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Management and Conservation

Relationship Between Wildfire, Salvage Logging, and Occupancy of Nesting Territories by Northern Spotted Owls

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ABSTRACT The northern spotted owl (*Strix occidentalis caurina*) is one of the most intensively studied raptors in the world; however, little is known about the impacts of wildfire on the subspecies and how they use recently burned areas. Three large-scale wildfires in southwest Oregon provided an opportunity to investigate the short-term impacts of wildfire and salvage logging on site occupancy of spotted owls. We used Program MARK to develop single-species, multiple-season models of site occupancy using data collected during demographic surveys of spotted owl territories. In our first analysis, we compared occupancy dynamics of spotted owl nesting territories before (1992–2002) and after the Timbered Rock burn (2003–2006) to a reference area in the south Cascade Mountains that was not affected recently by wildfire. We found that the South Cascades had greater colonization probabilities than Timbered Rock before and after wildfire ($\hat{\beta} = 1.31$, 95% CI = 0.60–2.03), and colonization probabilities declined over time at both areas ($\hat{\beta} = -0.06$, 95% CI = -0.12 to 0.00). Extinction probabilities were greater at South Cascades than at Timbered Rock prior to the burn ($\hat{\beta} = 0.69$, 95% CI = 0.23–2.62); however, Timbered Rock had greater extinction probabilities following wildfire ($\hat{\beta} = 1.46$, 95% CI = 0.29–2.62). The Timbered Rock and South Cascades study areas had similar patterns in site occupancy prior to the Timbered Rock burn (1992–2001). Furthermore, Timbered Rock had a 64% reduction in site occupancy following wildfire (2003–2006) in contrast to a 25% reduction in site occupancy at South Cascades during the same time period. This suggested that the combined effects of habitat disturbances due to wildfire and subsequent salvage logging on private lands negatively affected site occupancy by spotted owls. In our second analysis, we investigated the relationship between wildfire, salvage logging, and occupancy of spotted owl territories at the Biscuit, Quartz, and Timbered Rock burns from 2003 to 2006. Extinction probabilities increased as the combined area of early seral forests, high severity burn, and salvage logging increased within the core nesting areas ($\hat{\beta} = 1.88$, 95% CI = 0.10–3.66). We were unable to identify any relationships between initial occupancy or colonization probabilities and the habitat covariates that we considered in our analysis where the β coefficient did not overlap zero. We concluded that site occupancy of spotted owl nesting territories declined in the short-term following wildfire, and habitat modification and loss due to past timber harvest, high severity fire, and salvage logging jointly contributed to declines in site occupancy.

KEY WORDS colonization, extinction, northern spotted owl, occupancy, salvage logging, site occupancy, southwest Oregon, *Strix occidentalis caurina*, wildfire.

Northern spotted owls (*Strix occidentalis caurina*, hereafter spotted owl) are a medium sized, forest-dwelling owl with high levels of mate and site fidelity (Forsman et al. 1984, 2002; Thomas et al. 1990; Zimmerman et al. 2007). Nesting territories of spotted owls have greater proportions of mature and older forest than surrounding landscapes (Ripple et al. 1991, 1997; Meyer et al. 1998; Swindle et al. 1999). Forest stands used by spotted owls have large proportions of downed woody debris and snags, high canopy cover and high structural diversity (Hershey et al. 1998, North et al. 1999, Irwin et al. 2000). The features that provide structural complexity within spotted owl habitat also serve as ladder fuels that increase the likelihood of stand-replacing wildfire (Agee 1993, Wright and Agee 2004). As a result, forest stands that provide favorable habitat conditions for spotted owls within dry forest ecosystems are at risk of stand-replacing wildfire (Agee 1993, Agee et al. 2000). Presently, wildfire is the leading cause of spotted owl habitat modification on

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federally administered lands, and the rate of habitat modification due to wildfire within dry forest ecosystems has exceeded predictions (Davis and Lint 2005). Consequently, the viability of owl populations in dry forests has been questioned (Spies et al. 2006), and wildfire has been identified as a threat to the persistence of spotted owls occupying dry forest ecosystems (U.S. Fish and Wildlife Service [USFWS] 2011).

Despite the perceived threat of wildfire, little is known about the effects of wildfire on spotted owls, and the hypothesized effects come from research conducted in unburned landscapes. Numerous studies have documented that spotted owl survival, reproduction (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005), and territory occupancy (Blakesley et al. 2005, Dugger et al. 2011) were positively associated with increased amounts of late-successional forest within their core use areas or home range. Furthermore, owl territories with large reductions in the amount of older forest will have low reproduction or be abandoned (Bart and Forsman 1992, Bart 1995). These studies suggest that loss of older forests negatively affects spotted owls; however, the response of spotted owls to high severity fire and subsequent harvest of dead standing trees is unknown. Conversely, survival rates of spotted owls were greater at territories that were not entirely composed of late-successional forests (Franklin et al. 2000, Olson et al. 2004), which suggests that spotted owls may be adapted to natural disturbances such as wildfire that create a mosaic of forest conditions. Territory occupancy and nest success of spotted owls decreased as the amount of the territory composed of clear-cuts increased (Thraillkill et al. 1998), which suggests widespread post-fire salvage logging may negatively affect spotted owls.

The few studies that have been conducted on spotted owls in burned landscapes have provided equivocal results regarding the effects of wildfire on the species. Lack of consensus between studies may be owing to the confounding effects of salvage logging, the short-term nature of studies, small sample sizes from which to draw inference, treating the effect of fire as a binomial variable (i.e., burned or unburned), or potentially different responses of the 3 subspecies of spotted owls to wildfire. Radio-marked northern and California spotted owls (*Strix occidentalis occidentalis*) used forest stands that burned with low to high severities (Clark 2007, Bond et al. 2009); however, survival rates of radio-marked northern spotted owls occupying a burned area that was subsequently salvage logged were less than others reported throughout the subspecies' range (Clark et al. 2011). Conversely, short-term (<1 yr) survival rates of northern, Mexican (*Strix occidentalis lucida*), and California spotted owls in burned landscapes that were not subjected to post-fire salvage logging were similar to annual survival rates (Bond et al. 2002). The number of reproductive spotted owl pairs and the number of occupied spotted owl territories declined 1 year post-fire on the eastern slope of the Washington Cascade Range (Gaines et al. 1997); however, only 6 territories were surveyed in this study, 1 of which had a large amount of stand-replacing fire. Other studies indicate low and moderate severity burns may have minimal impacts on spotted owls. Territory occupancy of Mexican spotted owls in burned areas was similar to unburned areas (Jenness et al. 2004). Probability of territory occupancy for California spotted owls in the Sierra Nevada Mountains of California were similar between randomly selected burned and unburned sites (Roberts et al. 2011).

Because spotted owls are territorial and have high site fidelity (Forsman et al. 2002, Zimmerman et al. 2007), occupancy of nesting territories is essential for successful survival and reproduction. Occupancy models (MacKenzie et al. 2003, 2006) are well suited for investigating territory occupancy by spotted owls because the structure of existing spotted owl surveys (Franklin et al. 1996) fits the model framework well. Furthermore, occupancy models allow the inclusion of site-specific covariates, which allows the investigation of fire severity and habitat influences on site occupancy dynamics (i.e., extinction and colonization rates). The Biscuit, Quartz, and Timbered Rock burns in southwest Oregon provided an opportunity to investigate the impacts of wildfire and subsequent salvage logging on site occupancy by spotted owls. Our first objective was to determine if occupancy rates changed substantially following wildfire and subsequent salvage logging when compared to pre-burn occupancy rates and to occupancy rates in a landscape that had not been recently affected by wildfire. We met this objective by comparing occupancy rates of spotted owls before (1992–2002) and after (2003–2006) the Timbered Rock burn to an adjacent unburned landscape in the southern Oregon Cascades. We predicted that occupancy rates of spotted owls would be similar between study areas prior to the Timbered Rock burn but occupancy rates would decline substantially following the Timbered Rock burn in response to modification and loss of owl habitat from wildfire and subsequent salvage logging. Our second objective was to model the impacts of fire severity, salvage logging, and habitat characteristics on site occupancy of spotted owls at the Biscuit, Quartz, and Timbered Rock burns from 2003 to 2006. We predicted that extinction probabilities would increase as the amounts of past timber harvest, high severity burn, and salvage logging within a territory increased. We also predicted that initial occupancy and colonization probabilities within the 3 burned areas would be greater at territories with decreased levels of disturbance. In particular, we predicted that initial occupancy and colonization probabilities within the 3 burned areas would be greater at territories that had more intermediate-aged and older forest that burned with low or moderate severities.

STUDY AREA

We studied site occupancy by spotted owls at the Biscuit, Quartz, and Timbered Rock burns in southwest Oregon. Each burn was located within a distinct geographic region: the mid-Coastal Siskiyou Mountains (Biscuit burn), the Siskiyou Mountains (Quartz burn), and the southern Oregon Cascades (Timbered Rock burn). We also analyzed site occupancy of spotted owls at the South Cascades Demographic Study Area, which was adjacent to the

Timbered Rock burn and was not affected by a large scale wildfire within the last 100 years. Consequently, site occupancy by spotted owls in this area served as a reference for comparison to the Timbered Rock study area.

Common tree species within our study areas included ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), California red fir (*A. magnifica)*, mountain hemlock (*Tsuga mertensiana*), Oregon white oak (*Quercus garryana*), California black oak (*Q. kelloggii*), tanoak (*Lithocarpus densiflorus*), and Pacific madrone (*Arbutus menziesii*). Prior to the implementation of active fire suppression policies by state and federal agencies, most of southwest Oregon was characterized by frequent low-intensity fires and occasional stand-replacing fires at higher elevations (Agee 1993, Taylor and Skinner 1997, Heyerdahl et al. 2001). After active fire suppression policies were implemented, fire frequencies declined and high-intensity wildfires became more common (Agee 1993, Agee and Skinner 2005). The climate regime in southwest Oregon is characteristically temperate with hot, dry summers and cool, moist winters. During our study, the warmest and coldest average daily temperatures occurred in July (21° C) and December (4° C), respectively. Average annual rainfall was lowest at the Quartz burn (66 cm) and highest at the Biscuit burn (113 cm; Oregon Climate Service, Oregon State University, unpublished data).

