures 3A–3C) that convert some high-canopy-cover forest into mid-canopy-cover forest are predicted to incur a relatively modest cost to expected occupancy rates in the 3 national forest study areas (note the modest slope of the declines along the back right edges of the surfaces in Figures 3A–3C). Similarly, treatments within a territory comprised of 50% high-canopy-cover forest and 20% mid-canopy-cover forest that reduce high-canopy-cover forest to 30% of the territory, and where these altered stands also remain at >40% canopy cover, are not predicted to experience major reductions in occupancy. In fact, a slight increase in occupancy would be expected in the Eldorado study area and a greater increase would be expected in the Sierra study area. However, our study also indicates that territory occupancy rates are likely to be negatively affected if canopy cover is consistently reduced to 40%, as evidenced by the lowest predicted occupancy rates occurring in the bottom right corners of Figures 3A–3D (i.e. where only 20% of a territory is in the high- and mid-canopy-cover classes, and 60% is in the low-canopy-cover class). Moreover, our post hoc analysis, in which we partitioned canopy cover into 10% classes, showed that forest with 50–69% canopy cover was more strongly and positively correlated with occupancy than forest with 40–49% canopy cover. Finally, we caution that forest with 40–69% canopy cover cannot simply be substituted for forest with $\geq$70% canopy cover. The importance of $\geq$70% canopy cover forests as nesting and roosting habitat for California Spotted Owls has been well documented (Bias and Gutiérrez 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Bond et al. 2004). Indeed, few territories contained $<$20% of high-canopy-cover forest, and as a result our study does not provide a reliable means of assessing the effects of reducing high-canopy-cover forest—and thus nesting and roosting habitat—below this level. In conjunction with declining numbers of large trees (i.e. suitable nest trees) in the Sierra Nevada over the past century (Smith et al. 2005, Lutz et al. 2009), sufficiently large reductions in high-canopy-cover forest are likely to negatively affect owls.

Our study, in conjunction with recent documentation of adverse impacts that large fires have had on California Spotted Owls (Jones et al. 2016a), suggests that maintaining viable Spotted Owl populations in the Sierra Nevada and reducing future wildfire risk using fuels and restoration treatments may be compatible goals, particularly if recent trends in high-severity fire continue or intensify because of climate change (Liu et al. 2013). However, we suggest that forest treatments to reduce fire risk should proceed with caution (be designed to retain some structural heterogeneity and the large trees) because we found declines in territory occupancy during our study, and other studies have reported substantial (up to 50%) declines in Spotted Owl populations in the Sierra Nevada within the past 20 yr (Conner et al. 2013, Tempel et al. 2014b). In addition, Barred Owls have not occurred in our study areas until recently, but evidence from Northern Spotted Owl studies suggest that they could pose an additional and significant threat to Spotted Owl populations in the Sierra Nevada if they continue to invade this region in future years (Yackulic et al. 2014, Dugger et al. 2016). Fuels treatments within Spotted Owl Protected Activity Centers (PACs), which contain ~125 ha of the best habitat around known Spotted Owl nest and roost locations, were largely excluded from treatment during our study, so we lack information on how treatments within PACs could affect territory occupancy. However, given that PACs have been consistently used for nesting and roosting over long time periods (Berigan et al. 2012), future treatments within PACs could negatively affect Spotted Owl territory occupancy because these are centers of owl activity. Furthermore, forest restoration objectives may be achievable without implementing treatments within PACs because PACs occupy a relatively small percentage of the overall landscape in the Sierra Nevada (North et al. 2015). Nevertheless, forest treatments that reduce canopy cover within Spotted Owl territories, if judiciously implemented, could maintain Spotted Owl habitat in the short term so that any long-term benefits as a result of reductions in high-severity fire can be realized.

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Ethics statement: We collected all data from the Eldorado study area, where R.J.G. and M.Z.P. were the principal investigators, following protocols approved under animal care and use permits overseen by the University of Minnesota's and University of Wisconsin–Madison's Institutional Animal Care and Use Committees. We followed these protocols and acquired and maintained all relevant state and federal permits for all study areas included in this meta-analysis.

Author contributions: J.J.K., R.J.G., M.Z.P., D.J.T., and J.D.W. conceived the idea, design, and experiment; J.J.K., R.J.G., M.Z.P., D.J.T., J.D.W., G.M.J., A.K., C.M.R., W.J.B., C.V.G., T.E.M., P.A.S., S.A.W., and M.Z.P. conducted the research; D.J.T., M.Z.P., R.J.G., J.J.K., A.K., J.D.W., G.M.J., S.A.W., W.J.B., C.V.G., and T.E.M. wrote the paper; D.J.T., R.J.G., A.K., C.M.R., M.Z.P., C.V.G., J.J.K., and G.M.J. developed and designed the methods; D.J.T., A.K., C.M.R., and G.M.J. analyzed the data; and R.J.G., M.Z.P., and J.J.K. contributed substantial materials, resources, and funding.

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Conservation Biology

Contributed Paper

Relation between Occupancy and Abundance for a Territorial Species, the California Spotted Owl

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Abstract: *Land and resource managers often use detection–nondetection surveys to monitor the populations of species that may be affected by factors such as habitat alteration, climate change, and biological invasions. Relative to mark-recapture studies, using detection–nondetection surveys is more cost-effective, and recent advances in statistical analyses allow the incorporation of detection probability, covariates, and multiple seasons. We examined the efficacy of using detection–nondetection data (relative to mark-recapture data) for monitoring population trends of a territorial species, the California Spotted Owl (*Strix occidentalis occidentalis*). We estimated and compared the finite annual rates of population change (λ_t) and the resulting realized population change (Δ_t) from both occupancy and mark-recapture data collected over 18 years (1993–2010). We used multiseason, robust-design occupancy models to estimate that territory occupancy declined during our study ($\Delta_t = 0.702$, 95% CI 0.552–0.852) due to increasing territory extinction rates ($\hat{\varepsilon}_{1993} = 0.019$ [SE 0.012]; $\hat{\varepsilon}_{2009} = 0.134$ [SE 0.043]) and decreasing colonization rates ($\hat{\gamma}_{1993} = 0.323$ [SE 0.124]; $\hat{\gamma}_{2009} = 0.242$ [SE 0.058]). We used Pradel's temporal-symmetry model for mark-recapture data to estimate that the population trajectory closely matched the trends in territory occupancy ($\Delta_t = 0.725$, 95% CI 0.445–1.004). Individual survival was constant during our study ($\hat{\varphi}_{1993} = 0.816$ [SE 0.020]; $\hat{\varphi}_{2009} = 0.815$ [SE 0.019]), whereas recruitment declined slightly ($\hat{f}_{1993} = 0.195$ [SE 0.032]; $\hat{f}_{2009} = 0.160$ [SE 0.023]). Thus, we concluded that detection–nondetection data can provide reliable inferences on population trends, especially when funds preclude more intensive mark-recapture studies.*

Keywords: dynamic occupancy model, population dynamics, Sierra Nevada, *Strix occidentalis occidentalis*, temporal-symmetry model

Relación entre Ocupación y Abundancia en una Especie Territorial, el Búho Moteado de California

Resumen: *Los manejadores de tierras y recursos a menudos utilizan muestreos de detección-no detección para monitorear las poblaciones de especies que pueden ser afectadas por factores como la alteración del hábitat, cambio climático e invasiones biológicas. En relación con estudios de captura-recaptura, el uso de muestreos de detección-no detección es más rentable, y los avances recientes de los análisis estadísticos permiten la incorporación de la probabilidad de detección, covariables y múltiples temporadas. Examinamos la eficacia del uso de datos de detección-no detección (relativos a datos de captura-recaptura) para monitorear las tendencias poblacionales de una especie territorial, el búho moteado de California (*Strix occidentalis occidentalis*). Estimamos y comparamos las tasas finitas anuales de cambio poblacional (λ_t) y cambio poblacional realizado resultante (Δ_t) tanto para datos de ocupación y de captura-recaptura recolectados a lo largo de 18 años (1993–2010). Utilizamos modelos de ocupación multianuales de diseño robusto para estimar que la ocupación de territorio declinó durante nuestro estudio ($\Delta_t = 0.702$, 95% IC 0.552–0.852) debido al incremento en las tasas de extinción de ocupación de territorio ($\hat{\varepsilon}_{1993} = 0.019$ [ES 0.012]; $\hat{\varepsilon}_{2009} = 0.134$ [ES 0.043]) y el decremento de las tasas de colonización ($\hat{\gamma}_{1993} = 0.323$ [ES 0.124]; $\hat{\gamma}_{2009} = 0.242$ [ES 0.058]). Utilizamos el modelo de simetría temporal de Pradel para datos de captura-recaptura para estimar que la trayectoria de la población era similar a las tendencias de la ocupación de territorio ($\Delta_t = 0.725$, 95% IC 0.445–1.004). La supervivencia individual fue constante a lo largo de nuestro studio ($\hat{\varphi}_{1993} = 0.816$ [ES 0.020]; $\hat{\varphi}_{2009} = 0.815$ [ES 0.019]), mientras que el reclutamiento declinó levemente ($\hat{f}_{1993} = 0.195$ [ES 0.032]; $\hat{f}_{2009} = 0.160$ [ES 0.023]). Por lo tanto, concluimos que los datos de detección-no detección pueden proporcionar*

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inferencias confiables sobre las tendencias poblacionales, especialmente cuando los fondos excluyen estudios más intensivos de captura-recaptura.

Palabras Clave: dinámica de poblaciones, modelo de ocupación dinámica, modelo de simetría temporal, Sierra Nevada, *Strix occidentalis occidentalis*

Introduction

A primary responsibility of land and resource managers is to monitor (often over large spatial scales) the population trends of focal species that may be affected by changing future conditions, such as habitat change, climate change, and biological invasions. The use of detection–nondetection data (i.e., occupancy monitoring) may be a cost-effective, robust means of achieving this goal (Noon et al. 2012). Furthermore, recent advances in the statistical analyses of site-occupancy data allow the incorporation of imperfect detection, site- and survey-specific covariates, multiseason dynamics, and multiple states to assess a wide range of ecological and management questions, which enhances the utility of occupancy analyses (MacKenzie et al. 2006; Nichols et al. 2007).

Mark-recapture studies offer an alternative means of monitoring populations and provide more detailed data on demographic vital rates, such as survival and recruitment (Armstrup et al. 2005). However, mark-recapture studies are labor intensive, relatively costly, and generally encompass a small geographic area due to these constraints. In contrast, occupancy studies require surveying for only the presence or absence of a species and generally allow a larger area to be surveyed at a lower cost (Noon et al. 2012). Furthermore, metapopulation models and species-abundance distributions describe a fundamental, theoretical relation between occupancy and abundance so that site occupancy should provide a useful index for population status (Royle et al. 2005; Borregaard & Rahbek 2010). The results of some empirical research support the theoretical relation between occupancy and abundance. For example, Zuckerberg et al. (2009) found strong correlations between regional occupancy and relative abundance for a wide range of bird species in the state of New York (U.S.A.) over 2 periods. For these reasons, researchers have recently used detection–nondetection data, rather than mark-recapture data, to monitor the population status of species over large spatial extents (e.g., Burton et al. 2011; Karanth et al. 2011; Thorn et al. 2011). However, we were unaware of existing studies in which annual trends in site occupancy were compared with annual population trends (estimated with mark-recapture data from the same study population), a comparison that would more convincingly demonstrate a close relation between occupancy and abundance.

The California Spotted Owl (*Strix occidentalis occidentalis*) is a focal management species in the Sierra Nevada because it uses late-seral forests for nesting and roosting (Gutiérrez et al. 1992). The U.S. Forest Service (USFS) considers the owl a "sensitive" species, which motivated the USFS to develop a Sierra-wide forest management plan (U.S. Forest Service 2004). The owl is highly territorial, displays strong site fidelity, and breeds irregularly, typically producing 1–2 young in years when it reproduces (Gutiérrez et al. 1995). Currently, the USFS monitors owl populations in the Sierra Nevada with long-term, mark-recapture studies designed to detect territorial adults (i.e., those responding to vocal surveys) (Franklin et al. 2004; Blakesley et al. 2010). The vital rates of those individuals are then quantified annually. These studies require intensive survey effort over large areas because California Spotted Owls have large home ranges (mean = 555 ha [SE 100] on the basis of data collected within and near our study area) (Williams et al. 2011). Thus, occupancy studies on a regional scale could be an ideal complement to the mark-recapture studies.

