

HABITAT SELECTION IN A CHANGING ENVIRONMENT: THE RELATIONSHIP BETWEEN HABITAT ALTERATION AND SPOTTED OWL TERRITORY OCCUPANCY AND BREEDING DISPERSAL

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Abstract. Understanding the effect of habitat alteration on avian behavior is important for understanding a species' ecology and ensuring its conservation. Therefore, we examined the relationship between Spotted Owl habitat selection and variation in habitat in the Sierra Nevada. We estimated habitat selection by modeling the probability of territory colonization (γ), territory extinction (ϵ), and breeding dispersal in relation to the amount of mature conifer forest within and among territories. Alteration of ≥ 20 ha of mature conifer forest (coniferous forest with $>70\%$ canopy cover dominated by medium [30.4–60.9 cm dbh] and large [>60.9 cm dbh] trees) within individual territories ($n = 66$) was negatively related to territory colonization and positively related to breeding dispersal probability. Although territory extinction was negatively related to the amount of mature conifer forest, it was not clear whether this relationship was due to variation of mature conifer forest within or among territories. Although modeling results for territory colonization and extinction generally supported the hypothesis that individuals are "ideal" when selecting a habitat in the sense that they settle in the highest-quality site available, we did not find a clear benefit in terms of habitat quality for Spotted Owls that exhibited breeding dispersal.

Key words: breeding dispersal, habitat alteration, habitat selection, occupancy, Spotted Owl, *Strix occidentalis*.

Selección de Hábitat en un Ambiente Cambiante: Relación entre la Alteración del Hábitat y la Ocupación de Territorios y la Dispersión Reproductiva en *Strix occidentalis*

Resumen. Entender el efecto de la alteración del hábitat sobre el comportamiento de las aves es importante para comprender la ecología de una especie y asegurar su conservación. Por lo tanto, examinamos la relación entre la selección de hábitat por parte de *Strix occidentalis* y la variación en el hábitat en la Sierra Nevada. Estimamos la selección de hábitat modelando la probabilidad de colonización de un territorio (γ), de extinción de un territorio (ϵ) y de dispersarse para reproducirse en relación con la cantidad de bosque de coníferas maduro dentro de y entre los territorios. La alteración de 20 o más hectáreas de bosque de coníferas maduro (bosque de coníferas con más del 70% de la cobertura del dosel dominada por árboles medianos [30.4–60.9 cm de DAP] y grandes [>60.9 cm de DAP]) dentro de territorios individuales ($n = 66$) se relacionó negativamente con la colonización de los territorios y positivamente con la probabilidad de dispersarse para reproducirse. Aunque la extinción de los territorios se relacionó negativamente con la cantidad de bosque de coníferas maduro, no es claro si esta relación se debió a la variación en el bosque de coníferas maduro dentro de los territorios o entre territorios. Aunque los resultados del modelado de colonización y extinción de los territorios en general apoyaron la hipótesis de que los individuos son "ideales" al seleccionar el hábitat en el sentido en que se establecen en los sitios disponibles de mayor calidad, no encontramos un beneficio claro en términos de la calidad de hábitat para los individuos que se dispersaron para reproducirse.

INTRODUCTION

The effect of habitat alteration on avian habitat choice is a key issue for conservation (Stamps

2001). If birds choose habitats to increase their fitness (Fretwell and Lucas 1969), habitat alteration, both before and after habitat selection has occurred, has the potential to affect population dynamics, particularly if the alteration affects a large area. The consequence of habitat alteration is especially relevant for territorial species that exhibit limited breeding dispersal (individuals switching territories be-

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tween breeding attempts). Breeding dispersal is likely an adaptive trait although it is thought to occur infrequently in many species (Greenwood and Harvey 1982). Inbreeding avoidance, mate choice, site choice, or social constraints have all been hypothesized to influence breeding dispersal (Greenwood 1980, Greenwood and Harvey 1982, Dobson and Jones 1985, Payne and Payne 1993). Breeding dispersal that is motivated by habitat alteration could be viewed as adaptive in terms of site choice.

The Spotted Owl (*Strix occidentalis*) is a territorial species that has high site fidelity (Gutiérrez et al. 1995, Blakesley et al. 2006). Most habitat studies have indicated that Spotted Owls preferentially select areas of mature coniferous forest (Forsman et al. 1984, Verner et al. 1992, Chatfield 2005), and that this habitat type influences their population dynamics (Franklin et al. 2000, Olson et al. 2004, Seamans 2005). Because mature coniferous forests in the western United States are prized for lumber production and are also highly susceptible to stand-replacing wildfire, alteration of this habitat type is believed to pose a threat to the owl's long-term viability (U.S. Department of Interior 1990, 1993, Verner et al. 1992). Although the alteration of mature forest is believed to have long-term negative consequences for Spotted Owls, there have been few empirical studies that have attempted to quantify how variation in the amount of mature forest may affect territory occupancy.