The Biscuit burn originated from several lightning strikes in July 2002. The small fires eventually merged into a complex fire that covered 201,436 ha. Land ownership within the burn was predominantly public (U.S. Forest Service [USFS], Bureau of Land Management [BLM], Oregon Department of Forestry [ODF], and Josephine County). Fifty documented spotted owl territories were within the burn. We non-randomly selected a sample of 9 territories on the eastern side of the burn to include in our study that were similar to forest types at the Timbered Rock and Quartz burns and provided reasonable access. The 9 territories included in this study were located within the Briggs Creek, Silver Creek, Deer Creek, and Illinois River watersheds, ranging in elevation from 300 to 1,400 m. The remaining 41 territories were not included in our study because of logistical concerns or because they were located in mesic forest types on the western side of the burn. The 9 study territories were surveyed annually from 2003 to 2006. The area within 2.2 km of the 9 study territories burned with a mixed severity and received the least amount of salvage logging of the 3 burns (Table 1).

The Quartz burn was ignited by lightning in August 2001 and burned 2,484 ha of public (USFS, BLM, and ODF) and private (primarily industrial forest) lands. The fire burned portions of the Glade Creek, Little Applegate, and Yale Creek watersheds at elevations ranging from 600 to 1,850 m. The fire completely or partially burned (i.e., burned the majority of a 2.2-km buffer around the territory center) 9 spotted owl territories. All 9 territories were surveyed annually from 2003 to 2006. The study area burned with a mosaic of fire severities and was subjected to substantial amounts of salvage logging, primarily on private lands (Table 1).

The Timbered Rock burn was ignited by lightning in July 2002 and burned 11,028 ha of land within the Elk Creek watershed at elevations ranging from 450 to 1,350 m. Land ownership was dominated by a checkerboard pattern of public (BLM) and private industrial forest lands in the southern two-thirds of the burn and contiguous USFS managed lands in the northern third. Twenty-two spotted owl territories were within the burn perimeter and were surveyed annually from 2003 to 2006. These 22 territories were also surveyed prior to the burn from 1992 to 2002. The study area burned with a mixed severity and much of the private land was salvage logged (Table 1).

The South Cascades Demographic Study Area (South Cascades) is 1 of 8 study areas included in the range-wide monitoring program for spotted owls (Lint et al. 1999, Anthony et al. 2006), and it served as a reference area for our analyses. From 1992 to 2006, surveys to locate spotted owls were consistently conducted on an annual basis at 103 spotted owl territories by the Oregon Cooperative Fish and Wildlife Research Unit (OCFWRU). The South Cascades area encompasses approximately 223,000 ha of lands managed by the USFS at the southern terminus of the Oregon Cascades and at elevations ranging from 900 to 2,000 m. No large-scale wildfires occurred within the study area from 1992 to 2006. Forest conditions have been influenced historically by mixed-severity wildfire and more recently by forest management, livestock grazing, and fire suppression. Forest management has included individual tree selection, stand thinning, and even-aged management (U.S. Department of Agriculture [USDA] 1997, 1998). Current management activities are guided by the objectives set forth by the Land-use Allocations of the Northwest Forest Plan.

Table 1. The percentage (±SE) early seral, intermediate-aged or older forest that burned with a low, moderate, or high severity or was salvage logged within 2,230 m of 40 northern spotted owl territories at the Biscuit, Quartz, and Timbered Rock burns in southwest, Oregon, USA from 2003 to 2006.

		Intermediate-aged or older forests			
Study area	**Non-forest or early seral**	**Low severity**[a]	**Moderate severity**[b]	**High severity**[c]	**Salvage logged**[d]
Biscuit	27.2 ± 6.1	40.5 ± 6.7	13.6 ± 1.8	17.1 ± 3.6	1.6 ± 0.7
Timbered Rock	27.8 ± 1.6	35.9 ± 4.1	10.1 ± 0.7	9.3 ± 1.4	16.9 ± 3.2
Quartz	21.7 ± 1.5	48.5 ± 4.4	6.6 ± 1.5	10.0 ± 2.3	13.2 ± 2.7

[a] ≤20% of the forest canopy removed by wildfire.
[b] 21–70% of the forest canopy removed by wildfire.
[c] >70% of the forest canopy removed by wildfire.
[d] Areas that were intermediate-aged or older forest prior to the burn that were salvage logged.

The main purpose of matrix lands is timber production, whereas the late-succesional reserves are for conservation of older forests and silvicultural treatments are intended to promote forest stand structures similar to historical conditions or old forest characteristics (USDA and U.S. Department of the Interior [USDI] 1994).

METHODS

Data Acquisition and Preparation

To assess the effects of wildfire on occupancy of spotted owl territories, we created post-fire habitat maps in ArcGIS 9.1 (ESRI, Redlands, CA) by merging 3 data layers: 1) a pre-fire habitat map (Davis and Lint 2005), 2) a fire severity map, and 3) the boundaries of salvage logged areas (see Clark 2007 for additional details). The final map output had 8 distinct habitat classes (Table 2) and a minimum mapping unit of 2 ha. We used ground plot data to calculate map accuracies, which we estimated to be 68% for the Timbered Rock burn, 69% for the Biscuit burn, and 75% for the Quartz burn. Seventeen of 20 (85%) classification errors at the Biscuit burn, 10 of 15 (67%) at the Quartz burn, and 11 of 22 (50%) at the Timbered Rock burn were within 1 habitat or fire severity class of the correct classification. Based on these estimates, overall map accuracy within 1 habitat or fire severity class was 95% at the Biscuit burn, 92% at the Quartz burn, and 84% at the Timbered Rock burn (Clark 2007).

We conducted annual surveys between 1 March and 31 August to determine the occupancy of spotted owls on nesting territories according to established survey protocols (Franklin et al. 1996) and Oregon State University, Institutional Animal Care and Use Committee guidelines (IACUC Number 3040). Post-fire surveys were conducted as a collaborative effort between the OCFWRU, the BLM, the USFS, and private timber companies. From 1992 to 2006, we surveyed 22 and 103 territories at the Timbered Rock and South Cascades study areas, respectively. We also surveyed 9 territories at both the Biscuit and Quartz burns from 2003 to 2006. The average number of visits conducted varied by study area and year (range: 1.9 [Timbered Rock 2002]–5.8 [Timbered Rock 1994]). The maximum number of surveys at individual spotted owl territories ranged from 7 to 9 depending on the year. The variability in survey effort was a function of occupancy and nesting status (i.e., territories that were occupied by a pair of non-nesting owls were visited less). Occasionally, some territories were not surveyed every year, which was most often because of limited access during years of high snowfall. Fortunately, differences in survey effort and missing observations can easily be accounted for in open population models if you assume that occupancy dynamics are the same at territories that are and are not surveyed (MacKenzie et al. 2006), which is a reasonable assumption as long as survey effort is unbiased.

We used results from demographic surveys to create site-specific detection histories for owl pairs. Owl pairs represent the appropriate ecological unit of interest when modeling site occupancy. Protocols for adapting survey data from spotted owls using methods outlined in Franklin et al. (1996) to fit an occupancy modeling framework were established by Olson et al. (2005). These protocols were used in subsequent occupancy analyses for spotted owls (Kroll et al. 2010, Dugger et al. 2011) and this analysis. If a pair of owls was detected, we coded the visit as a 1 and if 1 or no owls were detected, we coded the visit as a 0. However, if 1 owl was detected and the owl exhibited nesting behavior (e.g., the owl was observed on a nest) or if young were observed with an adult owl, we coded the visit as a 1. If a survey was not conducted, we coded the visit as a missing observation (·). A hypothetical detection history of 10.1 would indicate that a pair of owls was detected on the first and fourth surveys, no owls or a single owl was detected on the second survey, and the territory was not visited during the third survey.

Data Analyses

Basic modeling procedures.—We estimated site occupancy in Program MARK (White and Burnham 1999) using single-species, multiple-season models (MacKenzie et al. 2003, 2006). This analysis generated estimates of 4 parameters: Ψ, the probability that a site is occupied in the first year of the study (initial occupancy); ε, the probability an occupied site became unoccupied the subsequent year (extinction); γ, the probability an unoccupied site was occupied the subsequent year (colonization); and P, the probability of detection (detection). In our analyses, primary sampling occasions were years and secondary sampling occasions were visits to

Table 2. Definitions of habitats used in the assessment of the impacts of wildfire and salvage logging on northern spotted owl site occupancy at the Biscuit, Quartz, and Timbered Rock burns in southwest Oregon, USA, from 2003 to 2006.

Habitat class	Description
Early seral	Non-forested areas, early seral, and pole sized conifer stands
Intermediate forest[a]—low severity burn	Intermediate-aged conifer stands with ≤20% of the canopy removed by fire
Intermediate forest—moderate severity burn	Intermediate-aged conifer stands with 21–70% of the canopy removed by fire
Older forest[b]—low severity burn	Older conifer forest with ≤20% of the canopy removed by fire
Older forest—moderate severity burn	Older conifer forest with 21–70% of the canopy removed by fire
High severity	Intermediate-aged and older conifer forests with >70% of the canopy removed by fire
Salvage	Intermediate-aged and older conifer forests that were salvage logged
Edge	The interface between the combined area of intermediate-aged and older forest that burned with a low or moderate severity and all other habitat types

[a] Forest stands that provide suitable roosting and foraging habitat for spotted owls.
[b] Forest stands that provide nesting habitat for spotted owls.

territories within years. This modeling framework was flexible and allowed for time-specific parameter estimates, inclusion of site-specific covariates, the ability to include missing observations, the direct estimation of colonization and extinction, and it assumed detection probabilities were <1 (MacKenzie et al. 2003, 2006).

We modeled the 4 occupancy parameters using a step-wise approach (Olson et al. 2005, MacKenzie et al. 2006, Dugger et al. 2011). We first determined the most parsimonious model for within year detection probabilities followed by among year detection probabilities, retained that model, and then proceeded to model initial occupancy. We then retained the most parsimonious model for initial occupancy and proceeded to model colonization and extinction parameters. We followed the conventions of Lebreton et al. (1992) and White and Burnham (1999) when developing and naming models. We considered several possible temporal effects on detection probabilities both within and among years that included constant detection (·), linear (T), log-linear (ln T), and quadratic (TT) trends. We did not evaluate time-specific models (t) within years because they required estimation of too many parameters to obtain reasonable estimates (Olson et al. 2005); however, we considered models that included time-specific effects among years (year). We also considered models that included differences in detection probabilities between study areas, because experience and effort of survey personnel may have differed. We considered 2 initial occupancy models that contrasted differences between study areas (area) and constant initial occupancy (·). When modeling extinction and colonization parameters, we considered models that compared differences between study areas (area) and no differences between areas (·), and we considered several biologically plausible temporal effects including constant rates among years (·), variable rates among years (t), and linear (T), log-linear (ln T), and quadratic (TT) trends over time. Models that included $\geq$2 study areas included additive and interactive effects between study area and temporal effects, where appropriate.