To test the efficacy of using occupancy studies to infer population status, we compared long-term trends (1993–2010), estimated from both occupancy and mark-recapture data, in a California Spotted Owl population in the central Sierra Nevada. We considered each owl territory a site, so the sampling population was similar for both types of data (i.e., all territorial adults on our study area vs. all owl territories). Thus, we expected annual trends in owl site occupancy should be similar to population trends estimated from the mark-recapture data.

Study Area

We conducted our study on a contiguous 35,500-ha area on the Eldorado National Forest in the central Sierra Nevada, California. The Eldorado Density Study Area (EDSA) has been the site of a long-term mark-recapture study of California Spotted Owls (Seamans et al. 2001; Franklin et al. 2004; Blakesley et al. 2010). We surveyed the entire area each year without regard to land cover, topography, access, or land ownership. Approximately 60% of the EDSA was public land managed by the USFS, and 40% was private land managed by timber companies.

The primary vegetation type on the EDSA was mixed-conifer forest dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), and incense cedar (*Calocedrus decurrens*). Common understory species included California black oak (*Quercus kelloggii*), bigleaf maple (*Acer macrophyllum*), and tanoak

(*Lithocarpus densiflorus*). Red-fir (*Abies magnifica*) forest, dominated by red fir and lodgepole pine (*Pinus contorta*), was present at higher elevations. Other local vegetation types and landscape features included chaparral, black oak woodland, and barren rock. Elevations on the EDSA ranged from 360 to 2400 m, and the climate was characterized by cool, wet winters and warm, dry summers.

Methods

Spotted Owl Surveys

We conducted surveys annually for spotted owls from 1986–2010 during the owl breeding season (1 April to 31 August). We did not conduct complete surveys over the entire EDSA in the early years of the study because funding constraints limited our survey effort. Hence, we examined survey coverage of the EDSA (see Survey Coverage of Study Area below) to determine when our survey effort was adequate to include data for analyses. In our surveys we imitated spotted owl vocalizations (vocal lure) for 10 minutes at a survey station or used vocal lures while walking along a survey route. We determined sex of a responding owl by the pitch of its 4-note territorial call; males have a lower-pitched call than females (Forsman et al. 1984). If owls were detected on nocturnal surveys, we conducted diurnal surveys to band unmarked owls, resight marked owls, assess reproduction, and band fledglings (Franklin et al. 1996). We banded owls with a numbered locking metal band on one leg and a unique combination of color band and color tab on the other leg (Franklin et al. 1996). We included both nocturnal and diurnal surveys in our occupancy analyses. We considered sites a territory where owls responded to vocal lures and were subsequently observed either roosting or nesting.

Survey Coverage of Study Area

To determine the initial year of complete survey coverage of the EDSA, we used ArcGIS 9.3 (ESRI, Redlands, California) to examine annual survey coverage of the EDSA. We drew a 0.80-km (0.5 mile) circle around each survey point where owls were not detected and a 1.61-km (1 mile) circle around each nest or roost location. We chose the 0.80-km distance because we expected surveyors to be able to hear any owls within this distance that responded during the surveys. We chose the 1.61-km distance because it was unlikely that other territorial owls would occur so close to a given territory (mean nearest-neighbor distance between owl territory centers from 1993–2010 was equal to 2.26 km). We then overlaid these circled areas on a map of the EDSA and calculated the proportion of the EDSA contained within the estimated areas of survey coverage each year. We chose 1993 as the starting year for our analyses because it was the first year that >90% of the EDSA land area was surveyed and >1 survey was conducted at >90% of the owl territories. The surveys conducted prior to 1993 served to develop survey protocols and identify owl territories. Our approach was consistent with previous mark-recapture analyses for the EDSA that did not use data collected prior to 1990 because it was subjectively determined that survey effort was inadequate from 1986–1989 (Franklin et al. 2004; Blakesley et al. 2010).

Occupancy Modeling

We used a multiseason, robust-design occupancy model (MacKenzie et al. 2003) to assess occupancy trends of owls. We divided each breeding season into 10 bimonthly periods (1–15 April, 16–30 April, 1–15 May, 16–31 May, etc.). This approach provided greater biological meaning to the survey occasions at individual territories, relative to sequentially using all surveys conducted at a territory each year. For example, if one territory was first surveyed in early April and another in late May, we believed that it was inappropriate to model the detection probability for the first survey occasion at each site with the same parameter. We chose bimonthly periods to retain as much data as possible without having too many missing observations within a given sampling period. If a territory was not surveyed during a bimonthly period, we treated it as a missing observation. If multiple surveys were conducted within the same period, we assigned a zero to the survey history if no owls were detected during any survey and a one if at least one owl was detected during any survey. Our primary sampling periods were breeding seasons (i.e., years), and our secondary sampling periods were the bimonthly periods within each breeding season.

Our statistical model contained parameters for initial occupancy (ψ_1), local extinction (ε_t), local colonization (γ_t), and detection probability ($p_{t,j}$) (MacKenzie et al. 2003). We used PRESENCE (version 3.1) (Hines 2006) to compare models with Akaike's information criterion (AIC) (Burnham & Anderson 2002). We used MARK (version 6.1) (White & Burnham 1999) to obtain model-averaged parameter estimates that were based on Akaike weights (ω_i) (Burnham & Anderson 2002). Both programs also provided annual estimates of occupancy ($\hat{\psi}_t$) and rates of change in occupancy ($\hat{\lambda}_t$), which were derived recursively from $\hat{\psi}_1$, $\hat{\varepsilon}_t$, and $\hat{\gamma}_t$ (MacKenzie et al. 2003). We then calculated the geometric mean for the rate of change in occupancy ($\hat{\bar{\lambda}}$) and estimated the realized change in occupancy (Δ_t) as

$$\Delta_t = \prod_{\mathrm{i}=1}^{\mathrm{t}-1} \hat{\lambda}_{\mathrm{i}}. \tag{1}$$

Thus, Δ_t was the product of $\hat{\lambda}_{1993} \times \hat{\lambda}_{1994} \times \ldots \times \hat{\lambda}_{2009}$ and represented the proportion of the initial population (i.e., the number of occupied territories) remaining in

2010. We obtained variance estimates for $\hat{\bar{\lambda}}$ and Δ_t with the delta method (Powell 2007).

We conducted the modeling in 2 stages. First, we used the fully parameterized model (ψ_1, ε_t, γ_t, $p_{t,j}$) to model within-season p. We developed 16 models containing covariates that we hypothesized affect p on survey occasion j during year t (Supporting Information). We used month as a covariate because each month corresponded to a different stage of the owl's breeding cycle and breeding-cycle stage affects owl behavior (April, incubation period; May, brooding; June, young fledged from nest; July, fledglings and adults typically near nest tree; August, fledglings and adults typically farther from nest tree) (Gutiérrez et al. 1995). We separated the survey season into prefledging (1 April to 31 May) and postfledging (1 June to 31 August) periods because the fledging period affects owl behavior. We included time trends (linear, quadratic, and log linear) because Seamans and Gutiérrez (2007) found that p varied in a log-linear trend over the survey season on the EDSA. We specified that p was different on survey occasions after the survey when owls were initially detected at a territory because observers intensified their efforts to relocate detected birds in order to resight or capture birds and assess reproduction (Riddle et al. 2010). Because we expected nesting owls to be more easily detected than non-nesting owls (Nichols et al. 2007; MacKenzie et al. 2009), we used reproductive status as a covariate. Nesting owls may defend their territories more aggressively (i.e., respond more readily to vocal surveys) or spend more time in the territory core area, where most of our survey effort occurred. We did not include any covariates for survey effort because multiple surveys were often conducted within a sampling period at sites where owls were known to be present (i.e., for the demographic study), which created a spurious, positive relation between survey effort and p. We also did not include a covariate for survey type because surveys of different types were often conducted within the same period.

In the second modeling stage, we used the best structure for within-season variation in p and compared models in which ε_t, γ_t, and p_t varied in 5 ways: constant (.), different in each year (t), linear trend (T), quadratic trend (TT), and log-linear trend (ln$T$). We considered all possible combinations of temporal trends for ε_t, γ_t, and p_t. We did not include additional covariates (e.g., habitat quality within a territory) because our main interest was to obtain the best estimate of temporal trends in occupancy, not to test biological hypotheses related to territory occupancy.

Mark-Recapture Modeling

In prior mark-recapture analyses of some of our data, a temporal-symmetry model (Pradel 1996) was used that contained parameters for finite rate of population change (λ_t), annual survival (φ_t), and capture probability (p_t) and treated λ_t as a random effect (Franklin et al. 2004; Blakesley et al. 2010). Blakesley et al. (2010) used mark-recapture data from 1990–2005 on the EDSA, but they omitted the first 2 and last estimates of λ_t, which may have been confounded with p_t when the parameters were modeled with a categorical time covariate (i.e., a different parameter estimate for each year). We used data from only 1993–2010 in our analyses to maintain congruence with our occupancy modeling. Our top models did not include any categorical time covariates, so we did not omit any λ_t estimates from our results.

We also used a functional form of Pradel's temporal-symmetry model that contained parameters for recruitment (f_t), φ_t, and p_t, and treated all parameters as fixed effects. Although treating $\hat{\lambda}_t$ as a random effect allows the partitioning of process variance (i.e., variation in $\hat{\lambda}_t$ due to covariate effects) from sampling variance (i.e., variation in $\hat{\lambda}_t$ due to random sampling; Burnham & White 2002), we wished to maintain an approach consistent with our occupancy modeling. An additional benefit of our approach was the explicit modeling of both mechanisms (recruitment and survival) responsible for population change. For comparison with Blakesley et al. (2010), we also conducted a random-effects analysis with their methods (see Supporting Information).

We used MARK (version 6.1) to compare competing models with AIC$_c$ and obtain model-averaged parameter estimates on the basis of ω_i. MARK provided annual estimates of finite rates of population change ($\hat{\lambda}_t$), which were derived from $\hat{f}_t$ and $\hat{\varphi}_t$ (Pradel 1996). We then calculated $\hat{\bar{\lambda}}$, Δ_t, and their variances as above (see Occupancy Modeling above).

As with the occupancy modeling, we conducted the mark-recapture modeling in 2 stages. First, we used the fully parameterized model (f_t, φ_t, p_t) to model p_t. In this case, p refers to the probability of recapturing a marked individual that was still alive during a given year, whereas p in the occupancy modeling referred to the probability of detecting an owl(s) at an occupied territory during a given survey. We developed 12 models containing covariates that we hypothesized could affect p (Supporting Information). Walk-in effort represented the amount of time spent conducting diurnal surveys in a given year. Relatively greater walk-in effort is positively correlated with p on the EDSA for survival analyses (Blakesley et al. 2010). Blakesley et al. (2010) also found that a bird's sex affected p on the EDSA. Finally, we included time trends (linear, quadratic, and log linear) because observer proficiency may have improved as our study progressed.

In the second modeling stage, we used the best structure for p_t and compared models in which f_t and φ_t varied temporally in 5 ways: constant (.), different in each year (t), linear trend (T), quadratic trend (TT), and log-linear trend (ln$T$). We considered all possible combinations of

Table 1. Top-ranked models for multiseason occupancy analysis of California Spotted Owl (*Strix occidentalis occidentalis*) territories in the central Sierra Nevada, 1993–2010.