In this paper we examine the relationship between the amount of mature conifer forest, alteration of mature conifer forest, and Spotted Owl territory occupancy and breeding dispersal over a 15-year period. We use the term "habitat alteration" because we are not sure that all habitat changes in forest structure can be considered "habitat loss." Thus, habitat alteration represents a change from mature conifer forest to some other forest cover type by logging or wildfire. Ideally, a true experiment (i.e., random allocation of replicated experimental units to treatments) should be used to estimate cause and effect relationships between habitat alteration and Spotted Owl population processes. However, designing and executing true experiments has proven difficult because of constraints involved with endangered species management and because the scale of potential

treatments poses significant logistical challenges. Therefore, we used a combination of quasi-experimental (Cook and Campbell 1979) and observational approaches. We accepted treatment units (Spotted Owl territories) as they occurred and recorded observations of forest alteration, territory occupancy, and individual movement among territories over time. Valid inference from this approach required controlling for the confounding effect of variation in the amount of mature conifer forest among Spotted Owl territories. Because of the difficulty in controlling for this confounding effect, and because of the overall study design, we did not infer cause and effect relationships from our results. Rather, our goal was to evaluate whether: (1) alteration of mature conifer forest was correlated with immediate, short-term territory colonization probability (probability of an unoccupied territory becoming occupied), extinction probability (probability of an occupied territory becoming unoccupied), or breeding dispersal probability; (2) alteration of mature conifer forest was correlated with long-term territory colonization or extinction probability; and (3) territory colonization or extinction probability, or breeding dispersal, was related to variation in the amount of mature conifer forest among territories. We sought to increase our knowledge of the relationships between habitat alteration and Spotted Owl habitat choice. Further, our results can be used to identify specific habitat types that should be targeted by experimental studies whose goal is to test the effect of habitat alteration on Spotted Owls.

METHODS

STUDY AREA

Our 925 km² study area was located in the central Sierra Nevada, California, between the North and South Forks of the American River (Seamans et al. 2001). Within this area, we surveyed owls in a 355 km² "density study area" from 1990 to 2004. We surveyed the density study area completely for Spotted Owls each year regardless of land ownership or past occupancy by owls. In 1997 we established a "regional study area," which surrounded the density study area. The regional study area consisted of previously known owl territories and territories that were located from 1997 to

1999. Areas between owl territories in the regional study area were not completely surveyed.

The Sierra Nevada was the dominant physical feature of the area. The study area was typical of the midelevation Sierra Nevada, with mountainous terrain bisected by steep river canyons. Elevations ranged from 366 to 2401 m. Climate was Mediterranean, with cool wet winters and hot dry summers (Olson and Helms 1996). Sierran mixed conifer forest was the principal vegetation type (Sierra Nevada Ecosystem Project 1996) and was dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), and Douglas-fir (*Pseudotsuga menziesii*) in the canopy and black oak (*Quercus kelloggii*), tanoak (*Lithocarpus densiflora*), and big leaf maple (*Acer macrophyllum*) in the understory. Red fir forest was less abundant but common at higher elevations, and montane manzanita chaparral, black oak woodland, and barren rock were less abundant but locally important vegetation or landscape features (Sierra Nevada Ecosystem Project 1996).

DATA COLLECTION

Spotted Owl surveys. We surveyed Spotted Owls from 1 April to 28 August of each year from 1990 to 2004, following methods described by Franklin et al. (1996). We used two types of surveys: (1) nighttime surveys to initially locate owls in an area; and (2) daytime surveys to locate roosts and nests, and to capture, band, and assess the reproductive status of owls. Nighttime surveys consisted of imitating Spotted Owl vocalizations between dusk and dawn at established survey locations and listening for a response. Survey locations were consistent from year to year and were placed to obtain complete survey coverage of the density study area and each Spotted Owl territory in the regional study area. There were 5–12 survey points for each Spotted Owl territory, depending on the topography of the territory. A complete survey for a territory was achieved when we imitated owl territorial calls at all survey points within a territory over a four-day period without receiving a response. We conducted up to six surveys at each Spotted Owl territory to determine owl presence.