We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) and the difference between the AIC_c value of the best model and the ith model (ΔAIC_c) to rank and compare candidate models at each step of the analysis. We used Akaike weights to evaluate the strength of evidence for 1 model versus another model (Burnham and Anderson 2002). We considered models that were $\leq$2.0 AIC_c of the best model as competitive. We used estimates of regression coefficients ($\hat{\beta}$) and their 95% confidence intervals to evaluate the relative effect and measure of precision of various covariates in our models. Following the approach outlined by Anthony et al. (2006), we used 95% confidence intervals for the coefficients as a relative measure of support for observed relationships rather than a strict test of the hypothesis that $\beta = 0$. Covariates whose 95% confidence intervals did not overlap 0 had strong evidence for an effect, those that narrowly overlapped 0 had some evidence for an effect, and those that broadly overlapped 0 had little or no evidence for an effect on the parameter of interest. We used this approach because significance testing is not valid under an information theoretical approach (Burnham and Anderson 2002), and it is best to present estimates of effect size and precision under this analysis paradigm (Anderson et al. 2000).

Comparison of South Cascades and Timbered Rock.—We compared occupancy at Timbered Rock and South Cascades from 1992 to 2006. Our objective was to determine if extinction and colonization probabilities following the Timbered Rock burn were different from unburned landscapes in the South Cascades (i.e., the control) during the same time period. In this analysis, we considered all study area and temporal effects on site occupancy parameters that are outlined above in the basic modeling procedures. In addition, we considered 10 models for colonization and extinction that were modifications of common study area and time effect models (Fig. 1). We considered these models because they may identify distinct changes in extinction and colonization rates following a disturbance such as wildfire and subsequent salvage logging. We predicted that under model [Pre-burn(·)Post-burn(area)] the South Cascades and Timbered Rock would have similar, constant extinction probabilities prior to the Timbered Rock burn, but extinction probabilities would be greater at Timbered Rock following the burn. In contrast, we predicted the opposite for colonization probabilities (e.g., under model [Pre-burn(·)Post-burn(area)], colonization rates would be equal at Timbered Rock and South Cascades prior to the Timbered Rock burn, but colonization rates would be less at the Timbered Rock study area following the burn). We retained the best ranked initial occupancy, extinction, colonization, and detection probability models and combined them to determine our best overall model. We used the best overall model to calculate estimates of year-specific probabilities of site occupancy in Program MARK using the equation from MacKenzie et al. (2003):

$$\hat{\Psi}_t = \hat{\Psi}_{t-1}(1 - \hat{\varepsilon}_{t-1}) + (1 - \hat{\Psi}_{t-1})\hat{\gamma}_{t-1}$$

Relationship between wildfire, salvage logging, and spotted owl site occupancy.—We modeled occupancy of nesting territories after fires from 2003 to 2006 at the Biscuit, Quartz, and Timbered Rock burns. Our objective was to model the potential influence of fire severity, salvage logging, and habitat covariates on site occupancy of spotted owls. In this analysis, we used a multiple step approach outlined in previous occupancy analyses for the species (Olson et al. 2005, Dugger et al. 2011). This approach included 3 steps: 1) determine the occupancy model that best described temporal and study area effects, 2) retain the best model from step 1 and model individual covariates to determine the best spatial scale and relationship of the covariate, and 3) retain the best model from step 1 and the best spatial scale and relationship of covariates from step 2 to test specific hypotheses regarding the effects of covariates on site occupancy.

Our first step was to determine the best model that only included study area and temporal effects by following the methods outlined in the basic modeling procedures. Our objective in this step was to develop a base model upon

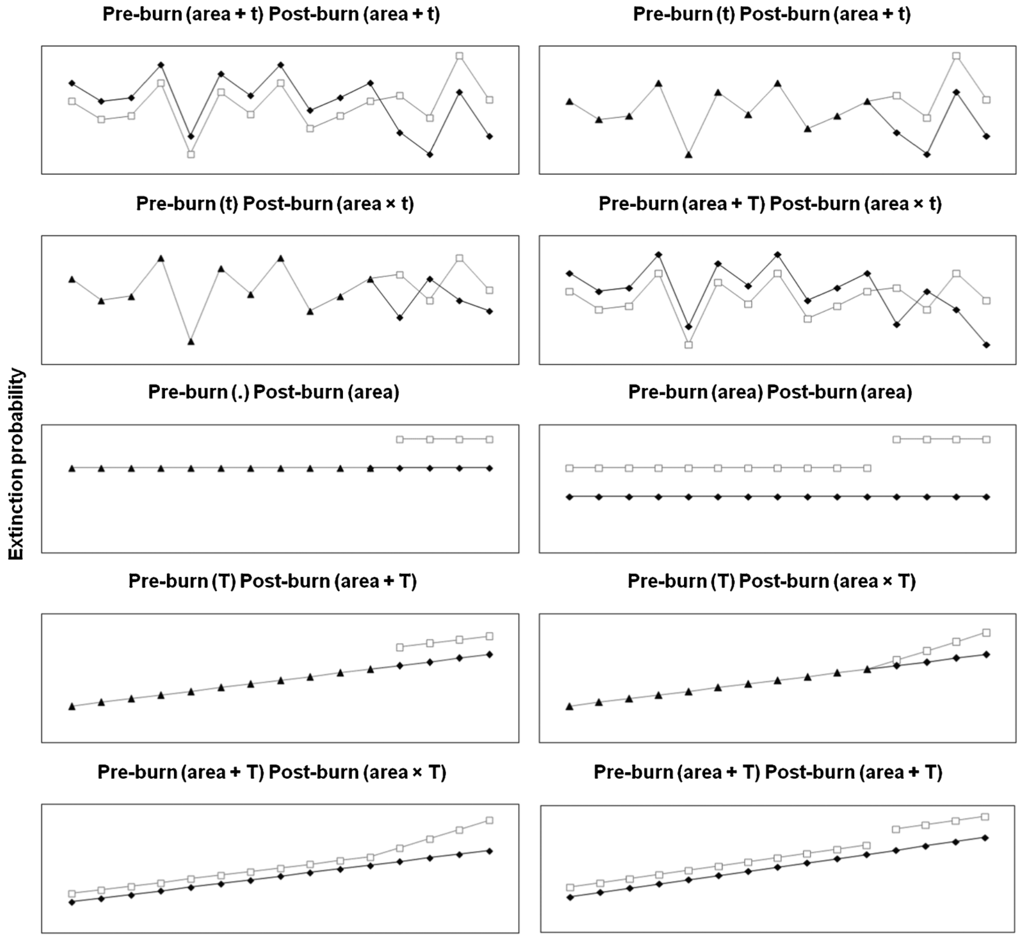

Figure 1. Visual representation of 10 hypothetical models comparing extinction rates of northern spotted owl territories at the Timbered Rock burn and South Cascades Demographic Study Area. We considered models that compared differences between study areas (area) and no differences between areas (·), and we considered several biologically plausible temporal effects including constant rates among years (·), variable rates among years (*t*), and linear (*T*) trends over time. The last 4 intervals represent the predicted changes in extinction probabilities following the Timbered Rock burn. The opposite relationship was predicted for colonization rates. Grey lines with open boxes represent the Timbered Rock study area, black lines with black diamonds represent the South Cascades Demographic Study Area, and gray lines with black triangles represent no differences between study areas.

which we modeled the effects of covariates. We considered all models outlined in the basic modeling procedures and 3 additional study area covariates for initial occupancy, extinction, and colonization models that incorporated various study area combinations including, 1) the Quartz and Timbered Rock burns would have similar occupancy dynamics because they include large amounts of private land (BIS ≠ TR = Q), 2) the Timbered Rock and Biscuit burns would have similar occupancy dynamics because they occurred 1 year after the Quartz burn (BIS = TR ≠ Q), and 3) the Quartz and Biscuit burns would have similar occupancy dynamics because they are both located in the Siskiyou Mountains (BIS = Q ≠ TR). Our primary objective during this portion of the analysis was to develop a parsimonious model on which to model covariates; consequently, we did not consider competing models in this step of the analysis. After determining the best study area and temporal effects model, we retained this model and proceeded to the second step of the analysis.

In the second step of this analysis, our objective was to determine the spatial scale and relationship that best explained the effect of various covariates on initial occupancy, extinction, and colonization probabilities. We calculated site-specific covariates at 2 spatial scales (territory and core area) and with 2 relationships (linear and log-linear), which represented 4 possible models for each covariate. We calculated covariate values in ArcGIS 9.1 from post-fire habitat maps as the percent of each cover type within a 2,230-m radius (1,560 ha; territory scale) and a 730-m radius (167 ha; core area scale) of the territory center. We selected these spatial scales because they were used to model spotted owl survival and reproduction in the same geographic region (Dugger et al. 2005).

For initial occupancy and colonization probabilities, we modeled 9 covariates (Table 3) to determine the best spatial scale and relationship of the covariate. All of the covariates we modeled on initial occupancy and colonization parameters were thought to represent the quality of habitat remaining at the territory and were based on biologically meaningful relationships. Forested areas that burned with a low or moderate severity likely had minimal changes in the amount of canopy cover, snags, and downed woody debris, which are

Table 3. Candidate model sets for initial occupancy, extinction, and colonization parameters in the analysis of covariate effects on site occupancy of northern spotted owls at the Biscuit, Quartz, and Timbered Rock burns in southwest Oregon, USA, from 2003 to 2006.

Initial occupancy (Ψ) and colonization (γ)[a]	Extinction (ε)[b]
INTL + INTM + OLDL + OLDM	EARLY + HIGH + SALVAGE
INTL + OLDL	HIGH + SALVAGE
INT + OLD	HARVEST + HIGH
OLDL + OLDM	EARLY + HISALV
OLDL	HISALV
OLD	HARVEST
LOW + MOD	SALVAGE
LOW	HIGH
EDGE	EARHISALV
	EDGE

[a] INTL, intermediate-aged forest that burned with a low severity; INTM, intermediate-aged forest that burned with a moderate severity; OLDL, older forest that burned with a low severity; OLDM, older forest that burned with a moderate severity; INT, intermediate-aged forest that burned with a low or moderate severity (combined area of INTL and INTM); OLD, older forest that burned with a low or moderate severity (combined area of OLDL and OLDM); LOW, intermediate-aged and older forest that burned with a low severity (combined area of INTL and OLDL); MOD, intermediate-aged and older forest that burned with a moderate severity (combined area of INTM and OLDM); EDGE, the interface between forested areas that burned with low or moderate severity and areas that were early seral stands, burned with high severity, or were salvage logged; EDGE was modeled as an additive effect with the best ranked covariate model to determine if it improved model fit.