Model[a]	*No. parameters*	*AIC*[b]	*ΔAIC*[c]	ω_i[d]
$\psi_1, \gamma_{.}, \varepsilon_{\ln T}, p_{T,\ \mathrm{initial+repro}}$	8	3081.93	0.00	0.108
$\psi_1, \gamma_{.}, \varepsilon_{T}, p_{T,\ \mathrm{initial+repro}}$	8	3082.60	0.67	0.077
$\psi_1, \gamma_{.}, \varepsilon_{\ln T}, p_{\mathrm{TT},\ \mathrm{initial+repro}}$	9	3082.82	0.89	0.069
$\psi_1, \gamma_{\ln T}, \varepsilon_{\ln T}, p_{T,\ \mathrm{initial+repro}}$	9	3083.44	1.51	0.051
$\psi_1, \gamma_{\mathrm{T}}, \varepsilon_{\ln T}, p_{T,\ \mathrm{initial+repro}}$	9	3083.50	1.57	0.049
$\psi_1, \gamma_{.}, \varepsilon_{\mathrm{TT}}, p_{T,\ \mathrm{initial+repro}}$	9	3083.65	1.72	0.046
$\psi_1, \gamma_{.}, \varepsilon_{T}, p_{\mathrm{TT},\ \mathrm{initial+repro}}$	9	3083.74	1.81	0.044
$\psi_1, \gamma_{\ln T}, \varepsilon_{T}, p_{T,\ \mathrm{initial+repro}}$	9	3084.04	2.11	0.038
$\psi_1, \gamma_{T}, \varepsilon_{T}, p_{T,\ \mathrm{initial+repro}}$	9	3084.15	2.22	0.036
$\psi_1, \gamma_{.}, \varepsilon_{\mathrm{TT}}, p_{\mathrm{TT},\ \mathrm{initial+repro}}$	10	3084.32	2.39	0.033
$\psi_1, \gamma_{\ln T}, \varepsilon_{\ln T}, p_{\mathrm{TT},\ \mathrm{initial+repro}}$	10	3084.41	2.48	0.031
$\psi_1, \gamma_{T}, \varepsilon_{\ln T}, p_{\mathrm{TT},\ \mathrm{initial+repro}}$	10	3084.46	2.53	0.030
$\psi_1, \gamma_{\mathrm{TT}}, \varepsilon_{\ln T}, p_{T,\ \mathrm{initial+repro}}$	10	3084.66	2.73	0.028
$\psi_1, \gamma_{.}, \varepsilon_{T}, p_{t,\ \mathrm{initial+repro}}$	24	3085.03	3.10	0.023
$\psi_1, \gamma_{.}, \varepsilon_{\mathrm{lnT}}, p_{t,\ \mathrm{initial+repro}}$	24	3085.05	3.12	0.023
$\psi_1, \gamma_{\mathrm{TT}}, \varepsilon_{T}, p_{T,\ \mathrm{initial+repro}}$	10	3085.10	3.17	0.022
$\psi_1, \gamma_{\ln T}, \varepsilon_{\mathrm{TT}}, p_{T,\ \mathrm{initial+repro}}$	10	3085.20	3.27	0.021
$\psi_1, \gamma_{\ln T}, \varepsilon_{T}, p_{\mathrm{TT},\ \mathrm{initial+repro}}$	10	3085.25	3.32	0.021
$\psi_1, \gamma_{T}, \varepsilon_{\mathrm{TT}}, p_{T,\ \mathrm{initial+repro}}$	10	3085.26	3.33	0.020
$\psi_1, \gamma_{T}, \varepsilon_{T}, p_{\mathrm{TT},\ \mathrm{initial+repro}}$	10	3085.34	3.41	0.020
$\psi_1, \gamma_{\mathrm{TT}}, \varepsilon_{\ln T}, p_{\mathrm{TT},\ \mathrm{initial+repro}}$	11	3085.62	3.69	0.017

[a] *Model variables are defined in Methods.*
[b] *Akaike's information criterion.*
[c] *Distance in AIC units from the model with the lowest AIC value.*
[d] *Akaike weight.*

temporal trends for f_t and φ_t. As with the occupancy modeling, we did not include additional biological covariates because our goal was to obtain the best estimate of temporal trends in population size, not to test biological hypotheses related to individual survival or recruitment.

Results

Territory Occupancy

We located 45 owl territories from 1993–2010, and owls had been detected at least once at all sites by 1997. Reproduction by owls was observed at 39 of 45 territories at least once during the study, which indicated we had identified biologically relevant territories. At least 1 owl was detected at 40 of 45 (90.0%) territories in 1993, but at only 26 of 45 (57.8%) territories surveyed in 2010. Thus, naïve territory occupancy estimates, which did not account for imperfect detection, indicated occupancy declined by 31% (14/45) during our study.

In the first modeling stage, model $\{\psi_1, \gamma_t, \varepsilon_t, p_{t,\ \mathrm{initial+repro}}\}$ had 100.0% of the Akaike weight among the 16 candidate models. Therefore, we used $p_{t,\ \mathrm{initial+repro}}$ in all second-stage models, of which $\{\psi_1, \gamma_{.}, \varepsilon_{\ln T}, p_{T,\ \mathrm{initial+repro}}\}$ was the top-ranked model (Table 1). However, considerable uncertainty existed regarding which model best fit the data as the top 7 models were within 2.0 AIC units of each other (Burnham & Anderson 2002). Parameter estimates from model $\{\psi_1, \gamma_{.}, \varepsilon_{\ln T}, p_{T,\ \mathrm{initial+repro}}\}$ indicated that within-year detection probability of owls was higher on surveys following the initial detection of an owl at a territory ($\hat{\beta}_{\mathrm{initial}} = 1.20$ [SE 0.11]) and higher for nesting owls ($\hat{\beta}_{\mathrm{repro}} = 1.63$ [SE 0.14]). Annual detection probabilities were generally high, particularly for nesting owls (Supporting Information).

Due to model-selection uncertainty, we obtained model-averaged estimates for $\hat{\gamma}_t$, $\hat{\varepsilon}_t$, and $\hat{\psi}_t$ with the 21 models that had >80% of the Akaike weight (Fig. 1). We used the top 80% because all models outside of this set had low support ($\omega_i \leq 0.02$). When a model contained a temporal covariate for either $\hat{\gamma}_t$ or $\hat{\varepsilon}_t$, the indicated trend was always negative for $\hat{\gamma}_t$ and positive for $\hat{\varepsilon}_t$. Thus, territory extinction increased over time ($\hat{\varepsilon}_{1993} = 0.019$ [SE 0.012]; $\hat{\varepsilon}_{2009} = 0.134$ [SE 0.043]), whereas territory colonization decreased over time ($\hat{\gamma}_{1993} = 0.323$ [SE 0.124]; $\hat{\gamma}_{2009} = 0.242$, SE = 0.058). As a result, territory occupancy declined during the study ($\hat{\psi}_{1993} = 0.957$ [SE 0.045]; $\hat{\psi}_{2010} = 0.671$ [SE 0.069]). The model-averaged estimates of ψ corresponded well with the naïve estimates of occupancy, despite a decline in the annual estimates of p during the study (Fig. 1). The estimated and naïve occupancy estimates did not diverge because p remained relatively high throughout our study, and we conducted sufficient surveys at a territory each year (average number of surveys per territory = 3.9) to detect owls reliably.

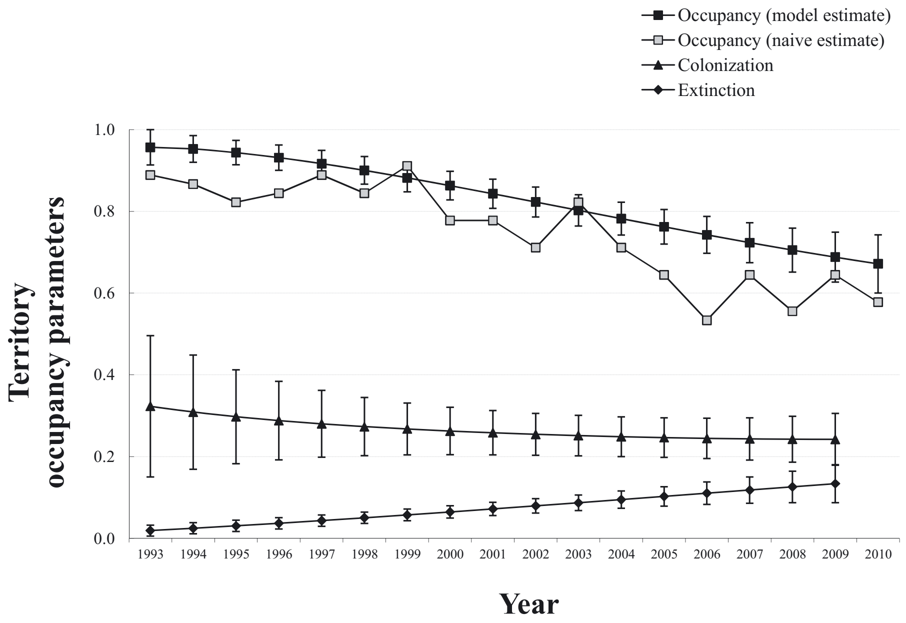

*Figure 1. Annual estimates (SE) of territory extinction, colonization, and occupancy at California Spotted Owl (*Strix occidentalis occidentalis*) territories in the central Sierra Nevada, 1993–2010.*

Table 2. Top-ranked temporal-symmetry models with recruitment and survival for mark-recapture analysis of a California Spotted Owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, 1993–2010.

Model[a]	*No. parameters*	*AIC*$_c$[b]	Δ*AIC*$_c$[c]	ω_i[d]
$\varphi_{.}, f_{.}, p_{\text{sex + effort}}$	5	2326.29	0.00	0.186
$\varphi_{.}, f_{\ln T}, p_{\text{sex + effort}}$	6	2326.86	0.57	0.139
$\varphi_{.}, f_{T}, p_{\text{sex + effort}}$	6	2327.56	1.27	0.099
$\varphi_{.}, f_{\text{TT}}, p_{\text{sex + effort}}$	7	2327.60	1.31	0.096
$\varphi_{\ln T}, f_{.}, p_{\text{sex + effort}}$	6	2328.25	1.96	0.070
$\varphi_{T}, f_{.}, p_{\text{sex + effort}}$	6	2328.30	2.01	0.068
$\varphi_{T}, f_{\ln T}, p_{\text{sex + effort}}$	7	2328.88	2.59	0.051
$\varphi_{\ln T}, f_{\ln T}, p_{\text{sex + effort}}$	7	2328.89	2.60	0.051
$\varphi_{T}, f_{T}, p_{\text{sex + effort}}$	7	2329.58	3.29	0.036
$\varphi_{\ln T}, f_{T}, p_{\text{sex + effort}}$	7	2329.59	3.30	0.036
$\varphi_{T}, f_{\text{TT}}, p_{\text{sex + effort}}$	8	2329.60	3.31	0.035
$\varphi_{\ln T}, f_{\text{TT}}, p_{\text{sex + effort}}$	8	2329.61	3.32	0.035
$\varphi_{\text{TT}}, f_{.}, p_{\text{sex + effort}}$	7	2330.26	3.97	0.025

[a] *Model variables are defined in Methods.*
[b] *Akaike's information criterion adjusted for small sample size.*
[c] *Distance in AIC*$_c$ *units from the model with the lowest AIC*$_c$ *value.*
[d] *Akaike weight.*

Mark-Recapture Abundance

In the first modeling stage, model $\{\varphi_t, f_t, p_{\text{sex + effort}}\}$ was the top-ranked model and had 35.7% of the Akaike weight among the 12 candidate models, so we used $p_{\text{sex + effort}}$ for detection probability in all second-stage models. In the second modeling stage, model $\{\varphi_{.}, f_{.}, p_{\text{sex + effort}}\}$ was the top-ranked model (Table 2). Parameter estimates from model $\{\varphi_{.}, f_{.}, p_{\text{sex + effort}}\}$ indicated that φ and f were constant during our study period and that p was higher for male owls ($\hat{\beta}_{\text{sex}} = 0.54$ [SE 0.25]) and positively correlated with annual walk-in survey effort ($\hat{\beta}_{\text{effort}} = 1.46$ [SE 0.67]). However, the top 6 models were within 2.0 AIC units of each other.