If an owl responded during a nighttime survey we conducted a daytime survey within

four days of receiving the response. We counted a nighttime survey with a response and the subsequent daytime survey as only one survey for the purpose of modeling occupancy (see below). We attempted to capture and band all Spotted Owls detected using the methods of Franklin et al. (1996). Once captured, we fitted owls with a U.S. Fish and Wildlife Service locking aluminum band on the tarsometatarsus of one leg. On the other leg we marked individuals ≥ 1 year old with a unique color-band and tab combination. We determined the sex of owls based on the pitch of their calls and their behavior (Forsman et al. 1984). We identified four age-classes based on plumage characteristics (Forsman 1981, Moen et al. 1991): juvenile; one-year-old (first-year subadult); two-year-old (second-year subadult); and ≥ 3 years old (adult).

Habitat metrics. Using a combination of aerial photographs, digital-orthophoto-quarter quadrangles, and extensive ground sampling we created a forest cover map with eight vegetation cover types for the entire density study area and a vegetation cover type map for each regional study area owl territory (Chatfield 2005, Seamans 2005). We defined vegetation cover types based on the dominant vegetation structure (tree diameter at breast height [dbh; measured 1.4 m above the forest floor on the uphill side of the tree] and canopy cover). Because Seamans (2005) estimated that the area of coniferous forest with $>70\%$ canopy cover dominated by medium (30.4–60.9 cm dbh) or large (>60.9 cm dbh) trees was the best predictor of demographic parameters for owls in our study population, we chose to examine only the effect of alteration of this vegetation type. Hereafter, we refer to this vegetation type as “mature conifer forest.” Minimum polygon size for mapping was 0.1 ha. Map accuracy for mature conifer forest was 91% (Chatfield 2005).

We estimated the total amount of each of the eight cover types within a 400 ha circle in each owl territory using the spatial analyst extension in ArcView 3.2 (Environmental Systems Research Institute, Redlands, California). This area was based on a circle with a radius of 1128 m, which was half the mean nearest neighbor distance of occupied territories in the density study area averaged over the years 1990 to 2002. We determined the center of the circle for each territory by estimating the geometric

center of all owl locations from each year the territory was occupied. The area encompassed by this circle was approximately one-quarter to one-half of the estimated home range size for Spotted Owls in the central Sierra Nevada (Laymon 1988, Call et al. 1992). Although we did not know if the entire 400 ha area was used by owls, the circles did encompass all nests and >90% of all roosts in each territory. We used the term "territory" to depict the spatial location and area for which we estimated habitat metrics because: (1) owls responded to conspecific calls from these areas during surveys; (2) the 400 ha we used for analyses contained all known nest locations of owls responding in that area; and (3) all areas surrounding the nest were vocally defended by owls during daytime surveys.

We used aerial photographs (a complete set was created approximately every four years of study) to determine the location and extent of habitat alteration. We estimated the year of timber harvest based on: (1) our own field notes; (2) USDA Forest Service harvest records; (3) University of California Berkeley Blodgett Experimental Forest harvest records; and (4) core samples of trees. We used an increment borer to extract complete cores of ≥ 4 trees immediately adjacent to a clear-cut or within a forest stand that had been thinned. We then estimated the year of harvest by locating a sustained increase in widths of tree rings, indicating reduced competition from other trees.

STATISTICAL ANALYSES

Territory occupancy. For female Spotted Owls, we estimated territory colonization (γ) and extinction (ϵ) probabilities (vital rates of territory occupancy) following MacKenzie et al. (2003). Territory colonization probability is the probability that a territory unoccupied in year $t - 1$ becomes occupied in year t , and territory extinction probability is the probability that a territory occupied in year $t - 1$ is unoccupied in year t . The probability of occupancy (ψ) in year t can be calculated from γ , ϵ , and ψ_{t-1} (MacKenzie et al. 2003) by:

$$\psi_t = \psi_{t-1}(1 - \epsilon_{t-1}) + (1 - \psi_{t-1})\gamma_{t-1}.$$

We modeled occupancy vital rates for females only because the most appropriate method for coding data of single male versus

single female responses from surveys was not clear. Modeling females only was a good indication of pair occupancy of a territory because unpaired females were rare during our study (we located only two females in 15 years that may have been unpaired during a year). Each territory was surveyed up to six times each year for 15 years.

We estimated γ and ϵ using program MARK (White and Burnham 1999). In addition to γ and ϵ , the analytical approach we used directly estimated the proportion of territories occupied in the first year of study. We accounted for imperfect detectability of owls while modeling γ and ϵ . We examined the following temporal structures for detection probability within and among years: constant (means model); linear trend; log-linear trend; and quadratic trend. We fitted a model for each combination of these temporal structures within and among years and ranked models using Akaike's information criterion (AIC; Burnham and Anderson 1998). We used the top-ranked detection probability structure for inference regarding the effect of habitat alteration on γ and ϵ .