[b] EARLY, non-forested areas early seral stands that burned with any severity; HIGH, the combined area of intermediate-aged and older forest that burned with a high severity; SALVAGE, any intermediate-aged or older forest that was salvage logged; HARVEST, any forested area, that was harvested before or after the burn (combined area of EARLY and SALVAGE); HISALV, any forested area, excluding early stands, that burned with a high severity or was salvage logged (combined area of HIGH and SALVAGE); EARHISALV, any early seral stand or forested area that burned with high severity or that was salvage logged (combined area of EARLY, HIGH, and SALVAGE).

all critical components of spotted owl habitat (Hershey et al. 1998, North et al. 1999, Irwin et al. 2000). Intermediate-aged forests contribute to landscape heterogeneity, which influenced spotted owl survival in other studies (Franklin et al. 2000, Olson et al. 2004), so we hypothesized that it would also influence site occupancy by the subspecies. Spotted owl territories usually have high proportions of mature and older forests (Ripple et al. 1991, 1997; Meyer et al. 1998; Swindle et al. 1999), so we expected that initial occupancy and colonization probabilities would be influenced by the amount of older forest within the territory.

We elected to use a different set of covariates on extinction probabilities because of the highly correlated nature of extinction and colonization probabilities (MacKenzie et al. 2006). Modeling the same set of covariates on extinction and colonization parameters can result in counter-intuitive results. This is because sites that went extinct are the sites available for colonization. As a result, factors that contribute to increased extinction probabilities could also contribute to increased colonization probabilities. For extinction models, we modeled 7 covariates (Table 3) to determine the best spatial scale and relationship of the covariate. All of the covariates considered for extinction were thought to be related to the impacts of habitat loss and modification attributable to past timber harvest, high severity fire, and salvage logging. We hypothesized that all 3 of these factors would negatively affect site occupancy. Spotted owl territories that had increased amounts of clear-cut timber harvest had decreased occupancy (Thrailkill et al. 1998). Timber harvest and post-fire salvage commonly results in large-scale clear-cuts; as a result, site occupancy by owls should be negatively affected by these factors. High severity fire removes downed woody debris and reduces canopy cover and structural diversity. All of these factors influence spotted owl habitat selection (Hershey et al. 1998, North et al. 1999, Irwin et al. 2000), so we hypothesized that increased amounts of high severity fire may increase extinction probabilities.

We considered the effects of the amount of edge habitat on initial occupancy, extinction, and colonization probabilities because we suspected edge could have positive or negative impacts on site occupancy. Greater amounts of edge habitat may increase site occupancy by increasing prey availability, particularly woodrats (*Neotoma* spp.), which are common in edge habitats (Zabel et al. 1995, Ward et al. 1998) and are a primary prey item in this portion of the spotted owl's range (Forsman et al. 2004). In contrast, increased amounts of edge habitat may decrease the amount of interior forest available to owls, which has been associated with decreased spotted owl survival (Franklin et al. 2000). To avoid the potential correlation between extinction and colonization parameters (MacKenzie et al. 2006), we only used edge in 1 of the parameters, not both, in the same model. We used edge as an additive effect with the best ranked covariate model for initial occupancy and extinction or colonization to determine if it improved model fit (i.e., decreased the AIC_c value).

We modeled each of the 4 possible models of each covariate individually, as an additive effect, with the best model from the first step of our analysis. We took this approach to reduce redundancy in the potential list of covariates due to spatial scales and relationships of covariates being correlated and to reduce the number of candidate models that would be considered in the final step of the analysis. We ranked each model using AIC_c values to determine the best spatial scale and relationship of each covariate.

The third step of our analysis combined the best individual covariates from the second step of our analysis into more complex models to test a specific set of biologically plausible hypotheses (Table 3). We did not use covariates on detection probabilities because they are nuisance parameters for which we had minimal interest. Our most complex initial occupancy and colonization models included 4 covariates (combinations of intermediate-aged and older forests and low and moderate burn severity; Table 3). Other models were variations of the most complex model that included a subset of these covariates or combined 2 covariates into a single covariate. Our most complex extinction model included 3 covariates (early seral stands, forests with high burn severity, and salvage logged forests; Table 3). The remaining candidate models were variations of the most complex model that had fewer covariates or combined 2 or more covariates into a single covariate. Prior to fitting our candidate model set (Table 3), we looked for correlations between variables that may be included in the same model. We did not include candidate models with highly correlated variables ($r^2 > 0.70$). After determining the best covariate model for initial occupancy, extinction, and colonization probabilities, we retained these models and combined them to determine our best overall model.

RESULTS

Comparison of the South Cascades to Timbered Rock

The best model for detection probabilities was P (year + area + ln T), and the second ranked model [P (year + ln T)] was not competitive ($\Delta AIC_c = 13.18$; Table 4). The best model indicated that detection probabilities varied among years, differed between areas, and followed a log-linear time trend within years. Detection probabilities were greater at South Cascades than at Timbered Rock in 10 out of 15 years. In most years (8 out of 15), detection probabilities declined over the survey season, but in the remaining 7 years, detection probabilities increased over the survey season. Detection probabilities during 1 survey over the 15 years of the study varied considerably and ranged from 0.24 to 0.82 at the South Cascades and 0.11–0.79 at Timbered Rock. The range of detection probabilities within years was less variable. The best model for initial occupancy was Ψ (area), and the second ranked model [$\Psi(\cdot)$] was not competitive ($\Delta AIC_c = 7.21$). The best model indicated that the South Cascades had greater initial occupancy ($\hat{\beta} = 2.21$, 95% CI = 0.65–3.76) than Timbered Rock. We estimated initial occupancy probabilities in 1992 to be 0.94 (95% CI = 0.88–1.00) at South Cascades compared to 0.65 at Timbered Rock (95% CI = 0.44–0.86).

The best model for extinction probabilities was ε[Pre-burn (area + t)Post-burn(area + t)], and 2 models were highly competitive (i.e., $\Delta AIC_c < 2.0$) with the best extinction model (Table 4). However, model ε[Pre-burn(area + t)Post-burn(area + t)] had a weight of 0.42, indicating strong support for the best model. Interpretation of the best model was that extinction rates varied by year and study area, but the study areas followed the same pattern over time (Fig. 2). We found some evidence that the South Cascades had greater extinction probabilities than Timbered Rock prior to the burn because the 95% confidence interval barely overlapped 0 ($\hat{\beta} = 0.69$, 95% CI = −0.06 to 1.43). Following wildfire and subsequent salvage logging at the Timbered Rock study area, extinction probabilities were greater than at the South Cascades ($\hat{\beta} = 1.46$, 95% CI = 0.29–2.62; Fig. 2). Model ε[Pre-burn(t)Post-burn(area + t)] was the second ranked extinction probability model ($\Delta AIC_c = 1.53$; Table 4). This model suggested that extinction probabilities varied by year and the Timbered Rock and the South Cascades study areas had similar extinction probabilities prior to the Timbered Rock burn, but extinction probabilities were greater at Timbered Rock following wildfire and subsequent salvage logging. Model ε (t) was the third ranked extinction model ($\Delta AIC_c = 1.84$; Table 4). This model suggested that extinction probabilities varied by year, and the Timbered Rock and South Cascades study areas had similar extinction probabilities before and after the Timbered Rock burn. We did not consider this model further, because the 2 best ranked models had similar interpretations with a combined model weight of

Table 4. Model selection results for extinction (ε), colonization (γ), and detection (P) probability models in the analysis of site occupancy of northern spotted owls at the South Cascades Demographic Study Area and the Timbered Rock study Area in southwest Oregon, USA, from 1992 to 2006. We presented only models with an Akaike weight ≥0.01. We considered models that compared differences between study areas (area) and no differences between areas ($\cdot$), and we considered several biologically plausible temporal effects including constant rates among years ($\cdot$), variable rates among years (t), and linear (T), log-linear (ln T), and quadratic (TT) trends over time. For all extinction, colonization, and detection probability models, the best initial occupancy (Ψ) model was Ψ (area).

Model	AIC_c[a]	ΔAIC_c[b]	w_i[c]	K[d]	Deviance
Extinction—ε					
ε(Pre-burn(area + t)Post-burn(area + t))γ(area + T)P(year, area + ln T)	8689.47	0.00	0.42	66	8552.27
ε(Pre-burn(t)Post-burn(area + t))γ(area + T)P(year, area + ln T)	8691.00	1.53	0.19	65	8555.96
ε(t)γ(area + T)P(year, area + ln T)	8691.31	1.84	0.17	64	8558.42
ε(area + t)γ(area + T)P(year, area + ln T)	8692.58	3.12	0.09	65	8557.54
ε(Pre-burn(area + t)Post-burn(area × t))γ(area + T)P(year, area + ln T)	8692.77	3.30	0.08	69	8549.08
ε(Pre-burn(t)Post-burn(area × t))γ(area + T)P(year, area + ln T)	8694.30	4.83	0.04	68	8552.78
Colonization—γ					
ε(area × t)γ(area + T)P(year, area + ln T)	8700.13	0.00	0.43	78	8536.83
ε(area × t)γ(area + TT)P(year, area + ln T)	8702.15	2.03	0.16	79	8536.66
ε(area × t)γ(Pre-burn (area + T)Post-burn area + T))P(year, area + ln T)	8702.29	2.16	0.15	79	8536.80
ε(area × t)γ(Pre-burn(area + T)Post-burn(area × T))P(year, area + ln T)	8702.32	2.19	0.15	79	8536.83
ε(area × t)γ(Pre-burn(area)Post-burn(area))P(year, area + ln T)	8703.02	2.89	0.10	78	8539.72
ε(area × t)γ(Pre-burn(T)Post-burn(area × T))P(year, area + ln T)	8708.47	8.35	0.01	79	8542.98
Detection probability—P[e]					
ε(area × t)γ(area × t)P(year, area + ln T)	8729.48	0.00	1.00	103	8510.61
ε(area × t)γ(area × t)P(year, ln T)	8742.66	13.18	0.00	88	8557.33

[a] Akaike's Information Criterion corrected for small sample sizes.
[b] The difference between the model listed and the best AIC_c model.
[c] Akaike weight.
[d] No. parameters in model.
[e] Detection probability modeling notation is P (among year detection, within year detection).