Due to model-selection uncertainty, we obtained model-averaged estimates for $\hat{\varphi}_t$, $\hat{f}_t$, and $\hat{\lambda}_t$ with the 14 models that had ≥95.0% of the Akaike weight (Fig. 2). The top 4 models specified that φ was constant; when a model contained a temporal covariate for $\hat{\varphi}_t$, the trend was weakly negative. The top model specified that f was constant; when a model contained a temporal covariate for $\hat{f}_t$, the trend was negative. Thus, survival was nearly constant over time ($\hat{\varphi}_{1993} = 0.816$ [SE = 0.020]; $\hat{\varphi}_{2009} = 0.815$ [SE 0.019]), whereas recruitment decreased slightly ($\hat{f}_{1993} = 0.195$ [SE 0.032]; $\hat{f}_{2009} = 0.160$ [SE 0.023]). As a result, the finite rate of population change slightly declined during the study ($\hat{\lambda}_{1993} = 1.011$ [SE 0.035]; $\hat{\lambda}_{2009} = 0.975$ [SE 0.024]).

Occupancy versus Abundance

The realized change in occupancy ($\Delta_t = 0.702$, 95% CI 0.552–0.852) (Fig. 3) and the geometric mean of annual change in occupancy ($\hat{\hat{\lambda}} = 0.979$, 95% CI 0.967–0.992) both suggested that territory occupancy declined from 1993–2010. Changes in occupancy within our study area should reflect changes in abundance unless the average number of owls detected at a territory also changed over time (i.e., more or fewer single owls). Thus, we performed a linear regression of the number of owls detected per territory versus year, and the slope was not significantly different from 0.0 ($\beta = -0.004$, $F_{1,16} = 1.13$, $p = 0.30$).

The realized change in population size ($\Delta_t = 0.725$, 95% CI 0.445–1.004) (Fig. 3) and the geometric mean of the finite rate of population change ($\hat{\hat{\lambda}} = 0.981$, 95% CI 0.959–1.004) also suggested that population size declined from 1993–2010, but the 95% CI slightly

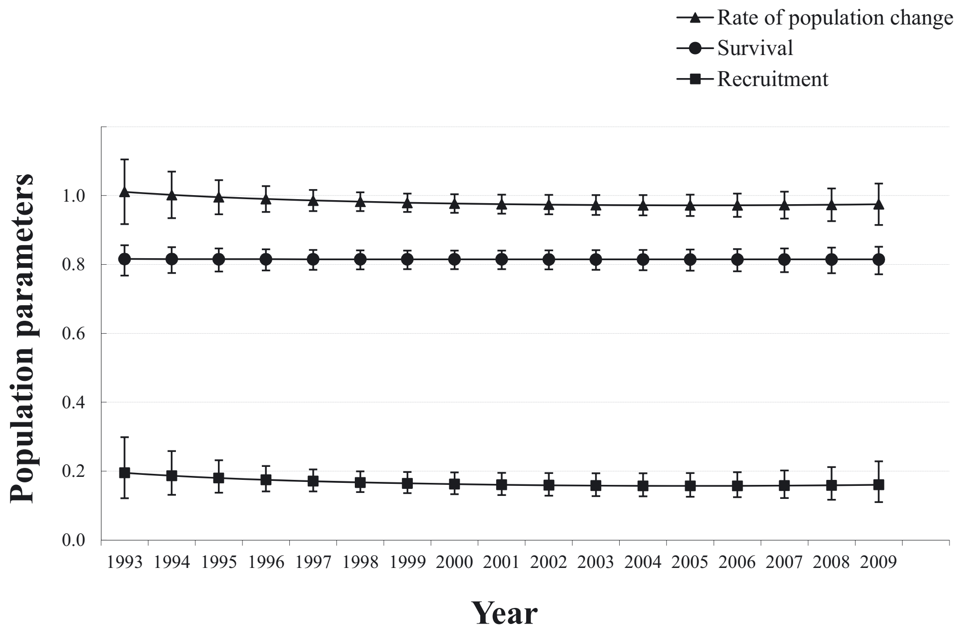

*Figure 2. Annual estimates (SE) of survival, recruitment, and finite rate of population change for a California Spotted Owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, 1993–2009.*

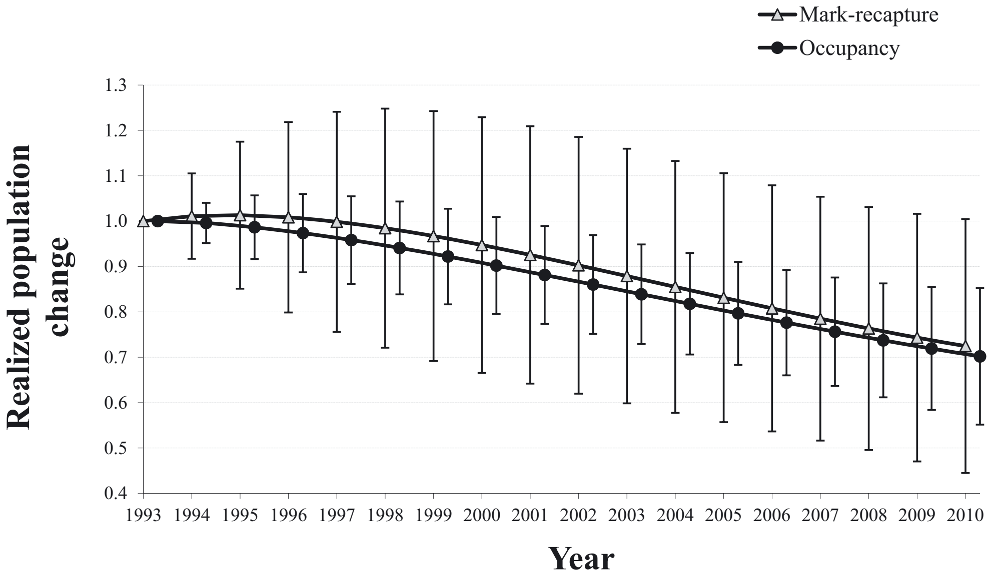

*Figure 3. Realized population change (95% CI) with both occupancy and mark-recapture data for a California Spotted Owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, 1993–2010.*

overlapped 1.0 for both parameters. The realized change in territory occupancy closely matched the realized population change estimated from mark-recapture data, although the realized population change estimates were less precise (Fig. 3).

Discussion

The realized change in population we estimated on the basis of occupancy closely matched the realized population change estimated from mark-recapture data. This result suggests occupancy monitoring may offer an accurate, cost-effective means to monitor the population trends of territorial species over large spatial extents. The relation between occupancy and abundance may be less strong for nonterritorial species (e.g., semicolonial; Estrada & Arroyo 2012), so we encourage assessments of the occupancy-abundance relation for such species. Occupancy models that incorporate observed counts of individuals and imperfect detection should be well suited for such applications (Royle et al. 2005).

We obtained more-precise parameter estimates with occupancy modeling relative to mark-recapture modeling. The determination of the effective sample size in occupancy studies has not been fully resolved (J. Nichols, personal communication). However, we apparently obtained a larger sample size with our occupancy data because the robust-design occupancy model accommodated multiple surveys (i.e., data points) at a territory each year, whereas we used a mark-recapture model that used a single datum each year for the marked individuals in our population. Robust-design models that accommodate missing observations are available for mark-recapture data (Pollock 1982), but we believe a site-based occupancy approach offers greater flexibility. For example, if the entire study area is not surveyed during each secondary sampling period, it is unclear how one would generally determine which individuals were not sampled during that period. Alternatively, the size of the study area can be increased to add more individuals, but this again requires substantial survey effort for species with large home ranges. In contrast, additional sampling units can be more easily added with occupancy surveys because the sampling unit is the site (whether defined as quadrats, territories, etc.), not the individual.

For the occupancy modeling, territory extinction increased over time, and colonization rates were insufficient to maintain occupancy at its initial level. Annual territory extinction was low during our study, but its effects were significant because most territories were occupied at the study's onset and colonization rates were also low. Territories may not have been colonized because habitat alteration during the study (e.g., logging, high-intensity wildfire) may have affected the quality of vacant owl territories (Seamans & Gutiérrez 2007). In addition, the mark-recapture modeling showed a declining trend in individual recruitment, so the population may have produced an insufficient number of owls to colonize vacant territories and maintain occupancy at its initial level.

We identified 2 factors that greatly affected the detection probability (p) in our occupancy analysis. First, p increased after the initial detection of owls at a territory during a given year (see Riddle et al. 2010). Owl demographic studies are designed to capture birds (either by banding unmarked birds or resighting marked birds) and to determine reproductive activity (Franklin et al. 1996), so observers intensify their efforts to locate birds after initial detection. This phenomenon suggests that future occupancy analyses for studies originally designed to collect mark-recapture data should include a within-year, initial-detection effect in the model structure. Second, we found that nesting spotted owls were more likely to be detected, which confirmed the results of prior analyses (Nichols et al. 2007; MacKenzie et al. 2009). Our results also supported the need to model detection probability appropriately during occupancy analyses to reduce bias in site-occupancy estimates (Mackenzie et al. 2006).

Our results suggested that occupancy data can provide reliable information on wildlife population trends, as evidenced by the concurrent declines in territory occupancy and population size of California Spotted Owls. Therefore, managers may be justified in using less costly, occupancy-based study designs to monitor spotted owls and other species of management concern over large geographic areas. Our occupancy models also provided more precise parameter estimates than our mark-recapture models because we conducted multiple surveys at each territory per primary sampling period. A robust-design mark-recapture model could have been used, but it was unclear to us how one would determine whether individuals were sampled during a defined secondary sampling period. We caution, however, that occupancy data may be more suitable for inferring the population status of territorial species than those with clumped spatial distributions, unless data collection also includes counts of individual organisms (in addition to the simple detection or nondetection of the target species) and researchers use occupancy models that incorporate such data (Royle et al. 2005).

We encourage future research that incorporates ecological covariates (e.g., habitat quality, habitat change) to elucidate site-occupancy dynamics and inform management decisions that may affect the California Spotted Owl. For example, managers need information on how timber harvest affects territory extinction and colonization, reproductive output, and individual survival (U.S. Forest Service 2004). We also recognize that mark-recapture studies provide important demographic information not provided by occupancy studies, which may allow the identification of life-history stages that are limiting a population. Thus, the choice of study design will depend on the specific research or management objectives for a given wildlife population.

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Supporting Information

The methods and results for our random-effects mark-recapture modeling for which we used the methods of Blakesley et al. (2010) (Appendix S1), our a priori models for detection probability (occupancy modeling) and capture probability (mark-recapture modeling) (Appendix S2), and the annual detection probabilities for our occupancy modeling (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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RESEARCH ARTICLE

Factors associated with crown damage following recurring mixed-severity wildfires and post-fire management in southwestern Oregon

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Abstract Wildfires and post-fire logging and planting have a lasting influence on the quantity and arrangement of live and dead vegetation, which can, in turn, affect the behavior of future fires. In 2002, the Biscuit Fire re-burned 38,000 ha of mixed-conifer/evergreen hardwood forest in southwestern Oregon that had burned heterogeneously during the 1987 Silver Fire and then was subject, in part, to post-fire logging and planting. We measured vegetation cover and crown damage from at temporal sequence (1987, 2000, and 2002) of digital aerial photo-plots (plot size = 6.25 ha) within managed and unmanaged portions of the twice-burned landscape. We estimated the strength and nature of relationships between crown damage in the two fires while also accounting for the influence of several vegetation, topographic, weather, and management variables. On average, unmanaged plots within the reburn area had 58% of their live crown cover scorched or consumed by the Biscuit Fire (median = 64%). The level of re-burn crown damage was strongly related to the level of crown damage during the Silver Fire. Typically, the areas that burned severely in the Silver Fire succeeded to a mix of shrubs and tree regeneration (i.e. shrub-stratum vegetation), which then experienced high levels of Biscuit Fire damage. In contrast, the level of tree-stratum damage in the Biscuit Fire was largely independent of Silver Fire damage. Within plots that were salvage-logged then planted after the Silver Fire, on average 98% of the vegetation cover was damaged by the Biscuit Fire (median = 100%). Within the plots that experienced complete crown damage in the Silver Fire but were left unmanaged, on average 91% of the vegetation cover was damaged by the Biscuit Fire (median = 95%). Our findings suggest that in productive fire-prone landscapes, a post-fire mosaic of young regenerating vegetation can influence the pattern of crown damage in future wildfires.