We created three statistical models to examine the relationship between mature conifer forest and γ and ϵ . For all models we predicted that: (1) increasing amounts of mature conifer forest would be positively related to γ and negatively related to ϵ ; and (2) alteration of mature conifer forest would be negatively related to γ and positively related to ϵ . The first model included a time-varying individual covariate that depicted the amount of mature conifer forest in each territory each year. For the second model we used a categorical treatment effect with two levels, no alteration of mature conifer forest versus >0 ha mature conifer forest altered, to estimate if alteration of mature conifer forest affected territory extinction or colonization probability the subsequent year. The treatment effect for this model occurred regardless of the amount of mature conifer forest altered. Lastly, we created a third model that hypothesized that the amount of mature conifer forest altered in an individual territory had a long-term effect on colonization and extinction probability. This latter model was essentially an interrupted time series model and included a continuous variable that depicted the total area of mature conifer forest in each territory at the beginning of the

study, and a nominal variable with three levels that depicted the size of treatment: no mature forest altered, between 0 and 20 ha altered, or ≥ 20 ha altered. Unlike the second model above, we coded the categorical treatment variable to carry the effect forward in time. For example, if a territory had 30 ha of mature forest altered in 1992, the model was coded to examine a ≥ 20 ha treatment effect on γ and ε for this territory from 1993 to 2004. Our use of a 20 ha cutoff for the treatment level was arbitrary. We also examined variations of this latter model that included the starting amount of mature forest and a nominal variable with two treatment levels (<20 ha versus ≥ 20 ha), and an interaction between the starting area of mature forest and the categorical treatment effect. We ranked the plausibility of these competing models using AIC_c (AIC corrected for small sample size) and examined the 95% confidence intervals around the model coefficients to determine whether γ or ε was related to the area of mature conifer forest or categorical treatment effect. For analysis of γ and ε we divided the covariate depicting the total area of mature conifer forest in a territory by 260 to aid numerical optimization. Model coefficients presented in results are based on this transformation.

Breeding dispersal. Before examining the effect of habitat alteration on breeding dispersal, we first examined the probability of breeding dispersal as a function of owl sex, age, social status, and breeding status with the same approach used by Blakesley et al. (2006) in a study of Spotted Owls in the northern Sierra Nevada. We defined breeding dispersal probability as the probability that an individual moved to a different territory between year t and year $t + 1$. We created a dataset comprised of uniquely marked individuals and their dispersal histories. Each observation in the dataset consisted of a two-year period for one individual, whether the individual dispersed (switched territories) between years, and the U.S. Fish and Wildlife Service band number for the individual. We coded the binomial response as "0" for no dispersal and "1" for dispersal. We considered owl sex, age (first-year subadult, second-year subadult, or adult) during year 1, reproductive status during year 1 (successfully produced young or not), and social status (unpaired, paired, or paired but apparent death

of mate during the interval) as factors that might explain variability in dispersal probability. We also considered an interaction term between individual sex and breeding status. We analyzed data using a logistic regression (PROC GENMOD in program SAS release 8.02; SAS Institute Inc., Cary, North Carolina) and considered all possible subsets of factors. We ranked models based on their ability to explain variation in dispersal probability using QAIC (AIC corrected for overdispersion; Burnham and Anderson 1998). We calculated overdispersion of the data as χ^2 divided by the degrees of freedom. We calculated the Pearson χ^2 value using the "AGGREGATE" option of the GENMOD procedure and specified age, sex, social status, and breeding status as subpopulations.

Unlike Blakesley et al. (2006), we did not include a factor depicting territory quality in the all possible subsets modeling of dispersal probability. Instead, we included the variables in the top-ranked model from the all possible subsets regression and constructed two statistical models that were similar to the two treatment models we constructed for γ and ε : (1) a model with a categorical treatment effect with two levels, no alteration of mature conifer forest versus alteration of mature conifer forest; and (2) a model that included a continuous variable that depicted the total area of mature conifer forest in each territory during year 1, and a nominal variable with three levels that depicted the size of treatment (no mature conifer forest altered, between 0 and 20 ha altered, or ≥ 20 ha altered). We also considered variations of this latter model that included only two categorical levels of treatment (<20 ha versus ≥ 20 ha) and an interaction term between the amount of mature conifer forest in year 1 and treatment level. For the two treatment effect models we used a repeated measures approach with generalized estimating equations (Liang and Zeger 1986) to determine if habitat modification was related to dispersal probability. Observations were repeated on individuals (i.e., the blocking factor was the individual owl) and we determined statistical significance using the 95% CI for the regression parameters.