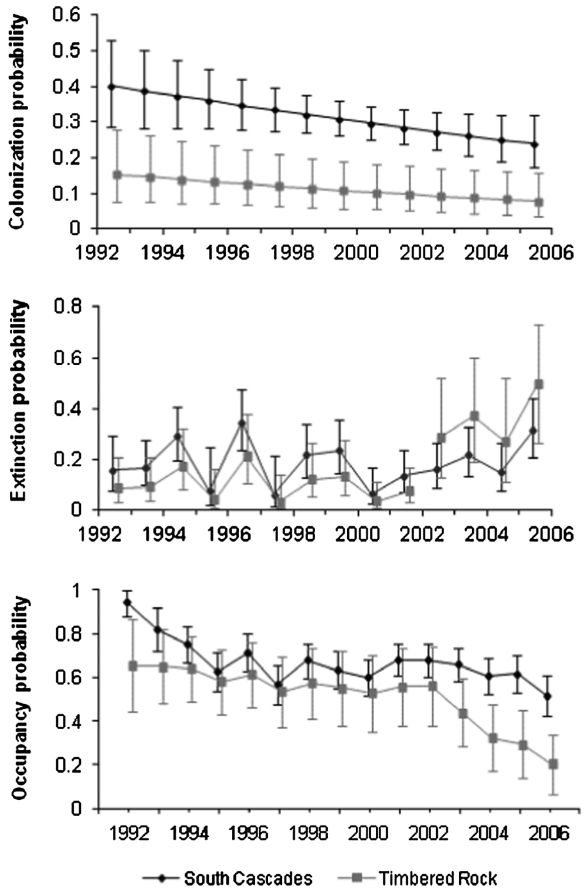

Figure 2. Estimated extinction, colonization, and site occupancy probabilities (95% CI) of northern spotted owls at the Timbered Rock and South Cascades study areas in southwest Oregon, USA from 1992 to 2006.

0.62 and indicated that post-burn, extinction probabilities were greater at Timbered Rock.

The best model for colonization was γ (area + T), and no models were within 2.0 AIC_c units of the best model (Table 4). Model γ (area + T) had a weight of 0.43 indicating strong support for this model. Interpretation of the best model was that colonization probabilities differed between study areas and declined linearly over time. Colonization probabilities were greater at the South Cascades ($\hat{\beta} = 1.31$, 95% CI = 0.60–2.03) than at Timbered Rock and declined over time ($\hat{\beta} = -0.06$, 95% CI = −0.12 to 0.00) at both areas (Fig. 2). Wildfire and salvage logging did not appear to influence post-burn colonization probabilities at Timbered Rock because models that included changes in colonization probabilities following wildfire were not competitive (i.e., $\Delta AIC_c > 2.0$) with the best model (Table 4).

We combined the best ranked models for initial occupancy, extinction, colonization, and detection probabilities to obtain our best overall model (Table 4), which we used to contrast trends in occupancy probabilities over time at the Timbered Rock and South Cascades study areas. We used the best overall model [Ψ(area)ε[Pre-burn(area + t)Post-burn(area + t)]γ(area + T)P(year + area + ln T)] to calculate year-specific occupancy estimates for each study area. Site occupancy by spotted owls at the South Cascades declined from 1992 to 1994, remained relatively stable from 1995 to 2005, and declined again in 2006 (Fig. 2). In contrast, site occupancy by spotted owls at Timbered Rock declined slightly from 1992 to 2002 and declined in an almost linear fashion from 2003 to 2006, which corresponded to the years following the Timbered Rock burn (Fig. 2). Between 2002 and 2006, the estimated proportion of spotted owl territories occupied by a pair at South Cascades declined from 0.68 to 0.51, a 25% reduction in site occupancy. In contrast, the estimated proportion of spotted owl territories occupied by a pair at Timbered Rock declined from 0.56 to 0.20, a 64% reduction in site occupancy during the same time period. This indicated that occupancy of territories by spotted owls in a recently burned landscape that was subjected to salvage logging declined at a greater rate than in a recently unburned landscape.

Relationship Between Wildfire, Salvage Logging, and Spotted Owl Site Occupancy

Our objective in this portion of the analysis was to determine the best model prior to modeling habitat covariates; consequently, we did not consider any competing models. The best model that described study area and temporal effects on spotted owl site occupancy at the Biscuit, Quartz, and Timbered Rock burns from 2003 to 2006 was $\Psi(\cdot)\varepsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\cdot)P(\cdot)$ (Table 5). Detection probabilities were constant within and among years, and equal between study areas. The probability of detecting a spotted owl pair on any 1 visit was 0.46 (95% CI = 0.39–0.53). The probability of initial occupancy was similar between study areas and was 0.46 (95% CI = 0.30–0.62) in 2003 at all 3 study areas. Colonization probabilities were also similar among study areas and constant over time. The probability that an unoccupied territory would be colonized the subsequent year was 0.15 (95% CI = 0.07–0.26). Extinction probabilities were greater at the Biscuit burn ($\hat{\beta} = 5.58$, 95% CI = 1.25–9.91) than the Quartz and Timbered Rock burns and increased from 2004 to 2006 ($\hat{\beta} = 2.96$, 95% CI = 0.97–4.94) at all 3 study areas. Extinction probabilities at the Quartz and Timbered Rock burns increased from 2004 to 2006 (0.11, 95% CI = 0.03–0.36; 0.72, 95% CI = 0.41–0.90, respectively). In contrast, extinction probabilities increased from 0.37 (95% CI = 0.11–0.73) in 2004 to 0.92 (95% CI = 0.58–0.99) in 2006 at the Biscuit burn. Based on the point estimates, extinction probabilities have increased dramatically for all areas (11–92%).

We modeled individual covariates as an additive effect with the best study area and temporal effects model (Table 5) to determine the spatial scale (core or territory) and relationship (linear or log-linear) that best described the effect of the covariate on initial occupancy, extinction, and colonization parameters (Table 6). In most cases, the models for alternative spatial scales and relationships were competitive (i.e., $\Delta AIC_c < 2.0$) with the best model for each covariate; however, our objective was to reduce redundancy between models and reduce the number of models in the final step of our

Table 5. Model selection results for initial occupancy (Ψ), extinction (ε), colonization (γ), and detection (P) probability models in the analysis of site occupancy of northern spotted owls without site-specific covariates at the Biscuit (BIS), Quartz (Q), and Timbered Rock (TR) burns in southwest Oregon, USA, from 2003 to 2006. We presented only models with an Akaike weight $\geq$0.05. We considered models that compared differences between study areas (area) and no differences between areas ($\cdot$), and we considered several biologically plausible temporal effects including constant rates among years ($\cdot$), variable rates among years (t), and linear (T), log-linear (ln T), and quadratic (TT) trends over time.

Model	AIC$_c$[a]	ΔAIC$_c$[b]	w_i[c]	K[d]	Deviance
Extinction—ε					
$\Psi(\cdot)\varepsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\cdot)P(\cdot, \cdot)$	476.93	0.00	0.28	6	464.38
$\Psi(\cdot)\varepsilon(T)\gamma(\cdot)P(\cdot, \cdot)$	477.79	0.86	0.18	5	467.39
$\Psi(\cdot)\varepsilon(\text{BIS} \neq \text{TR} = \text{Q} + \ln T)\gamma(\cdot)P(\cdot, \cdot)$	477.94	1.01	0.17	6	465.39
$\Psi(\cdot)\varepsilon(\ln T)\gamma(\cdot)P(\cdot, \cdot)$	478.65	1.72	0.12	5	468.26
$\Psi(\cdot)\varepsilon(t)\gamma(\cdot)P(\cdot, \cdot)$	479.35	2.42	0.08	6	466.80
$\Psi(\cdot)\varepsilon(TT)\gamma(\cdot)P(\cdot, \cdot)$	479.35	2.42	0.08	6	466.80
$\Psi(\cdot)\varepsilon(\text{area} + t)\gamma(\cdot)P(\cdot, \cdot)$	480.17	3.24	0.05	8	463.21
Colonization—γ					
$\Psi(\cdot)\varepsilon(\text{area} \times t)\gamma(\cdot)P(\cdot, \cdot)$	482.39	0.00	0.70	10	460.91
$\Psi(\cdot)\varepsilon(\text{area} \times t)\gamma(\text{BIS} \neq \text{TR} = \text{Q})P(\cdot, \cdot)$	487.41	5.02	0.06	13	458.90
Initial occupancy—Ψ					
$\Psi(\cdot)\varepsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	499.61	0.00	0.44	20	453.52
$\Psi(\text{BIS} \neq \text{TR} = \text{Q})\varepsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	501.12	1.51	0.21	21	452.37
$\Psi(\text{BIS} = \text{Q} \neq \text{TR})\varepsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	501.50	1.89	0.17	21	452.75
$\Psi(\text{BIS} = \text{TR} \neq \text{Q})\varepsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	502.27	2.66	0.12	21	453.52
$\Psi(\text{area})\varepsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	503.70	4.09	0.06	22	452.26
Detection probability—P[e]					
$\Psi(\text{area})\varepsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	503.70	0.00	0.52	22	452.26
$\Psi(\text{area})\varepsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\ln T, \cdot)$	506.28	2.58	0.14	23	452.11
$\Psi(\text{area})\varepsilon(\text{area} \times t)\gamma(\text{area} \times t)P(T, \cdot)$	506.44	2.74	0.13	23	452.26
$\Psi(\text{area})\varepsilon(\text{area} \times t)\gamma(\text{area} \times t)P(TT, \cdot)$	506.51	2.81	0.13	23	452.33
$\Psi(\text{area})\varepsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\text{year}, \cdot)$	507.56	3.86	0.08	25	447.79

[a] Akaike's Information Criterion corrected for small sample sizes.
[b] The difference between the model listed and the best AIC$_c$ model.
[c] Akaike weight.
[d] No. parameters in model.
[e] Detection probability modeling notation is P (among year detection, within year detection).

analysis. As a result, we did not consider competing models and assumed the highest ranked model best described the relationship of the covariate on each occupancy parameter. After determining the best spatial scale and relationship of each covariate, we looked for correlations between variables that were included in the same model. None of the variables that were included in the same model were highly correlated ($r^2 < 0.31$ in all contrasts). Consequently, we did not exclude any variables from our candidate model set because of colinearity (Table 3).