Keywords Burn mosaic · Reburn · Salvage logging · Burn severity · Biscuit Fire

Introduction

Wildfire is a dominant disturbance shaping forest ecosystems (Agee 1993). Individual wildfires have variable effects on vegetation and tend to increase the spatial and structural heterogeneity of live and dead fuels (Turner et al. 2003; Baker et al. 2007), which

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can in turn influence the behavior of subsequent wildfires (Peterson 2002; Agee 2005). This pathway may be affected further by post-fire forest management (McIver and Ottmar 2007; Thompson et al. 2007). Although the effects of compounding disturbances remain relatively unstudied, it is often assumed that severe forest disturbances, recurring over short time periods relative to their rate of recovery, can have qualitatively different ecological consequences than do isolated disturbances (Paine et al. 1998). We examined patterns of crown damage following two recurring mixed-severity wildfires in southwestern Oregon: the 1987 Silver Fire and the 2002 Biscuit Fire.

The "ecological memory" of past wildfires (sensu, Peterson 2002) ranges from strong (Minnich 1983) to non-existent (Bessie and Johnson 1995). In some low severity regimes, frequent surface fires reduce available fuels and the risk of crown fires (Covington and Moore 1994). Similarly, in some high severity regimes, fires can reduce short term fire hazard if regenerating vegetation is less flammable than older vegetation (Despain and Sellers 1977; Romme 1982). In contrast, in other high-severity regimes, stand replacing fires elevate fuel-loads (Agee and Huff 1987) and can lead to repeated high severity fires in rapid succession (Gray and Franklin 1997). In mixed-severity regimes, characterized by variable fire frequencies and heterogeneous effects within and between fires, the post-fire legacy of live and dead fuels is variable over time and space and is comparatively not well understood (Schoennagel et al. 2004; Agee 2005). Simulations suggest that the patch mosaic created by a mixed-severity fire can structure and reinforce the severity pattern within future fires (Peterson 2002; Wimberly and Kennedy 2008). In Sierra-Nevadan mixed-conifer forest, frequent fires with fire-free intervals <9 years appeared to limit the extent of recurring fires (Collins et al. 2009). In the more productive mixed-conifer/mixed-evergreen hardwood forests of southern Oregon and northern California, where the Silver and Biscuit Fires occurred, the post-fire landscape is typically a mosaic of high and low severity patches that vary widely in size (Agee 1991; Skinner 1995; Taylor and Skinner 2003). Within severely burned patches, most biomass remains on site but is converted from live to dead, while fine surface fuels and the forest floor are largely consumed (Campbell et al. 2007; Bormann et al. 2008). Dead aerial fuels gradually fall to the surface and decompose over time. Within a few years, live surface fuels increase dramatically, as shrubs, hardwoods and conifer trees regenerate, often at high densities (Shatford et al. 2007; Donato et al. 2009).

The risk of recurring high severity fires is just one of many competing concerns that managers must consider in the aftermath of a fire. Post-fire logging (i.e. salvage logging) has long been a management choice, motivated primarily by interest in economic returns and a perceived reduction in the risk of future severe fires resulting from lower fuel loads (Poff 1989; Brown et al. 2003; Sessions et al. 2004; Gorte 2006). Some recent studies have found, however, that post-fire logging can increase short-term fire hazard by increasing the availability of fine fuels (Donato et al. 2006; McIver and Ottmar 2007). Planting conifers has also been widely employed in the aftermath of wildfires to expedite the return of desired tree species and hasten the return of fire resistant forests (Sessions et al. 2004). This practice, too, may elevate short-term fire hazard if planting increases the availability and continuity of fine fuels (Stephens and Moghaddas 2005). Several observational and modeling studies have documented the high severity fire within plantations (Weatherspoon and Skinner 1995; Odion et al. 2004; Thompson et al. 2007; Kobziar et al. 2009), even when conifers are planted at low densities (Roloff et al. 2004).

We capitalized on a unique arrangement of disturbances to address questions of re-burn severity and post-fire management. We examined a landscape in southwest Oregon that burned heterogeneously during the 1987 Silver Fire, and then was subject to some salvage logging and planting before re-burning in the 2002 Biscuit Fire. In an earlier analysis of the same landscape, Thompson et al. (2007) used the Landsat-based differenced normalized burn ratio (dNBR, Lutes et al. 2004), and found that areas that burned at high severity in 1987 tended to re-burn severely in 2002. Conversely, areas that burned at low severity in 1987 tended to reburn at the lowest severities. Further, they found that areas that were salvage-logged and planted after the Silver Fire burned somewhat more severely in the Biscuit Fire than did areas that burned severely in the Silver but were left unmanaged. dNBR is correlated with vegetation damage (Lutes et al. 2004) and is commonly used for quantifying landscape-scale burn effects (Miller and Yool 2002; Bigler et al. 2005; Finney et al. 2005; Wimberly and Reilly 2007). However, dNBR cannot effectively distinguish between the type or structure of burned vegetation. At high levels of dNBR, changes in the index may be more associated with surface soil features (e.g., ash, soil color) than with canopy mortality, which reaches 100% before the maximum level of dNBR is reached (Kokaly et al. 2007). In this analysis, we increased ecological resolution far beyond dNBR by using a temporal sequence of digital aerial photography to document the layering of disturbances and the pattern of vegetation damage among the three dominant cover types: conifers, hardwoods, and low stature vegetation [a mix of shrubs and small trees, hereafter called the shrub-stratum, sensu Sandberg et al. (2001)]. We examined the relationship between 1987 Silver Fire severity and post-Silver management with Biscuit Fire severity. Additionally, we estimated the relative importance and the nature of relationships between Biscuit Fire crown damage and several aspects of its fire environment and management history. Our objectives were:

1. To characterize the relative importance of weather, topography, and the legacy of the 1987 Silver Fire on patterns of crown damage created by the 2002 Biscuit Fire.
2. To compare patterns of crown damage between areas that were salvage-logged and planted after the Silver Fire to areas that experience stand-replacing fire but were unmanaged, with respect to weather, topography, and vegetation structure.

Methods

Study area

The analysis was limited to the 21,000 ha that make up the northern half of the 1987 Silver Fire, centered at 123°89′W latitude 42°49′N longitude (Fig. 1), where an adequate aerial photo record was available. At >38,000 ha, the Silver Fire was the largest of more than 1,600 fires ignited by lightning in northwest California and southwestern Oregon on August 30, 1987 (Reider 1988). The Biscuit Fire burned through and completely encompassed the region of the Silver Fire beginning on July 17, 2002 and continuing through August 18, 2002.

The study area is managed by the Rogue-Siskiyou National Forest (RSNF) and is within the mixed evergreen zone (Franklin and Dyrness1988). It is dominated by conifer species such as Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), and white fir (*Abies concolor*). Dominant evergreen hardwoods include tanoak (*Lithocarpus densiflorus*), and Pacific madrone (*Arbutus menziesii*). Dominant shrubs species include manzanita (*Arctostaphylos* sp.) and snowbrush (*Ceanothus velutinus*). In older stands, the sclerophyllous hardwood trees often form lower strata under the conifer overstory (Franklin and Dyrness 1988).

Soil parent materials in the study area include igneous, meta-sedimentary, and metamorphic types. Less than 5% of the study area has ultramafic soils. These areas are floristically distinct and presented an unrepresentative fuel environment (Thompson and Spies 2009), so were excluded from this analysis. Topography in the region is steep and complex; the area is sometimes referred to as “Klamath Knot,” a reference to the lack of directionality to the mountains and the multifarious geology. Elevations range from 100 to 1,500 m. Mean January temperature is 6°C. Mean July temperature is 16°C. Mean annual precipitation is 270 cm, with greater than 90% occurring in winter (Daly et al. 2002).

Image processing and interpretation

We overlaid and manually interpreted a temporal sequence of digital aerial photo plots taken at three points in time: Post-Silver Fire (October 15, 1987, color, 30 cm grain size), Pre-Biscuit Fire (August 2000, panchromatic, 1 m grain size) and Post-Biscuit Fire (September 24, 2002, color, 30 cm grain size). We interpreted vegetation condition and fire effects within 181 randomly located photo-plots and 35 management units randomly selected from a database acquired from the RSNF. Unmanaged photo-plots were square, five-by-five polygon grids of 50 m cells, covering 6.25 ha. Plots were discarded if they contained any portion of a road, management unit or a large stream or river. To construct management plots, we overlaid a polygon grid of 50 m cells onto the variably shaped management units. If the unit was larger than 6.25 ha, then 25 cells were randomly selected and used as the plot. If the units was smaller than 6.25 ha, then all cells were used. Management units <1.25 ha were excluded. We

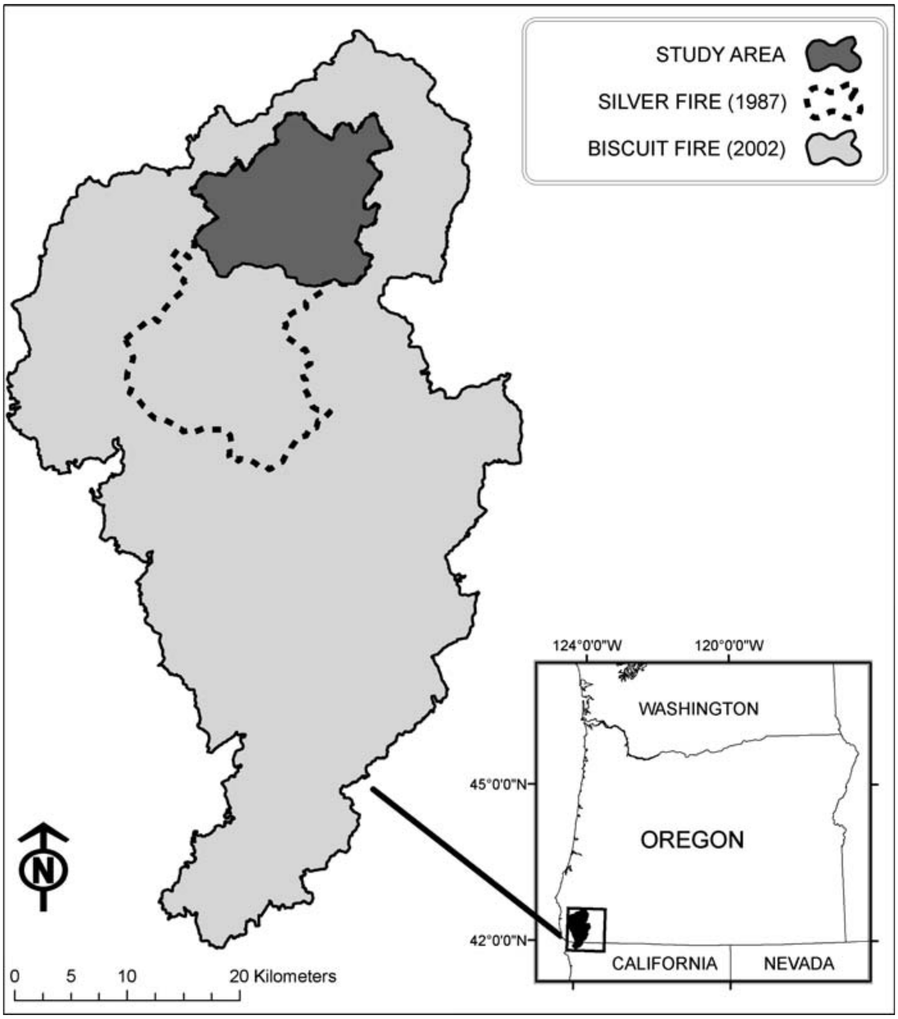


Fig. 1 Map of the study area in context of the Silver and Biscuit Fires

spatially co-registered each photo-plot using approximately 15 ground control points and used a first-order polynomial transformation for rectification, which resulted in a 30 cm grain size.

To quantify Silver and Biscuit fire effects, we measured the percent of overstory vegetation scorched or consumed (i.e. crown damage) by each fire within each cell of each photo-plot. In addition to measuring the percent of crown damage across all cover types we also independently measured the percent of pre-Biscuit Fire (year 2000) shrub-stature, conifer, and hardwood cover that was damaged by the Biscuit Fire (year 2002). The distinction between damage in each cover class proved necessary to understand the patterns of recurring fires. It is important to note that the percent of crown cover damaged as measured from a planar view of the landscape is not necessarily equivalent to the proportion of the crown volume damaged when measured in the field and, thus, these two measures of "crown damage" should not be directly compared. Also, while field measurements of pre-fire fuel conditions and post-fire burn effects may be ideal, the retrospective nature of this study and the spatial layering of multiple disturbances dictated a remote sensing approach.