We compared the quality of the original territory with that of the new territory for owls that dispersed. We estimated the quality of

individual territories based on their expected survival. We calculated expected survival ($E[\hat{\phi}]$) following Seamans (2005) using the equation:

$$E(\hat{\phi}) = \{ \exp[1.5886 + 0.0420(\text{SEX}) + 1.5938(\text{COR57}) - 1.5602(\text{LAMT1}) - 1.2481(\text{LAMT23})] \} \div \{ 1 + \exp[1.5886 + 0.0420(\text{SEX}) + 1.5938(\text{COR57}) - 1.5602(\text{LAMT1}) - 1.2481(\text{LAMT23})] \}^{-1},$$

where SEX was a dummy variable coded 0 for females and 1 for males, COR57 was the amount (ha) of interior mature forest, LAMT1 was the natural log of the amount of hardwood forest, and LAMT23 was the natural log of the amount of pole, sapling, and brush cover types. Habitat covariates were transformed before estimation of the above equation to improve numerical optimization by dividing COR57 and AMT1 by 160, and AMT23 by 350. This model explained 93% of the variability in survival among territories (Seamans 2005). We did not consider reproduction when estimating habitat quality because the relationship between reproductive success and habitat was unclear for this population (Seamans 2005).

RESULTS

TERRITORY OCCUPANCY

We located and monitored Spotted Owls in 66 territories in our study areas from 1990 to 2004. Detection probability was constant among years, followed a log-linear trend within years, and varied between the density and regional study areas (Fig. 1). The area of mature conifer forest in individual territories ranged from 0 to 257 ha among years. Thirty-eight territories (58%) experienced some habitat alteration during our study. Habitat alteration in two territories was the result of stand-replacing wildfire while habitat alteration in all others was the result of timber harvest.

The probability of territory colonization (γ) and extinction (ϵ) was related to the area of mature conifer forest in a territory and alteration of this habitat (Table 1). The top three colonization models had essentially the same AIC_c weight (w_i), suggesting a high degree of model selection uncertainty. However, the only

model coefficient (β) with a confidence interval that did not include zero was the categorical effect of alteration of ≥ 20 ha mature conifer forest (gt20). The top model included the amount of mature conifer forest in a territory at the beginning of the study (1990) and the alteration of ≥ 20 ha of mature conifer forest. Alteration of ≥ 20 ha of mature conifer forest was negatively related to γ ; $\hat{\beta}_{\text{gt20}} = -1.16$ (95% CI = -2.02 to -0.29). The beginning amount of mature conifer forest (BMF) in a territory was positively related to γ , but had a confidence interval that included zero; $\hat{\beta}_{\text{BMF}} = 1.34$ (95% CI = -0.70 to 3.39). The top model, $\gamma(\text{BMF} + \text{gt20})$, indicated that territories in which ≥ 20 ha of mature conifer forest was altered experienced a 2.5% decline in occupancy probability.

The top territory extinction model ($\epsilon[\text{CMF}]$; Table 1) suggested that ϵ was negatively related to the amount of mature conifer forest in a territory ($\hat{\beta}_{\text{CMF}} = -2.58$, 95% CI = -4.48 to -0.68). “CMF” was a time-varying individual covariate depicting the amount of mature conifer forest in a territory. Model $\epsilon(\text{CMF})$ was four times as plausible as the second-ranked model; therefore, we chose to use model $\epsilon(\text{CMF})$ for inference. The structure of this model precluded us from separating the confounding effect of habitat alteration within territories versus variation in the amount of mature conifer forest among territories. However, if we assume that differences in mature

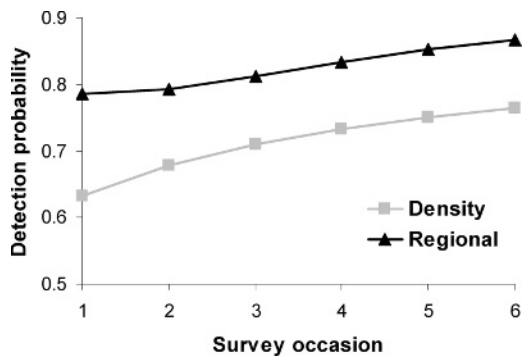


FIGURE 1. Female Spotted Owl within-year detection probability used to model territory colonization and extinction probability in the “density” and “regional” study areas in the central Sierra Nevada, 1990–2004. Each year we surveyed the complete density study area for Spotted Owls, whereas we did not survey areas between owl territories in the regional study area.