Fire severity and habitat effects.—The best model that described the relationship between site occupancy and fire severity, salvage logging, and habitat covariates at the Biscuit, Quartz, and Timbered Rock burns from 2003 to 2006 indicated that initial occupancy was best predicted by intermediate-aged and older forest that burned with a moderate severity at the core scale and amount of edge at the core scale. Extinction was best predicted by early seral stands that burned with high severity or were salvage logged at the core scale and amount of edge at the territory scale with extinction rates differing across time and at Biscuit sites. Colonization was best predicted by intermediate-aged older forests with low and moderate burn severity at the core scale and detection was constant across variables (Table 6). One model was within 2.0 AIC$_c$ units of the best model for extinction probability (Table 6). However, this model was a slight variation of the best model and did not include the covariate representing edge at the territory scale, so it was not considered further because the amount of edge at the territory scale improved model fit. No models competed with the best initial occupancy and colonization probability models (Table 6). The best overall covariate model ranked substantially higher ($\Delta\text{AIC}_c = 27.12$) than the model that only included study area and temporal effects (Table 6). This indicated that the covariates used in this model explained some of the variability observed in post-fire site occupancy by spotted owls at the Biscuit, Quartz, and Timbered Rock burns.

Our best initial occupancy model included variables for the amount of low severity burn and edge (km) within the core use area (Table 6). The confidence intervals of the beta coefficients for the amount of low severity burn within the core area ($\hat{\beta} = 0.52$, 95% CI $= -0.22$ to 1.26) and the amount of edge (km) in the core area ($\hat{\beta} = -0.42$, 95% CI $= -0.92$ to 0.10) broadly overlapped zero, which indicated that neither of these variables influenced initial occupancy probabilities. Extinction probabilities increased as the combined area that was previously harvested, burned with a high severity, or salvage logged increased ($\hat{\beta} = 1.88$, 95% CI $= 0.10$–3.66; Fig. 3a). We found some evidence that the amount of edge (km) within a territory had a positive effect on extinction probabilities as the 95% confidence intervals overlapped 0 slightly ($\hat{\beta} = 0.18$, 95% CI $= -0.01$ to 0.37; Fig. 3b). We found weak support that colonization proba-

Table 6. Initial occupancy (Ψ), extinction (ε), and colonization (γ) models in the analysis of covariate effects on site occupancy of northern spotted owls at the Biscuit (BIS), Quartz (Q), and Timbered Rock (TR) burns in southwest Oregon, USA, from 2003 to 2006. We presented only models with an Akaike weight $\geq$0.05. For all initial occupancy, extinction, and colonization models the best detection probability model was constant detection among and within years ($P(\cdot, \cdot)$).

Model[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	K[e]	Deviance
Best overall model					
Ψ(ln LOWc + EDGEc)ε(BIS $\neq$ TR = Q + T + ln EARHISALVc + EDGEt)γ(INTLc + INTMc + OLDLc + OLDMt)$P(\cdot, \cdot)$	449.81	0.00	1.00	14	418.89
$\Psi(\cdot)\varepsilon$(BIS $\neq$ TR = Q + T)$\gamma(\cdot)P(\cdot, \cdot)$—Base model	476.93	27.12	0.00	6	464.38
Initial occupancy—Ψ					
Ψ(ln LOWc + EDGEc)ε(BIS $\neq$ TR = Q + T)$\gamma(\cdot)P(\cdot, \cdot)$	473.78	0.00	0.36	8	456.82
Ψ(ln LOWc)ε(BIS $\neq$ TR = Q + T)$\gamma(\cdot)P(\cdot, \cdot)$	476.01	2.22	0.12	7	461.27
Ψ(INTLc + OLDLc)ε(BIS $\neq$ TR = Q + T)$\gamma(\cdot)P(\cdot, \cdot)$	476.09	2.30	0.12	8	459.13
Ψ(RFc + ln NRFc)ε(BIS $\neq$ TR = Q + T) $\gamma(\cdot)P(\cdot, \cdot)$	476.43	2.65	0.10	8	459.47
$\Psi(\cdot)\varepsilon$(BIS $\neq$ TR = Q + T)$\gamma(\cdot)P(\cdot, \cdot)$—Base model	476.93	3.15	0.08	6	464.38
Ψ(INTLc + INTMt + OLDLc + OLDMt)ε(BIS $\neq$ TR = Q + T)$\gamma(\cdot)P(\cdot, \cdot)$	477.43	3.65	0.06	10	455.94
Ψ(OLDLc)ε(BIS $\neq$ TR = Q + T)$\gamma(\cdot)P(\cdot, \cdot)$	477.64	3.85	0.05	7	462.89
Ψ(ln NRFc)ε(BIS $\neq$ TR = Q + T)$\gamma(\cdot)P(\cdot, \cdot)$	477.88	4.09	0.05	7	463.14
Extinction—ε					
$\Psi(\cdot)\varepsilon$(BIS $\neq$ TR = Q + T + ln EARHISALVc + EDGEt)$\gamma(\cdot)P(\cdot, \cdot)$	464.61	0.00	0.60	8	447.65
$\Psi(\cdot)\varepsilon$(BIS $\neq$ TR = Q + T + ln EARHISALVc)$\gamma(\cdot)P(\cdot, \cdot)$	466.50	1.89	0.23	7	451.76
$\Psi(\cdot)\varepsilon$(BIS $\neq$ TR = Q + T + ln HARVESTc + HIGHc)$\gamma(\cdot)P(\cdot, \cdot)$	469.49	4.88	0.05	8	452.53
$\Psi(\cdot)\varepsilon$(BIS $\neq$ TR = Q + T + ln EARLYc + HISALVc)$\gamma(\cdot)P(\cdot, \cdot)$	469.73	5.12	0.05	8	452.77
Colonization—γ					
$\Psi(\cdot)\varepsilon$(BIS $\neq$ TR = Q + T)γ(INTLc + INTMc + OLDLc + OLDMt)$P(\cdot, \cdot)$	462.72	0.00	0.65	10	441.24
$\Psi(\cdot)\varepsilon$(BIS $\neq$ TR = Q + T)γ(INTLc + INTMc + OLDLc + OLDMt + ln EDGEc)$P(\cdot, \cdot)$	464.93	2.21	0.22	11	441.14
$\Psi(\cdot)\varepsilon$(BIS $\neq$ TR = Q + T)γ(OLDLc + OLDMt)$P(\cdot, \cdot)$	467.27	4.54	0.07	8	450.31

[a] Variables preceded by ln were modeled using a log-linear relationship, variables followed by a c were modeled at the core area scale, and variables followed by *t* were modeled at the territory scale. INTL, intermediate-aged forest that burned with a low severity; INTM, intermediate-aged forest that burned with a moderate severity; OLDL, older forest that burned with a low severity; OLDM, older forest that burned with a moderate severity; LOW, intermediate-aged and older forest that burned with a low severity (combined area of INTL and OLDL); MOD, intermediate-aged and older forest that burned with a moderate severity (combined area of INTM and OLDM); EDGE, the interface between forested areas that burned with low or moderate severity and areas that were early seral stands, burned with high severity, or were salvage logged; EDGE was modeled as an additive effect with the best-ranked covariate model to determine if it improved model fit; EARLY, non-forested areas early seral stands that burned with any severity; HIGH, the combined area of intermediate-aged and older forest that burned with a high severity; SALVAGE, any intermediate-aged or older forest that was salvage logged; HARVEST, any forested area that was harvested before or after the burn (combined area of EARLY and SALVAGE); HISALV, any forested area, excluding early stands, that burned with a high severity or was salvage logged (combined area of HIGH and SALVAGE); EARHISALV, any early seral stand or forested area that burned with high severity or that was salvage logged (combined area of EARLY, HIGH, and SALVAGE); RF, intermediate-aged forest that burned with a low or moderate severity (combined area of INTL and INTM); NRF, older forest that burned with a low or moderate severity (combined area of OLDL and OLDM); T, linear time.

[b] Akaike's Information Criterion corrected for small sample sizes.

[c] The difference between the model listed and the best AIC_c model.

[d] Akaike weight.

[e] No. parameters in model.

bilities increased as the amount of intermediate-aged forest that burned with a low severity within the core area increased ($\hat{\beta} = 0.10$, 95% CI = -0.01 to 0.38; Fig. 4a) as the amount of older forest that burned with a low severity within the core area increased ($\hat{\beta} = 0.10$, 95% CI = -0.01 to 0.22; Fig. 4b), and as the amount of older forest that burned with a moderate severity within the territory increased ($\hat{\beta} = 0.82$, 95% CI = -0.05–1.69; Fig. 4c). We found no evidence that colonization probabilities were associated with the amount of intermediate-aged forest that burned with a moderate severity within the core area ($\hat{\beta} = -1.20$, 95% CI = -3.21 to 0.80).

DISCUSSION

Comparison of the South Cascades to Timbered Rock

As predicted, the Timbered Rock and South Cascades study areas had relatively similar trends in site occupancy prior to the Timbered Rock burn. However, extinction probabilities increased at Timbered Rock following wildfire and subsequent salvage logging, which combined with the lesser colonization rates at Timbered Rock contributed to greater declines in site occupancy than were observed in recently unburned landscapes at the South Cascades (Fig. 2). The Timbered Rock study area had an approximately 64% reduction in site occupancy following wildfire, whereas the South Cascades study area had a roughly 25% reduction in site occupancy during the same time period. This supported our prediction that occupancy rates in burned and salvage logged landscapes would decline at a greater rate than unburned landscapes. Our results contrast with those of previous studies that compared occupancy rates of spotted owls in burned and unburned landscapes. Jenness et al. (2004) found that territory occupancy of Mexican spotted owls in burned areas was similar to unburned areas. Roberts et al. (2011) found that site occupancy of California spotted owls in randomly selected burned and unburned areas were similar. Neither of these studies was affected by the high degree of salvage logging we observed following the Timbered Rock

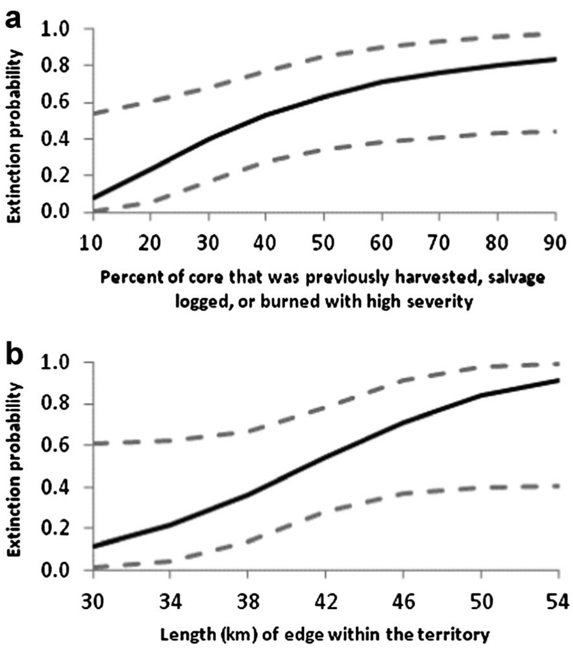

Figure 3. The estimated effects of the percent of (a) forested area that burned with a high severity or was previously harvested or salvage logged and (b) forest edge on extinction probabilities of northern spotted owls at the Biscuit, Quartz, and Timbered Rock burns in southwest Oregon, USA from 2003 to 2006. The 95% confidence intervals for the estimated effects are represented by gray, dashed lines. The median values of the additional covariates in the model were held constant while varying the covariate of interest over the observed range of values.