We measured percent cover of conifer, hardwood, shrub-stature vegetation, bare ground/grass in every cell within each photo-plot at each point in time, and measured percent crown damage to the conifer, hardwood and shrub-stratum for each cell in 1987 and 2002. We subtracted areas obscured by topographic shadow from the effective area of the photo plot (which cumulatively represented <0.5% of the sampled area).

Pre-fire conifer cover in each cell was further assigned a size class: small, (<50 cm DBH), large (>50 cm DBH), or mixed. DBH estimates were verified with a post hoc comparison of conifers in photo photos to 70 co-located Forest Service inventory plots measured before the Biscuit Fire. Cover estimates summed to 100% in each cell. We averaged cell-level cover estimates to obtain plot-level values. As a metric of structural complexity for each plot, we calculated the standard deviation of the different cover types measured in 1987. To ensure consistency and reduce error all photo interpretation was conducted by a single researcher (Thompson). To calibrate interpretation, we began by developing a catalog of paired oblique-to-aerial photos for use in training then, later, informally ground-truthed a subset of photo-plots, which revealed excellent correspondence.

Topographic and weather variables

Using a 10-meter digital elevation model (DEM), we calculated average photo-plot elevation, percent slope, Beers' transformed aspect (Beers et al. 1966), and topographic position (TP) for each photo-plot. We calculated TP at two spatial scales: "TP-Fine" is the difference between the mean plot elevation and the mean elevation in an annulus 150–300 m from the plot; "TP-Coarse" uses an annulus 850–1,000 m from the plot.

The RSNF provided a map showing the daily progression of the Biscuit Fire, which we used to assign weather data to each photo-plot based on the day it burned. We assigned the average temperature, relative humidity, wind speed, and cosine transformed wind direction between 10:00 and 19:00 for each day as calculated from the Quail Prairie Remote Automated Weather Station, located approximately 25 km south of the study area. We also created a variable that divided the reburn area into three "Burn Periods," which corresponded to the spread of the Biscuit Fire and fire suppression effort during each period (USDA 2002; GAO 2004). Period A represents 5% of the total Biscuit Fire area (7% of the study area) and includes the region that burned from July 13 to July 26. There was comparatively little suppression effort and mild weather conditions during the time this area burned (Table 1). Period B includes the region that burned from July 27 to Aug 04; 50% of the Biscuit Fire burned in this 9 days period (46% of the study area), which was characterized by strong north-northeastern winds and low relative humidity. Suppression resources increased during this period but were largely unsuccessful in preventing fire spread. Period C represents the remaining 45% of the Biscuit Fire (47% of study area) that burned from August 5 to 18 Fire suppression activities were extensive throughout Period C. The fire continued to spread during extreme weather but had a higher potential to be influenced by fire fighting activities, including burn-outs. While there are no official records describing burn-out locations or severity, the practice was widely used during the suppression campaign, particularity in areas close to towns and private land at the very north and west margins of the Biscuit Fire perimeter. These areas are primarily outside of the re-burn study area which is in the central and more remote regions of the fire. Therefore, we are confident that burn outs did not have a large effect on the crown damage estimates we report here. However, like local weather and specific fuel conditions, the influence of fire suppression was a source of unexplained variance within our analyses.

Table 1 Dates, area, and weather information for burn periods distinguished by the spread of fire and the resources used for fire suppression

Burn period	Start-stop	No. days	Hectares (% total)	Temperature (°C)	Relative humidity (%)	Wind speed (km/h)	Wind direction	Suppression effort
A	7/13 to 7/26/2002	14	1,485 (7)	23.3	43	13.0	0.08	Low
B	7/27 to 8/04/2002	9	9,731 (46)	25.5	35	13.1	0.63	Moderate
C	8/05 to 8/18/2002	14	9,761 (47)	27.2	22	9.8	0.66	High
Silver Fire	8/31 to 10/15/1987	46	20,977 (100)	22.7	37	7.9	0.02	Unknown

Weather variables are averages of the daily average between 10:00 and 19:00 within each Biscuit Fire burn period, or within the duration of Silver Fire. Wind direction has been cosine transformed such that a value of -1 is associated with southwesterly winds and a value of $+1$ is associated with northeasterly winds

Management data

All the management units included in the study were salvage logged in the 3 years following the Silver Fire, then planted with conifers (primarily Douglas-fir) and later certified as "successful plantations" by the RSNF. The Silver Fire salvage logging guidelines set by the Forest Service required that, within harvest units, 12–18 standing snags >60 cm diameter and >12 m tall, along with 2.8 m^3 of down wood be retained per hectare. No documentation describing post-logging fuel treatment was available. Plantations were deemed successful if, 3–5 years after planting, conifers exceeded 370 stems per hectare and were considered healthy enough to survive competition with shrubs and hardwood trees. Though post-Silver Fire records from the RSNF are not complete, they indicate that some certified plantations had undergone mechanical treatment to suppress competing vegetation and that conifer stocking typically ranged from approximately 600–1,100 trees per hectare. All areas logged and planted prior to the Silver Fire were excluded from our analyses.

Data analysis

Unmanaged plots

To illustrate the differences in patterns of crown damage between the two fires, we plotted empirical cumulative distributions of total crown damage measured in the photo-plots after each fire. To assess the pattern of re-burn damage as it related to the level of Silver Fire damage, we summarized the proportion of conifer, hardwood, and shrub-stratum damage at 5% increments of Silver Fire crown damage. To estimate the importance of the predictor variables (Table 2) on re-burn severity, we structured three response variables that describe different aspects of crown damage during the Biscuit Fire: total crown damage across all cover types, relative conifer damage (i.e. (2000 Conifer Cover—2002 Conifer Cover)/2000 Conifer Cover), and relative hardwood damage. When modeling relative hardwood damage, we subset the data to include only those plots with greater than 5% pre-fire hardwood cover ($n = 107$). We used a two-stage approach to analyzing relationships between the three response variables and the suite of 18 predictor variables (Table 2). We first used random forest analysis (RFA; Breiman 2001) to estimate and rank the importance of predictors, and then used regression tree analysis (RTA; De'ath and Fabricius 2000) to illustrate the nature of relationships between the response and the top ranked predictor variables. These nonparametric methods are ideally suited for the analysis of high dimensional ecological data with hierarchical and non-linear relationships among predictor variables and between predictor and response variables (De'ath and Fabricius 2000; Cutler et al. 2007).

We used Liaw and Wiener's (2002) implementation of RFA within the R statistical environment (R Development Core Team 2006). The algorithm, as applied to these data, was as follows: (1) Select 1,500 bootstrap samples each containing two-thirds of the data; (2) For each bootstrap sample, grow an un-pruned regression tree with the modification that at each node, rather than implementing the best split among all predictors (as is typical in regression trees), randomly select one-third of the predictor variables and choose the best split from among those variables; (3) At each bootstrap iteration, predict the response value for data not included in the bootstrap sample—the so-called Out-Of-Bag or OOB data—and average those response values over all trees; (4) Calculate importance values for each predictor by calculating the percent increase in mean squared error when OOB data for each variable are permuted while all others are unchanged. We used RFA variable importance values to rank predictors in terms of the strength of their relationship to the response and partial dependence plots to show the effect of changing individual predictors while holding all other predictors at their average.

After identifying important predictor variables with RFA, we used RTA to better understand the nature of relationships between the six top-ranked predictors and each response variable. RTA is a non-parametric technique that recursively partitions a dataset into subsets that are increasingly homogeneous in terms of the response (De'ath and Fabricius 2000). RTA produces a set of decision rules on predictor variables that are easily interpreted as a dendrogram. Most implementations of RTA have a selection bias towards predictors with many possible splits and tend to overfit to a given dataset by creating splits that do not significantly reduce the variance (Hothorn et al. 2006). Trees are typically pruned back to include only those partitions assumed to be valuable beyond the sample

Table 2 Summary of response and predictor variables used in the random forest and regression tree analysis of unmanaged stands

	Median	Mean	Min	Max
Response variables				
All crown damage	62.6	58.4	0.0	100.0
Relative conifer damage	38.6	45.8	0.0	100.0
Relative hardwood damage	85.3	72.9	0.0	100.0
Predictor variables				
1987 crown damage (silver fire)	16.4	28.3	0.0	100.0
1987 Large conifer cover	29.0	36.6	0.0	100.0
1987 Small conifer cover	1.2	6.1	0.0	82.8
1987 Mixed-size conifer cover	2.2	9.2	0.0	82.2
1987 Hardwood cover	6.2	15.8	0.0	77.2
1987 Shrub cover	0.0	2.1	0.0	52.0
1987 Bare/grass cover	0.0	1.9	0.0	44.0
1987 Cover variability (SD)	21.1	22.0	9.2	35.4
Elevation (m)	700.0	701.9	136.8	1,476.0
Topographic position (Fine)	−0.9	−1.1	−58.5	53.8
Topographic position (Coarse)	−6.1	−2.5	−271.0	275.6
Slope (%)	57.6	57.0	21.7	92.4
Beer's aspect	0.1	0.1	−1.0	1.0
Temperature (C)	27.2	25.6	16.6	35.0
Relative humidity (%)	28.3	29.3	11.4	53.6
Wind speed (km/h)	15.0	14.1	6.2	19.1
Wind direction (cosine transformed)	0.6	0.5	−0.3	0.8
Burn period	A (9%), B (49%), C (42%)			

See "Methods" and Table 1 for information regarding the different burn periods

data. We used an implementation of RTA called conditional inference trees, which establishes partitions based on the lowest statistically significant *P*-value that is obtainable across all levels of all predictor variables, as determined from a Monte Carlo randomization test. This minimizes bias and prevents over-fitting and the need for pruning (Hothorn et al. 2006). To guard against Type-I errors resulting from spatial autocorrelation, we set α conservatively to 0.005. We assessed autocorrelation in RFA and RTA model residuals using semivariograms.

Management data

To determine whether salvage logging and planting after the Silver Fire influenced the level of crown damage in the Biscuit Fire, we compared the management plots ($n = 35$) with the portion of unmanaged plots (or contiguous portions of unmanaged plots >1.25 ha) that experienced complete overstory mortality during the Silver Fire ($n = 35$). By using only those unmanaged plots that burned severely during the Silver Fire we ensured that our comparison was between two stand-replacing events. We compared medians and distributions of the percent of crown damage in the managed and unmanaged plots, but did not report *P*-values because spatial autocorrelation prevented us from setting a meaningful level for α. We then pooled these data ($n = 70$) and used RFA and RTA to examine relationships between the predictor variables (Table 2) and crown damage, while also including an indicator variable for management history as a potential predictor.