TABLE 1. Ranking of models (95% confidence set) depicting the relationship between the amount of mature conifer forest present and altered at individual territories and Spotted Owl territory colonization and extinction probability ($n = 66$ territories), and Spotted Owl breeding dispersal probability ($n = 565$), in the central Sierra Nevada, 1990–2004. Ranking of colonization and extinction models based on Akaike’s information criterion corrected for small sample size (AIC_c), while ranking of breeding dispersal models based on AIC corrected for overdispersion (QAIC). $\text{Log}(\mathcal{L})$ is the log-likelihood, K is the number of parameters, ΔAIC_c is the difference in Akaike’s information criterion from the top model, and w_i is the model weight.

Model ^a	$-2\text{log}(\mathcal{L})$	K	ΔAIC_c^b	w_i
Territory colonization probability (γ)				
$\gamma(\text{BMF} + \text{gt}20)$	3364.84	9	0.00	0.26
$\gamma(\text{BMF} + \text{gt}20 + \text{BMF}*\text{gt}20)$	3362.79	10	0.01	0.26
$\gamma(\text{BMF} + \text{ltgt}20)$	3362.87	10	0.09	0.25
$\gamma(\text{BMF} + \text{ltgt}20 + \text{BMF}*\text{ltgt}20)$	3360.53	12	1.87	0.10
$\gamma(\text{CMF})$	3369.65	8	2.77	0.07
Territory extinction probability (ϵ)				
$\epsilon(\text{CMF})$	3363.84	8	0.00	0.68
$\epsilon(\text{BMF} + \text{ltgt}20)$	3362.55	10	2.81	0.17
$\epsilon(\text{BMF} + \text{gt}20)$	3366.69	9	4.90	0.06
$\epsilon(\text{BMF} + \text{ltgt}20 + \text{BMF}*\text{ltgt}20)$	3361.39	12	5.77	0.04
Breeding dispersal probability (d) ^c				
$d(\text{BMF} + \text{gt}20 + \text{BMF}*\text{gt}20)$	274.83	9	0.00	0.56
$d(\text{BMF} + \text{ltgt}20 + \text{BMF}*\text{ltgt}20)$	273.69	11	2.86	0.14
$d(\text{BMF} + \text{gt}20)$	279.95	8	3.12	0.12
$d(\text{gt}0)$	283.13	7	4.30	0.07
$d(.)$	285.31	6	4.48	0.06

^a Abbreviations for model parameters: BMF = individual covariate representing amount of mature conifer forest at beginning of study; CMF = time-varying individual covariate representing amount of mature conifer forest; gt20 = categorical treatment effect for mature conifer forest of <20 ha or ≥ 20 ha; ltgt20 = categorical treatment effect for mature conifer forest of 0 ha, >0 and <20 ha, or ≥ 20 ha; gt0 = categorical treatment effect of mature conifer forest of 0 ha or >0 ha.

^b AIC_c of top colonization model = 3383.07 and of top extinction model = 3385.84; QAIC of top breeding dispersal model = 292.83.

^c All breeding dispersal models included the variables Age (age of owl: 1, 2, or ≥ 3 years old); Reproduction (did owl fledge young the previous year); and Social (a combination of pair status and mate loss).

conifer forest among territories caused the variation in territory extinction probability, model $\epsilon(\text{CMF})$ suggested that occupancy probability increased approximately 1.1% for every 20 ha difference in the amount of mature conifer forest among territories.

BREEDING DISPERSAL

We observed 51 incidences of breeding dispersal among 565 owl-years (i.e., total dispersal opportunities of 159 owls in 15 years of study). Overall, 33 females switched territories (of which 12 were single or had lost their mate), while 18 males switched territories (of which 10 were single or had lost their mate). Overdispersion in the dataset was slight ($\hat{c} = 1.15$). Results from the all possible subsets modeling suggested that owl age, sex, and social status best described variation in the probability of

breeding dispersal. The only two competing models (≤ 4 QAIC_c units from top model) included these same three variables plus: (1) reproductive status (repro) in the previous year; and (2) the interaction of reproductive status in the previous year and owl sex. However, model coefficients for these additional variables had confidence intervals that significantly overlapped zero ($\hat{\beta}_{\text{repro}} = -0.19$, 95% CI = -0.57 to 0.17 ; $\hat{\beta}_{\text{sex} \times \text{repro}} = 0.10$, 95% CI = -0.28 to 0.53). Therefore, we chose to use a model with owl age, sex, and social status for further inference.

The probability of breeding dispersal (d) was related to the area of mature conifer forest in a territory and alteration of this habitat (Table 1). The top-ranked model, $d(\text{BMF} + \text{gt}20 + \text{BMF}*\text{gt}20)$, suggested that d was negatively related to the area of mature conifer

TABLE 2. Parameter estimates from the top-ranked logistic regression model examining breeding dispersal probability of California Spotted Owls in the central Sierra Nevada, 1990–2004.