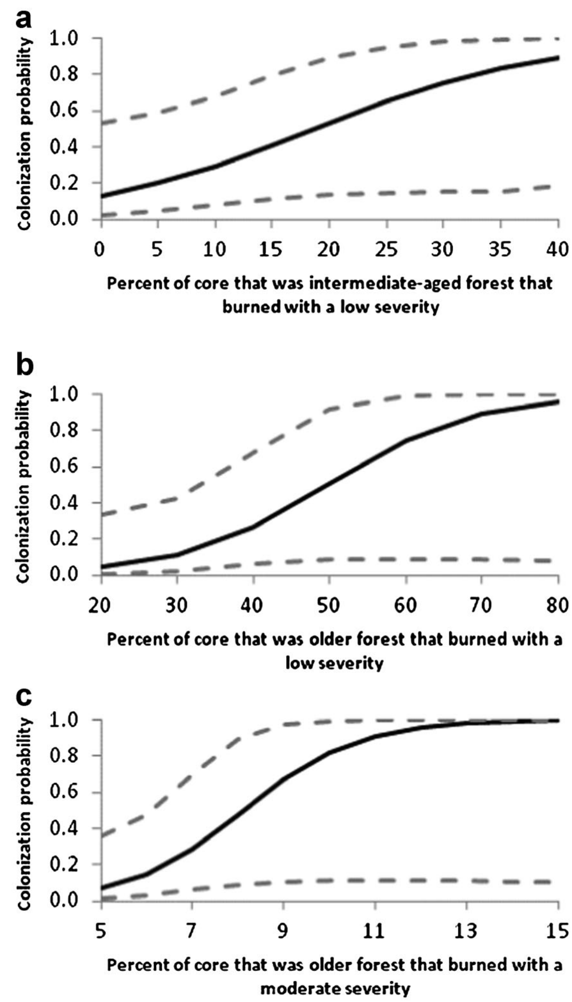

Figure 4. The estimated effects of the percent of (a) intermediate-aged forest that burned with a low severity, (b) older forest that burned with a low severity, and (c) older forests that burned with a moderate severity on colonization probabilities of northern spotted owls at the Biscuit, Quartz, and Timbered Rock burns in southwest Oregon, USA from 2003 to 2006. The 95% confidence intervals for the estimated effects are represented by gray, dashed lines. The median values of the additional covariates in the model were held constant while varying the covariate of interest over the observed range of values.

burn, which may explain the difference between our results and those of previous studies.

The approximately 25% reduction in site occupancy at the South Cascades from 2002 to 2006 was somewhat surprising given that the study area did not have any large scale disturbances during this time. However, several spotted owl populations have been declining throughout the subspecies' range (Anthony et al. 2006, Forsman et al. 2011), and declines in site occupancy at the South Cascades could be related to ongoing population declines that are unrelated to natural disturbances. Dugger et al. (2011) found that barred owls (*Strix varia*) had negative impacts on site occupancy by spotted owls by decreasing colonization rates and increasing extinction rates. This likely explains much of the nearly 25% decline in site occupancy we observed from 2002 to 2006 at the South Cascades. The 64% reduction in site occupancy at Timbered Rock from 2002 to 2006 was substantially greater than the roughly 25% decline observed at South Cascades, which suggests that wildfire, subsequent salvage logging, and past timber harvest contributed to the greater declines in site occupancy at Timbered Rock. We estimated that following the Timbered Rock burn only 46% of the area within 2,230 m of spotted owl territories were intermediate-aged or older forests that burned with a low or moderate severity (Table 1). This amount of habitat is marginal for successful reproduction (Bart and Forsman 1992) and may cause decreases in survival rates of the subspecies (Franklin et al. 2000, Dugger et al. 2005).

The large declines in site occupancy following the Timbered Rock burn are most likely explained by dispersal out of the burn (i.e., emigration) and decreased survival of spotted owls. Several color-banded, adult spotted owls at the Timbered Rock burn (2 pairs and 1 individual, 25% of the known pre-fire population) dispersed to an unburned territory adjacent to the burn, 1–2 years post-fire (OCFWRU, unpublished data). Adult dispersal is a relatively rare occurrence in spotted owls throughout their range (Forsman et al. 2002: 5%, Zimmerman et al. 2007: 2%); however, owl territories may be abandoned when large amounts of mature and older forest are lost (Bart and Forsman 1992, Bart 1995). We believe that the relatively high rate of adult dispersal following the Timbered Rock burn suggests that insufficient habitat remained at abandoned territories to support a spotted owl pair. In addition, radio-marked spotted owls that maintained a territory within the Timbered Rock burn had lower survival rates ($\hat{S} = 0.69 \pm 0.12$; Clark et al. 2011) than reported throughout the subspecies' range ($\hat{\Phi} = 0.75$ to

0.91 ± 0.01 to 0.05; Anthony et al. 2006). Annual survival of spotted owls was positively associated with greater amounts of older forest within their home ranges or core use areas in other studies (Franklin et al. 2000, Olson et al. 2004, Blakesley et al. 2005, Dugger et al. 2005). High severity wildfire and salvage logging removed and modified 26% of the intermediate-aged and older forests within 2,230 m of spotted owl territories at the Timbered Rock burn, and 28% of the remaining area was previously harvested (i.e., early seral forest; Table 1). Consequently, the large degree of habitat loss and modification from past timber harvest, high severity fire, and salvage logging following the Timbered Rock burn likely contributed to the high levels of dispersal out of the burn, decreased survival rates and subsequent declines in site occupancy that we observed. These declines in site occupancy appear to have continued past the conclusion of our study because no spotted owls were detected during surveys conducted during the 2011 breeding season at the Timbered Rock study site (OCFWRU, unpublished data).

Increased extinction rates following the Timbered Rock burn may have been exacerbated by the checkerboard land ownership pattern of private and BLM lands (Richardson 1980). Private lands within the area of the Timbered Rock burn are managed as industrial forests and are frequently subjected to large-scale timber harvest, which creates large tracts of early seral forest. Following the Timbered Rock burn, much of the private land was salvage logged (17% of the study area), which created large clear-cuts throughout the landscape. Territory occupancy by spotted owls was negatively associated with increased areas of clear-cuts within the territory in another study (Thraillkill et al. 1998). Consequently, the large areas of clear-cuts created by salvage logging and past timber harvest (approx. 45% of the area within 2,230 m of spotted owl territories; Table 1) potentially exacerbated declines in site occupancy following the Timbered Rock burn or confounded the effects of wildfire. Declines in site occupancy may not be as large in burned areas that were not subjected to previous timber harvest or substantial amounts of post-fire salvage logging.

Relationship Between Wildfire, Salvage Logging, and Spotted Owl Site Occupancy

Extinction.—We predicted that occupancy of nesting territories by spotted owls after fires would decline because of increased extinction probabilities attributable to habitat loss and modification from past timber harvest, high severity fire and salvage logging. Our results supported this prediction because extinction probabilities increased as the combined area of high severity burns, salvage logging, and early seral forest increased (Fig. 3a; $\hat{\beta} = 1.88$, 95% CI = 0.10–3.66). This was the strongest relationship we observed in this analysis because it was the only habitat covariate where the 95% confidence interval for the regression coefficient did not overlap 0. Unfortunately, we were unable to separate the impacts of these 3 variables on extinction probabilities. When these 3 variables were included separately, the models were not competitive with the model that combined these variables into a single covariate (Table 6). This may indicate that we lacked the precision to separate the impacts of these 3 variables or they were confounded. However, our results suggest that these 3 variables work in concert and generate synergistic effects. Any 1 disturbance event may not generate negative effects on occupancy of territories, but the combined loss and modification of habitat from these 3 factors negatively affected spotted owls in our study. The combined influence of these 3 factors may reduce spotted owl habitat to such an extent that a threshold is passed and spotted owls are no longer able to occupy the territory.

Spotted owls are associated with late-successional forests (Forsman et al. 1984, Thomas et al. 1990), and their territories have greater amounts of older forests than surrounding landscapes (Ripple et al. 1991, 1997; Meyer et al. 1998; Swindle et al. 1999). Forest stands used by spotted owls have large proportions of downed woody debris and snags, high canopy cover, and high structural diversity (Hershey et al. 1998, North et al. 1999, Irwin et al. 2000). Timber harvest, salvage logging, and high severity fire remove or alter many of these structural characteristics associated with spotted owl habitat. As a result, we were not surprised that these factors were associated with increased extinction probabilities and declines in site occupancy. Spotted owls have high site fidelity (Forsman et al. 1984, 2002; Zimmerman et al. 2007), and survival rates are positively correlated with increased amounts of older forest in their territories (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005); consequently, owls that occupied territories with a large degree of past timber harvest, salvage logging, and high severity fire were likely forced to emigrate out of the burned area or risk decreased survival.