Results

Level of overall crown damage

Ninety percent of the unmanaged plots experienced some level of crown damage (i.e. >1% of the plot area) during the Silver Fire, while 99% experienced some level of crown damage during the Biscuit Fire (Fig. 2). On average, unmanaged plots had 28% of

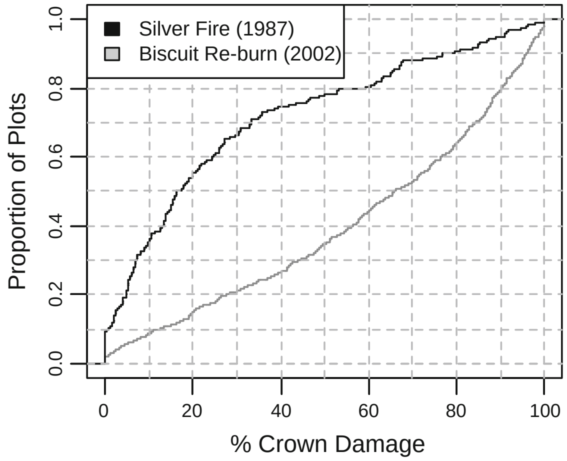


Fig. 2 Empirical cumulative distribution of crown damage in the 1987 Silver Fire and re-burn portion of the 2002 Biscuit Fire

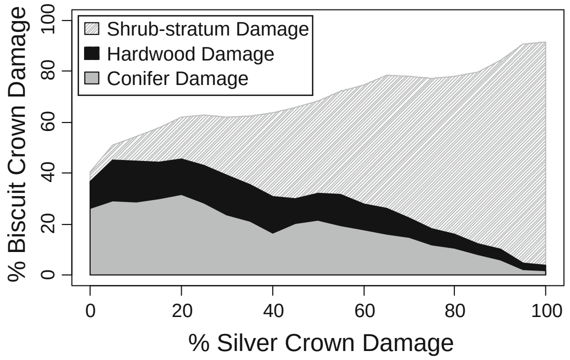


Fig. 3 Percent Biscuit Fire crown damage to the shrub-stratum, hardwood, and conifer crowns in relation to the overall percent crown damage during the 1987 Silver Fire

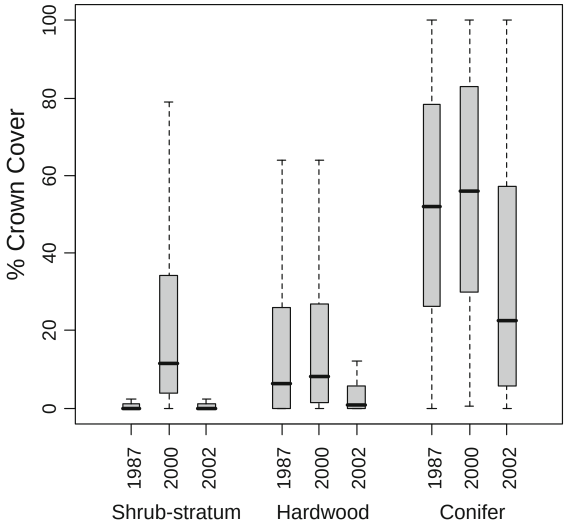


Fig. 4 Percent crown cover of shrub-stratum, hardwood, and conifer cover in 1987 (immediately after the Silver Fire), in 2000 (2 years before the Biscuit Fire), and in 2002 (immediately after the Biscuit Fire). *Black lines* correspond to median values; *boxes* correspond to the inner quartile range; *whiskers* correspond to the range of the data

their crown cover damaged by the Silver Fire (median = 16%), while the average level of crown damage from the Biscuit Fire, across all cover types, was 58% (median = 64%; Table 2). Within-plot burn variability was higher in the Silver Fire than the Biscuit Fire (coefficient of variation = 1.05 vs. 0.6, respectively). Plots with the highest levels of crown damage in the Silver Fire also had the highest levels of crown damage within the Biscuit Fire (Fig. 3). By the year 2000, plots that had been severely burned by the Silver Fire had largely succeeded to shrub-stratum cover and contained low levels of tree-stratum cover. Consequently, the highest levels of absolute (as opposed to relative) tree-stratum crown damage (conifer and hardwood) during the Biscuit Fire were in areas that had sustained the lowest levels of Silver Fire damage (Fig. 3). Of the three cover types considered, the shrub-stratum experienced the largest proportional damage (95%; Fig. 4). Of the tree-strata cover types, hardwoods experienced a greater proportional loss of canopy than did conifers (85 vs. 39%, respectively; Table 2).

Overall crown damage models

The RFA model explained 46% of the variability in overall crown damage (unmanaged plots only). Silver Fire damage and large conifer cover were the most important predictor variables (Fig. 5). Increasing Silver Fire damage was associated with increasing Biscuit crown damage, while increasing large conifer cover was associated with decreasing crown damage in the Biscuit.

RTA of total crown damage resulted in five terminal nodes (Fig. 6). The first partition was based on whether Silver Fire crown damage was >39%; when it was, Biscuit Fire damage was generally >90%. When Silver Fire damage was <39%, areas that burned during period B, and when the average

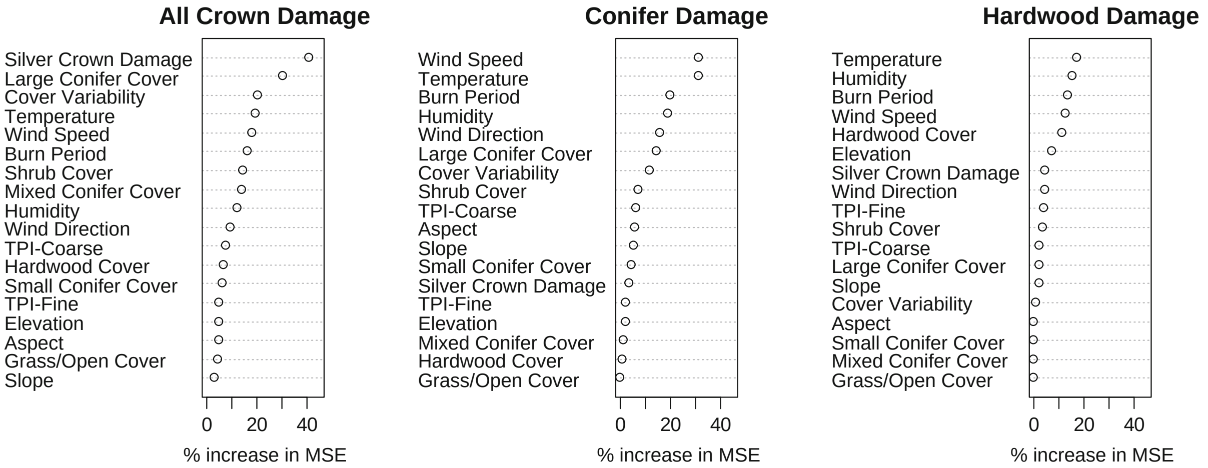
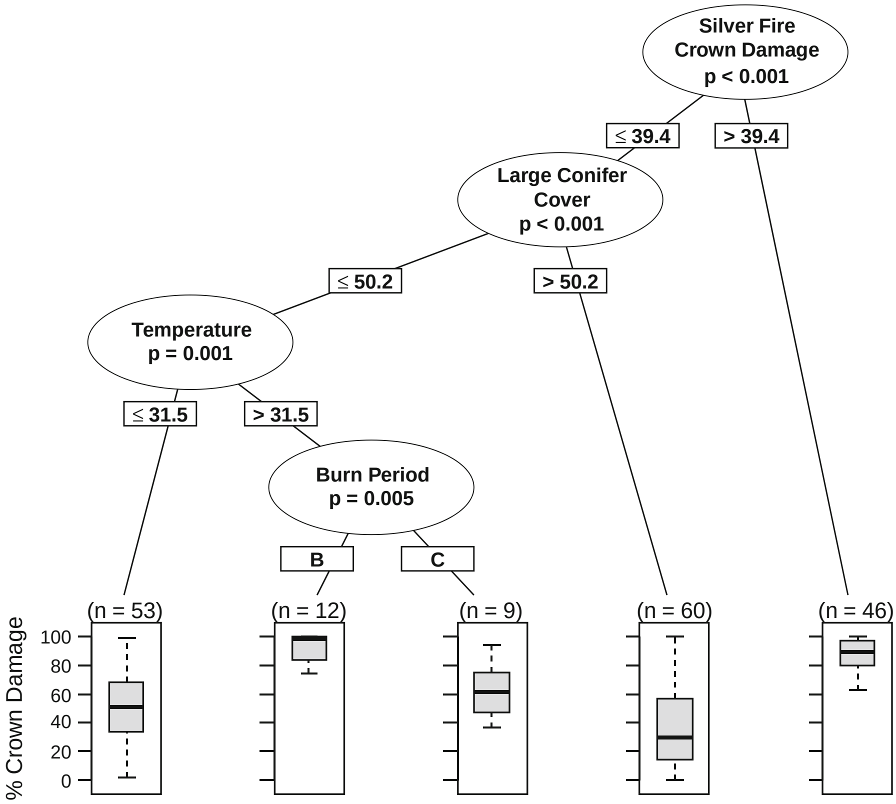


Fig. 5 Variable importance plots for predictor variables from random forests models for overall crown damage, relative conifer damage, and relative hardwood damage. Predictor variables are along the *y*-axis and the average increases in the mean square error when data for that variable are permuted and all other are left unchanged are on the *x*-axis. TPI = Topographic position index; see "Methods" section for details

Fig. 6 Regression tree for total Biscuit Fire crown damage based on the top six predictor variables from the random forest analysis (see Fig. 5). *Box-plots* at terminal nodes show the distribution of the data within that branch of the tree



temperature was greater than 31°C, had very high levels of crown damage. In contrast, the lowest levels of crown damage were in areas with >50% large conifer cover.

Conifer and hardwood damage

The RFA models explained 32 and 18% of the variability in relative conifer and hardwood damage,

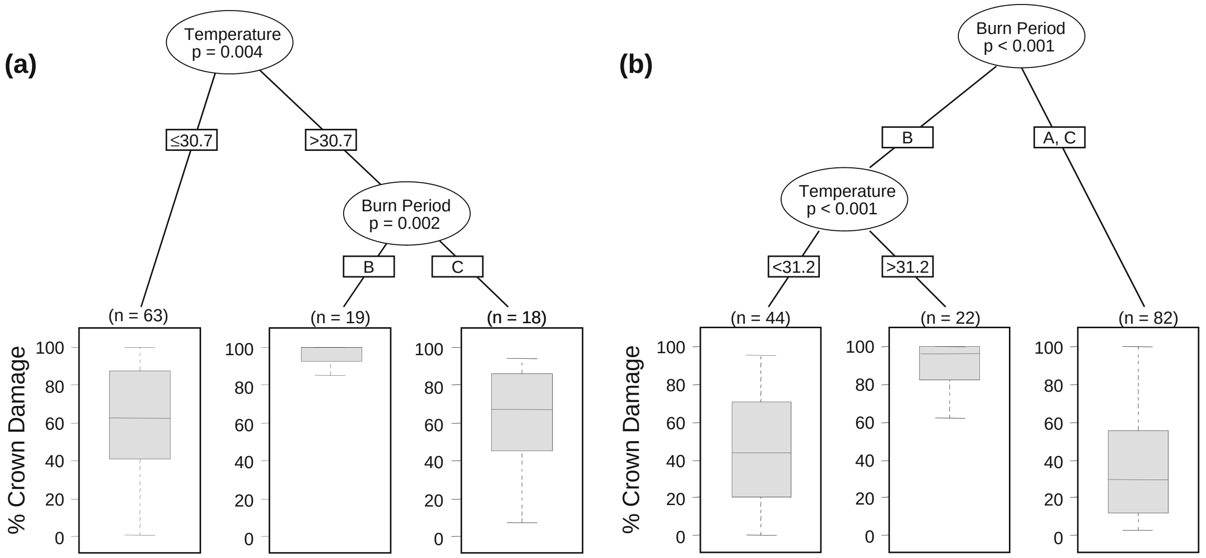


Fig. 7 Regression trees of **a** relative conifer and **b** hardwood crown damage during the Biscuit Fire using the top six predictor variables from the random forest analysis (see Fig. 5)

respectively (Fig. 5). Weather variables and burn period were ranked as most important predictor variables in both cases. The first split in the regression tree of relative conifer damage was burn period and indicated lower levels of damage during burn periods A and C (Fig. 7). Conifer damage was highest during period B when the average temperature was above 31°C. The first split in the RTA for hardwood damage was related to average daily temperature, but overall, patterns were similar to those in relative conifer damage (Fig. 7).

Management history

The average level of pre-Biscuit Fire (year 2000) live shrub-stratum cover was 95% in the salvage-logged and planted plots (i.e. managed plots) and was 86% in the plots that experienced complete crown damage in the Silver Fire but were left unmanaged (Fig. 8). Within the managed plots, on average 98% of the vegetation cover was damaged by the Biscuit Fire (median = 100%). Within the plots that experienced complete crown damage in the Silver Fire but were left unmanaged, on average 91% of the vegetation cover was damaged by the Biscuit Fire (median = 95%).