Parameter	Estimate	CI
Intercept	6.42	2.55 to 10.30
Age class (S1)	1.08	0.09 to 2.08
Age class (S2)	1.68	0.79 to 2.57
Sex (F)	1.00	0.24 to 1.75
Social status (Pair)	-1.30	-2.04 to -0.57
Social status (Single)	1.85	0.54 to 3.16
BMF ^a	-0.55	-0.90 to -0.20
gt20 ^b (0)	-8.61	-12.29 to -4.94
BMF*gt20 (0)	0.53	0.19 to 0.88

^a BMF = individual covariate representing amount of mature conifer forest in territory in year prior to potential or actual dispersal; transformed for analysis by dividing raw numbers by 10.

^b Categorical treatment effect for mature conifer forest coded "0" for <20 ha or "1" for \geq 20 ha.

forest in a territory just prior to actual or potential dispersal, and positively related to alteration of \geq 20 ha of mature conifer forest. Confidence intervals for model coefficients representing mature conifer forest and alteration of \geq 20 ha of mature conifer forest did not overlap zero (Table 2). The interaction term suggested a steep increase in d in territories with <150 ha of mature conifer forest that experienced alteration of \geq 20 ha of this forest type (Fig. 2). This steep increase in d was disproportional in comparison to territories with lesser amounts of this forest type that did not experience habitat alteration. For example, an individual in a territory with 100 ha of mature conifer forest (median = 99 ha for our study population) in which \geq 20 ha were altered was estimated to have a much higher d than an individual in a territory that started with 80 ha yet had no mature conifer forest altered. For owl-specific variables in the top model, d was: (1) 0.09 times higher for first-year subadults than adults and 0.14 times higher for second-year subadults than adults; (2) 0.08 times higher for females; and (3) 0.11 times less for owls that were paired and did not lose their mates than for owls that were paired but lost their mates, and 0.15 times higher for unpaired owls than for paired owls who lost their mates.

Owls that switched territories apparently did not select new territories based on higher quality; only 53% of owls that switched territories moved to a territory with higher

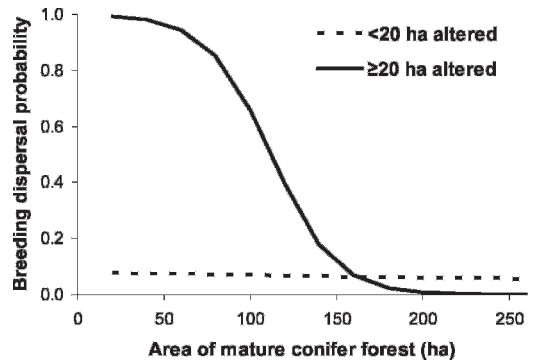


FIGURE 2. The relationship between paired female Spotted Owl breeding dispersal probability and the amount of mature conifer forest in a territory in the central Sierra Nevada, from 1990 to 2004. Dispersal probability increased rapidly at territories with <150 ha of mature conifer forest when \geq 20 ha of this habitat type was altered. The x-axis represents the amount of mature conifer forest prior to actual or potential dispersal. The dashed and solid lines represent predicted dispersal probability when <20 ha or \geq 20 ha of mature conifer forest were altered, respectively.

expected survival. We estimated that approximately 6% (three of 51) of owls that dispersed were unpaired after they switched territories, compared to 5% (51 of 1092) of all owls during the study. However, in the year prior to dispersal, 45% (23 of 51) of owls that switched territories were either unpaired or had lost their mate. We observed 14 breeding dispersal events in which one or both pair members switched territories and both formed a pair with a new mate.

DISCUSSION

We found that the amount of mature conifer forest was correlated with Spotted Owl habitat choice. Territories with more mature conifer forest had a higher probability of being colonized and a lower probability of becoming unoccupied. Further, alteration of mature conifer forest appeared to decrease the probability of colonization. Although we estimated that breeding dispersal was more likely when habitat alteration occurred, it was not clear if this increase or changes in other demographic processes were responsible for variability in territory extinction probability. For example, because Spotted Owl survival is correlated with the area of mature conifer forest in individual

territories (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005, Seamans 2005), it is possible that habitat alteration affected survival, which in turn increased the probability of a territory becoming unoccupied. Conversely, it is possible that habitat alteration did not result in decreased survival but in increased emigration from the study population. In a related study, Olson et al. (2005) estimated that Spotted Owl occupancy declined 5%–15% in three study areas ($n = 125$ to 146 sites) when Barred Owl (*Strix varia*) presence increased, and noted that these declines could have been the result of either death or emigration.