Radio-marked spotted owls at the Timbered Rock burn were located closer to edge habitats than at random (Clark 2007), which suggests edge habitat may provide a benefit to the subspecies. Spotted owls may prefer to forage in habitat edges because of greater densities of some prey in early seral forests (Carey and Peeler 1995, Franklin and Gutiérrez 2002), particularly woodrats in southwest Oregon and northwest California (Zabel et al. 1995, Ward et al. 1998). Our results provided some evidence that extinction probabilities increased as the amount (km) of edge increased within nesting territories increased (Fig. 3b; $\hat{\beta} = 0.18$, 95% CI = −0.01–0.37), suggesting a negative impact of edge habitat on spotted owl territory occupancy. In our analysis, edge represented a metric of habitat fragmentation. Dugger et al. (2011) observed greater colonization probabilities at spotted owl territories when older forest was less fragmented, and our results were similar. Franklin et al. (2000) indicated that spotted owls are likely to have decreased survival at territories with reduced amounts of interior forest, suggesting that habitat fragmentation negatively affects spotted owls. The patchy nature of high severity fire and salvage logging created large amounts of edge habitat, which likely reduced the amount of interior forest available to owls and contributed to declines in site occupancy in our study. Furthermore, increases in edge may be correlated with increased amounts of nonhabitat (i.e., nonforested and early seral stands) and increases in nonhabitat have contributed to declines in territory occupancy of California spotted owls (Blakesley et al. 2005) and increases in extinction probabilities in this study. Despite indications that spotted owls are negatively affected by habitat fragmentation, the mechanism of these effects is not well understood (Franklin and Gutiérrez 2002). We calculated the amount of edge as the interface between intermediate-aged and older forests that burned with a low or moderate severity and all other habitat types (Table 2). This classification of edge habitat delineated distinct boundaries between stands of larger living trees and high severity burns or early seral stands. Additional types of edge habitats exist at the interface between intermediate-aged and older forests or the interface between low and moderate severity burns, and these types of edges may provide foraging habitat for spotted owls. Additional research between the association of various edge habitats on spotted owl demography and site occupancy is needed to clarify this relationship.

Colonization.—Overall, our estimated effects of habitat covariates on colonization probabilities were relatively imprecise. We attributed this lack of precision to the fact that we observed only 6 colonization events at our 3 study areas from 2003 to 2006. Despite the fact that we observed relatively few colonization events, we were still able to document several biologically meaningful associations between post-fire habitat and colonization probabilities. We suspect that if additional colonization events had occurred during the course of our research, our estimated effects of habitat on colonization probabilities would be more precise.

We found some evidence that colonization probabilities in our study were positively associated with increased amounts of older forest that burned with a low severity within the core area (Fig. 4b; $\hat{\beta} = 0.10$, 95% CI = −0.01 to 0.22). Although this estimated effect had weak support, this finding was expected and follows the well documented association between spotted owls and older forest (Forsman et al. 1984, Thomas et al. 1990). Furthermore, previous research indicated that territory occupancy of California spotted owls was positively associated with older forest (Blakesley et al. 2005), extinction probabilities at northern spotted owl territories were greater at territories with lesser amounts older forest (Dugger et al. 2011) and site occupancy by California spotted owls in areas that primarily burned with a low and moderate severity was similar to unburned areas (Roberts et al. 2011). Older forests that burned with a low severity are likely the highest quality spotted owl habitat in post-fire landscapes. These areas likely retained much of the canopy cover, downed woody debris, snags, and structural diversity that is selected by spotted owls (Hershey et al. 1998, North et al. 1999, Irwin et al. 2000). As a result, unoccupied territories that have high quality habitat (i.e., older forest that burned with a low severity) will have the greatest probability of being colonized by spotted owls. Within the Timbered Rock burn, radio-marked spotted owls strongly selected for older forest that burned with a low severity (Clark 2007), further demonstrating the influence of this habitat on spotted owls in post-fire landscapes.

Moderate severity burns likely remove and modify more of the forest stand features selected by spotted owls than low severity burns, yet many critical habitat features are likely retained and allow moderately burned areas to provide habitat for spotted owls following wildfire. Our analysis provided weak support that colonization probabilities were positively associated with increased amounts of older forest that burned with a moderate severity (Fig. 4c; $\hat{\beta} = 0.82$, 95% CI = −0.05 to 1.69). In addition to potentially providing many of the critical habitat features of forest stands that burned with a low severity, moderately burned stands likely have decreased risk of stand-replacement in the future because of removal of ladder fuels (Agee 1993), which likely increases the resilience of the forest stand to future disturbance. Spotted owls have been shown to disproportionately forage in habitats that have high levels of prey abundance (Carey et al. 1992, Carey and Peeler 1995, Zabel et al. 1995). Moderate severity burns may increase habitat heterogeneity and prey abundance, similar to the effects of heterogeneous thinning of young forest stands (Carey 2001). However, we did not test this hypothesis, and the potential benefits of moderate severity burns in older forests for spotted owls are unclear.

Previous studies have suggested a quadratic relationship between survival and reproduction of spotted owls and the amount of older forest surrounding nesting territories (Franklin et al. 2000, Olson et al. 2004). These studies suggest that territories that are not entirely comprised of older forests are beneficial to spotted owls and that spotted owls may be adapted to natural disturbances such as wildfire that create a mosaic of forest conditions. Our results provided weak support for this hypothesis because owl territories in our study that had increased amounts of intermediate-aged forest that burned with a low severity have a greater probability of being colonized by a pair of owls (Fig. 4a; $\hat{\beta} = 0.10$, 95% CI = −0.01 to 0.38). However, we expect a threshold exists in this relationship because spotted owls are associated with older forest (Forsman et al. 1984, Thomas et al. 1990) and spotted owls that occupy territories with insufficient amounts of older forest will have decreased survival and reproductive rates (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). The amount of intermediate-aged forest that burned with a low severity at any 1 owl territory in our study ranged from 0 to 38%. Territories that have insufficient amounts of older forest will likely not be occupied by spotted owls, but our results provided some evidence of a benefit of habitat heterogeneity for spotted owls.

Initial occupancy.—We were unable to identify any relationships between initial occupancy probabilities and the habitat covariates that we considered in our analysis. Our best model for initial occupancy probabilities (Table 6) included variables for the amount of the core area that burned with a low severity ($\hat{\beta} = 0.52$, 95% CI = −0.22 to 1.26) and the amount of edge habitat ($\hat{\beta} = -0.42$, 95% CI = −0.92 to 0.10); however, both of these estimates were imprecise and the 95% confidence intervals broadly overlapped zero, which suggested these relationships were not meaningful. Since these relationships were not supported by the data, additional research is needed to investigate the influence of low severity fire and edge habitat on spotted owl site occupancy.

Our analysis of site occupancy at the Biscuit, Quartz, and Timbered Rock burns indentified several meaningful relationships between site occupancy and amount of post-fire habitat. All of these relationships were based on biologically plausible hypotheses and have implications for spotted owl management. However, the relationships we observed were based on small sample sizes, non-random samples at the Biscuit burn, and our estimated relationships were often imprecise. Furthermore, our study was opportunistic and observational, which prevents us from assigning cause and effect relationships. Consequently, we suggest a cautionary approach when applying our findings to future land management decisions. In particular, the relationships we observed in our analysis may not be applicable to spotted owls in post-fire landscapes that are not affected by post-fire salvage logging.

Both wildfire and barred owls have been identified as threats to the persistence of spotted owls (USFWS 2011). Barred owls have expanded throughout the entire range of the northern spotted owl (Dark et al. 1998, Pearson and Livezey 2003) and are negatively affecting spotted owls (Kelly et al. 2003, Olson et al. 2005, Dugger et al. 2011). Furthermore, barred owls have a more generalized diet (Hamer et al. 2001, Wiens 2012) and use a wider range of habitats (Hamer et al. 2007) than spotted owls, which suggests that barred owls may be better adapted to persist in burned landscapes. We only detected 2 barred owls at the Biscuit, Quartz, and Timbered Rock burns during demographic surveys conducted between 2003 and 2006, so we believe that barred owls had little to no effect on our results.

Jointly, our analyses suggest that site occupancy by spotted owls in burned landscapes is likely to decline, at least in the short-term. These declines in site occupancy are driven by large increases in extinction probabilities in post-fire landscapes and are attributable to past timber harvest, high severity fire, and salvage logging. Although territories that had increased amounts of older forest that burned with a low severity had the greatest colonization probabilities, we only observed 6 colonization events at our 3 study areas from 2003 to 2006, and this level of colonization was insufficient to offset the high extinction probabilities we observed. This suggests that insufficient habitat remained at many of the spotted owls territories included in our analyses to support a pair of spotted owls following wildfire. Site occupancy by Mexican and California spotted owls in landscapes that burned primarily with low or moderate severities was similar to unburned landscapes (Jenness et al. 2004, Roberts et al. 2011), which suggests that spotted owls may be able to persist in burned landscapes. These findings contrast our results, which suggested that spotted owl site occupancy will decline in burned landscapes; however, our results were confounded by the effects of past timber harvest and salvage logging. Additional research in post-fire landscapes that have not been impacted by past timber harvest and salvage logging are needed to help clarify these relationships.

MANAGEMENT IMPLICATIONS

We identified several factors that influenced occupancy of nesting territories by spotted owls in post-fire landscapes; however, the strongest association we observed was that site occupancy declined because of increased extinction probabilities. Increased amounts of past timber harvest, salvage logging, and high severity burns jointly contributed to increased extinction probabilities and subsequent declines in spotted owl site occupancy. Past timber harvest negatively influenced site occupancy in our analysis, so we recommend increased protection of older forest in dry forest ecosystems to prevent future habitat loss to timber harvest and mitigate potential losses of older forest to stand-replacing fire and subsequent salvage logging. High severity fire was 1 of 3 factors that combined to increase local-extinction probabilities of spotted owls in our study; however, we were unable to separate the impacts of wildfire from land management activities. As a result, we recommend future research to clarify the relationship between high severity fire and spotted owl site occupancy in the absence of past timber harvest and salvage logging. We believe that widespread, stand-replacing wildfires will negatively affect site occupancy by spotted owls, so we suggest efforts should be made to reduce the risk of widespread, stand-replacing wildfire in spotted owl habitat. However, a precautionary approach should be taken when implementing fuel reduction techniques that will reduce that risk of stand-replacing wildfire. Research is needed to ensure that fuel reduction techniques, particularly commercial or non-commercial thinning, are not detrimental to spotted owls, their habitat, or prey before fuel reduction techniques are implemented on a large scale. Our results also indicated a negative impact of salvage logging on site occupancy by spotted owls. We recommend restricting salvage logging after fires on public lands within 2.2 km of spotted owl territories (the median home range size in this portion of the spotted owl's range) to limit the negative impacts of salvage logging. Our results indicated a negative response of spotted owls to wildfire in the short-term, but the response is likely to vary over time; however, little is known about the long-term response of spotted owls to wildfire. As a result, long-term monitoring studies should be implemented in post-fire landscapes to determine the response of spotted owls to wildfire over time.

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