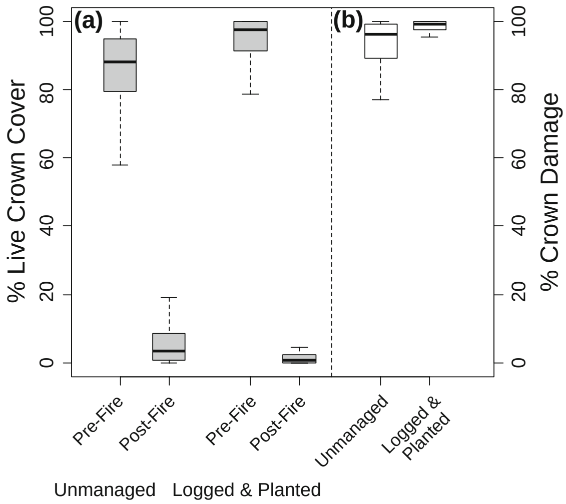


Fig. 8 Distribution of **a** vegetation cover and **b** percent crown damage within areas that were severely burned in the Silver Fire and either left unmanaged or were salvage logged and planted with conifers

With those managed and unmanaged plot data pooled, the RFA model explained 37% of the variability in crown damage. The two measures of topographic position and management history were the most important predictors of damage (Fig. 9). Higher topographic position and management was associated with higher crown damage. Consistent with this finding, the first split in the regression tree was on TP-Fine; plots on lower topographic positions had median crown damage of 93% and included only unmanaged plots (Fig. 10). Among plots with higher topographic

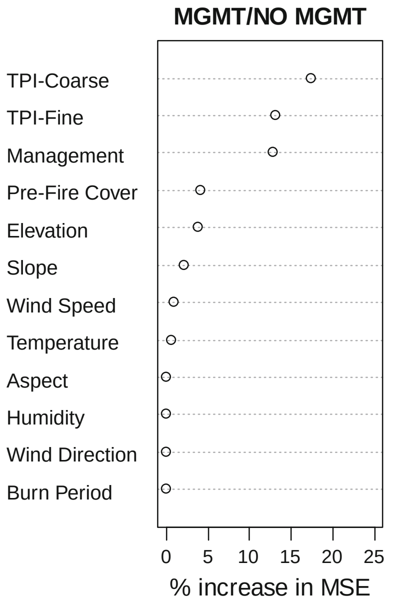


Fig. 9 Variable importance plot from the random forests analysis of crown damage within areas that were severely burned in the Silver Fire and either left unmanaged or were salvage logged and planted with conifers. TPI = Topographic position index; see "Methods" section for details. (See Fig. 5 for further explanation of axes)

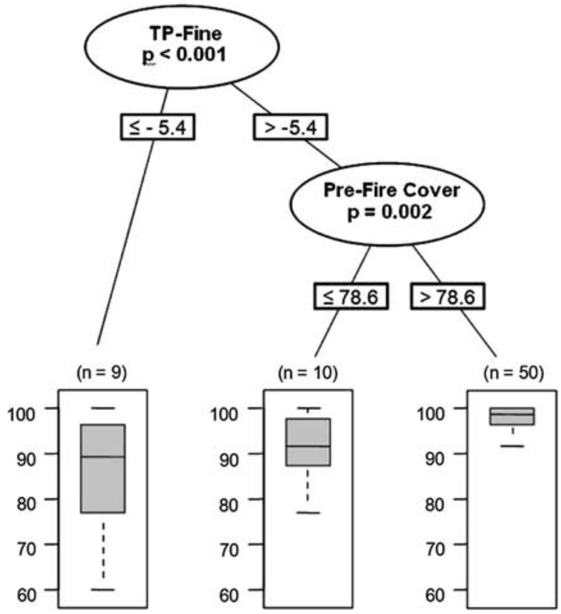


Fig. 10 Regression tree of canopy damage for areas that experienced 100% crown damage during the Silver Fire and were either left unmanaged or were salvage logged and planted with conifers. Note that when the pre-fire cover variable was held out of this analysis, the indicator for management entered as a significant variable at the same place on the regression tree with $P = 0.026$

positions, an additional split was based on whether shrub-stratum cover was above 79%.

Discussion

While the Biscuit Fire resulted in higher levels of canopy damage than the Silver Fire, this was not exclusively related to it being a re-burn. In fact, Biscuit-related crown damage outside of the re-burn area also exceeded the level of damage in the Silver Fire (Thompson and Spies 2009). Differences in overall damage between the two fires were largely attributable to more extreme weather conditions at the time of the Biscuit Fire (see temperature and wind speed data in Table 1). Nonetheless, the legacy of the Silver Fire was strongly associated with the pattern of overall Biscuit Fire crown damage. Consistent with Thompson et al. (2007), we found a trend of increasing overall Biscuit Fire damage with increasing Silver Fire damage (Fig. 3). What the current analysis shows—and what the previous analysis was unable to show—is that damage to the regenerating shrub-stratum vegetation drove this correlation and that damage in the tree-stratum was largely independent of patterns of damage in the Silver Fire. Early successional pathways in the Klamath-Siskiyou region are characterized by aggressive colonization of sprouting hardwoods and shrubs (Hobbs et al. 1992; Stuart et al. 1993), and although conifers will eventually succeed (Shatford et al. 2007), the period during which most live biomass remains in the shrub-stratum may be protracted over several decades. Shrub-stratum vegetation is available to surface fires and, depending on the species composition, can be associated with flashy and sometimes intense fire (Anderson 1982; Weatherspoon and Skinner 1995). As such, it not surprising that areas that burned severely in the Silver Fire and were characterized by a dominant shrub layer, re-burned severely in the Biscuit Fire. In contrast, the areas that retained large conifers through the Silver Fire were the areas that had the lowest levels of damage during the Biscuit Fire (Fig. 6).

Absolute (as opposed to relative) tree crown damage of hardwoods and conifers was highest in areas that burned with low levels of crown damage during the Silver Fire (Fig. 3). This simply reflects the fact that areas that did not experience crown fire in the Silver Fire still had trees canopies available to burn in the Biscuit Fire. Damage in the tree-stratum relative to pre-fire abundance was related primarily to weather and burn period. Interestingly, Silver Fire crown damage was not an important predictor of Biscuit Fire relative tree crown damage, further suggesting that the legacy of the Silver Fire was limited to the severely burned patches.

Results of this study suggest that the mosaic of crown damage in these productive, fire-prone forests can influence future burn mosaics. Once an area experiences a stand replacing burn, it can be caught within a positive feedback of repeated severe fires. Lightning strikes are ubiquitous in this region, and can ignite wildfires that repeatedly reset succession, resulting in enduring shrub-fields (Agee 1993). After each burn, shrubs, hardwoods, and conifers regenerate vigorously, setting the stage for the next severe burn. Clearly, this cycle does not continue indefinitely, as is evidenced by abundant old-growth forests that were present in this landscape before the recent fires. Periodically, the fire-free interval must be sufficiently long to allow a tree stratum to develop. This relatively fire-resistant patch type would be characterized by dense tree canopies that suppress shrub fuel ladders, increasing heights to the base of the canopies and larger bole diameters that are progressively more resistant to fire over time. This comparatively fire-resistant patch type may endure until a high intensity fire, such as the Biscuit Fire, shifts the vegetation back to an early-seral condition.

Relationship between crown damage and post-fire management

Shrub-stratum vegetation experienced high rates of crown mortality throughout the reburn area regardless of management history. Median crown damage was five-percent higher in areas that had been logged and planted after burning severely in the Silver Fire. The direction of this effect was consistent with Thompson et al. (2007), in that the managed stands burned more completely than comparable unmanaged stands. However, the magnitude of difference was much lower in the present study (5% difference in crown damage versus a 16–61% difference in dNBR). The reason for the difference may be due to the fact that maximum dNBR is not reached at 100% crown damage (Lutes et al. 2004; Miller and Thode 2007). Or, it may be because dNBR is a synthetic measure of multiple fire effects, and while it is primarily related to crown damage, it also corresponds to changes in soil moisture and color, ash color and content, and consumption of down wood (Lutes et al. 2004). The Biscuit Fire resulted in sharp reductions in mineral soil and changes in soil structure (Bormann et al. 2008) that may have been represented by the dNBR measure. In this respect, two estimates simply measure different aspects of "fire severity," a term that often means different things to different people (Jain et al. 2004). The difference in *crown damage*—a far more interpretable, though still imperfect, measure of fire effects—between the managed and unmanaged stands was small, and the degree to which this difference might affect subsequent ecological processes is unknown. It may make no difference, whatsoever. Or, the small initial differences in heterogeneity of shrubs and trees could affect longer term successional pathways and structural diversity. Plantations that were consumed by the Biscuit Fire were immediately replanted by managers (RSNF 2004). If these areas had not been replanted, it seems likely that their successional trajectories would be distinct from the high severity burned areas that had pre-fire abundance of sprouting shrubs and trees.

The RFA analysis ranked the predictor variable for management above the predictor describing the cover of pre-fire shrub-stratum vegetation. In contrast, RTA included pre-fire vegetation—but not management history—as a partition in the tree. This difference illustrates the strengths and weaknesses of the two approaches. The importance ranking from RFA indicates that, all other predictors being held constant, the management history explained more variability than did the level of pre-fire shrub-stratum cover. In contrast, interpretation of each node in the regression tree is conditional on the nodes above it. In our analysis, pre-fire vegetation cover is included as a split in the tree, only after accounting for topographic position. Further, RTA selects the best possible partition, but, unlike RFA, offers no information regarding other variables that may have reduced deviance almost as much as the chosen variable. Indeed, when we re-ran the RTA without the pre-fire cover variable, the indicator for management entered as a significant variable on the same branch of the regression tree with $P = 0.026$.

Our analyses suggest that the difference in crown damage between managed and unmanaged stands was related to topographic position and pre-fire vegetation cover. Although Thompson et al. (2007) controlled for topographic position within a regression framework, they were not able to adequately account for pre-fire cover. Higher cover in managed stands was presumably a result of planting. Young, evenly-spaced dense conifers have been hypothesized to have fuel properties more conducive to fire spread than shrubs and young broadleaf hardwoods (Perry 1994), but we are aware of no empirical research that supports or refutes this. However, several studies have documented high burn severity within conifer plantations (Weatherspoon and Skinner 1995; Odion et al. 2004; Roloff et al. 2004), particularly when young (Graham 2003; Stephens and Moghaddas 2005).

Conclusions

Our analysis extends beyond Thompson et al. (2007), who used a synthetic metric of burn "severity" (Landsat-based dNBR) and focused on two narrow questions (Q1: First, was severity in the Biscuit Fire associated with severity in the Silver Fire in unmanaged areas? Q2: Did areas that were salvage-logged and planted with conifers after the Silver Fire burn more or less severely in the Biscuit Fire than comparable unmanaged areas?) By interpreting changes in vegetation cover through a time series of aerial photos, we were able to learn more about the ecological relationships that were uncovered in the first study that used only satellite imagery. We found that areas that burned severely in the 1987 Silver Fire reburned severely in the 2002 Biscuit Fire, but that these areas contained primarily shrub-stratum vegetation. Relative damage within the tree stratum was largely independent of the legacy of the Silver Fire. Areas that were salvage logged and planted after the Silver Fire experienced high rates of crown damage during the Biscuit Fire. The plantations had somewhat higher vegetation cover than the unmanaged stands, suggesting that higher live and dead fuel continuity in plantations may play a role creating more flammable vegetation types. Additional research is clearly needed to judge if these findings are generalizable to other mixed-severity reburns and to quantify the differences in reburn severity with longer and shorter intervals between fires.

The Biscuit Fire burned more than 75% of the overstory on almost 100,000 ha across the RSNF (Thompson and Spies 2009). In the short term (10–20 years), managers may not be able to reduce the likelihood of recurring high severity fire in these cover types through traditional silvicultural practices. Our findings suggest that the type of post-fire management practiced after the Silver Fire did not reduce fire hazard at 15 years and may increase it compared to early-seral unmanaged areas. Research done elsewhere within the Biscuit Fire has shown that thinning in mature (90- to 120-year-old) green forests followed by prescribed fire can be an effective way to reduce fire severity in the first few years after treatment, but that thinning without treating logging slash can increase severity compared with unmanaged stands (Raymond and Peterson 2005). Managers may consider strategically placing thinning and burning treatments in configurations that might slow the spread of future fires enabling protection of key structures and habitat conditions (e.g. spotted owl habitat areas) with the landscape (RSNF 2004; Ager et al. 2007).

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