Our use of a categorical variable to depict the amount of habitat altered allowed us to examine the relationship between alteration of mature conifer forest and Spotted Owl habitat selection. However, our use of broad categories may not have adequately represented the effect of very large or very small changes in mature conifer forest. For example, alteration of 20 ha of mature conifer forest was considered the same as alteration of 80 ha. Although this range within the categorical habitat variables likely made detecting statistical relationships more difficult, creating more detailed categories would have resulted in small sample sizes within categories. Thus, the inference that territory extinction was not related to alteration of mature conifer forest because a categorical treatment variable was not in the top model should be made with caution. In addition, the broad range of values in the categorical variable may be partially responsible for the steep increase in dispersal probability in territories with <150 ha of mature conifer forest.

Our estimate of Spotted Owl breeding dispersal probability (9%) is similar to estimates by Forsman et al. (2002; 7%) and Blakesley et al. (2006; 7%) for other Spotted Owl populations. The relationship between breeding dispersal probability and age, sex, and social status appears to be consistent for Spotted Owls. Similar to our study, Forsman et al. (2002) and Blakesley et al. (2006) estimated that younger owls were more likely to disperse than older owls, females were more likely to disperse than males, and unpaired owls were more likely to disperse than paired owls. However, Forsman et al. (2002) and Blakesley et al. (2006) also estimated that owls that nested during the previous year were less likely to disperse than

owls that did not nest, whereas the effect of reproductive status in the previous year was poorly supported in our analysis. Prior to our study, the effect of habitat alteration on dispersal probability had not been examined in depth for the Spotted Owl, although Bond et al. (2002) examined Spotted Owl territory fidelity after wildfire and found that 11% (two of 18) of Spotted Owls switched territories the year after wildfire.

Breeding dispersal is an important life history trait that has likely evolved to increase individual fitness (Greenwood and Harvey 1982). Although the mechanisms behind the evolution of breeding dispersal are unclear, it is generally agreed that breeding dispersal can have significant effects on individual fitness and population dynamics (Greenwood and Harvey 1982, Clobert et al. 2001). Most theoretical models either predict or assume that dispersing individuals should be “ideal” when selecting a habitat, in the sense that they should settle in the highest-quality site available (Fretwell and Lucas 1969, Pulliam and Danielson 1991). Our results regarding the effect of habitat alteration on breeding dispersal, territory colonization, and territory extinction support this hypothesis. However, we did not find that Spotted Owls chose sites with more mature conifer forest, i.e., sites of higher quality, following breeding dispersal. This may indicate that the disturbance associated with habitat alteration, regardless of the extent of area altered, was an important factor motivating breeding dispersal, yet owls were either imperfect in their ability to assess habitat quality of new territories or chose a territory in which to settle based on other factors. It did appear that mate acquisition was a primary factor in selecting a territory; 43% of dispersing individuals were unpaired prior to dispersal compared to 6% after dispersal. Thus, it is surprising that we did not find that previous reproductive success was a good predictor of breeding dispersal probability. Prior reproductive success has been suggested as a primary factor determining breeding dispersal of many bird species (Wiklund 1996, Haas 1998, Catlin et al. 2005), including Spotted Owls (Forsman et al. 2002, Blakesley et al. 2006). Further, Ens et al. (1995) viewed site choice for the Oystercatcher (*Haematopus ostralegus*) as a “career decision” because of the long-term consequences for

individual fitness. We suspect a similar scenario is possible for the Spotted Owls we studied because they exhibited a relatively low probability of breeding dispersal, and because there appeared to be substantial differences among territories in terms of their quality (Seamans 2005).

Individual Spotted Owls may choose territories for something other than their intrinsic quality. We found evidence that selection of new territories by breeding individuals was not correlated with the amount of mature forest, but may have been associated with the presence of a mate. In addition, Seamans and Gutiérrez (2006) estimated that immigrants (it was unknown if they reflected breeding or natal dispersal events) appeared to use conspecifics as cues for settlement, although conspecifics may not always indicate the highest quality territory available. A further confounding factor for estimating the mechanisms responsible for selection of territories is the unknown effect anthropogenic actions have on the selective pressures responsible for breeding dispersal and habitat selection (Stamps 2001). For example, cues (e.g., the amount of mature conifer forest, the presence of a mate, or the occupancy of neighboring territories) that Spotted Owls once used to evaluate habitat quality may no longer reliably indicate quality (Hildén 1965). Our results for breeding dispersal partially support this hypothesis, while our results for territory colonization and extinction probability suggest that Spotted Owls are occupying higher quality territories.

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