Original Article

Use of Private Lands for Foraging by California Spotted Owls in the Central Sierra Nevada

PERRY J. WILLIAMS,[1,2] *Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 200 Hodson Hall, 1980 Folwell Avenue, Saint Paul, MN 55108, USA*

SHEILA A. WHITMORE,[3] *Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 200 Hodson Hall, 1980 Folwell Avenue, Saint Paul, MN 55108, USA*

R. J. GUTIÉRREZ, *Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 200 Hodson Hall, 1980 Folwell Avenue, Saint Paul, MN 55108, USA*

ABSTRACT The use of private land by owls has long been of interest to wildlife managers in the Sierra Nevada, California, USA, because private lands could contribute to owl conservation if it is used extensively. Therefore, we studied the use of private lands for foraging by 14 California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, California during 2006. We modeled foraging locations as a function of 2 land-ownership categories within an owl's territory: public and private land. The log probability of an owl using a public-land location was 15% greater than for a private-land location. Private-land distribution was relatively consistent with respect to the geometric center of owl home ranges, suggesting that our result was not influenced by a peripheral distribution of private land in owl home ranges. Based on our findings, national forest lands within our study area currently have more foraging habitat for California spotted owls than do private lands. We recommend that managers consider owl use of private land within the context of our results when developing conservation strategies for California spotted owls in the central Sierra Nevada.

KEY WORDS California spotted owl, managed forests, public land, radiotelemetry, resource selection function, *Strix occidentalis occidentalis*.

California spotted owls (*Strix occidentalis occidentalis*) occur primarily on public lands in the Sierra Nevada. Therefore, management of California spotted owls has relied on protecting the owl's primary habitats within national forests (Verner et al. 1992, U.S. Forest Service 2004). Management plans for California spotted owls have ignored potential habitat contributions from private land because of the variability in land practices, uncertainty in long-term distribution and suitability of these habitats, and the legal status of the owl (i.e., it is not currently listed under the Endangered Species Act; Verner et al. 1992, U.S. Forest Service 2004). This decision has been controversial because 30–40% of forested land in the Sierra Nevada is on private land (Verner et al. 1992, Davis and Stoms 1996). Owls use forests on private land when they are adjacent to owl territories on public land (Williams et al. 2011), and, in some areas, private land is the primary land used by owls (Irwin et al. 2007). In general, California spotted owls use a broader array of forest types and edge habitats for foraging than they do for nesting and roosting. If California spotted owls were listed as threatened under the Endangered Species Act, the potential contribution of private lands, for foraging, nesting, and roosting, to recovery would be assessed across the Sierra Nevada. Thus, it is important to understand the extent to which owls use private land for foraging to allow comprehensive planning for owls in the Sierra Nevada. The U.S. Forest Service (2003) reported that >15% of known California spotted owl locations had >15% of their potential home range on private lands, and there were 135 known owl territories on private land. In addition, in one area of the Sierra Nevada more owl roost and nest locations were located on public land than on private land (Gutiérrez 1994), which has raised additional uncertainty about the value of private land to owls in this region (i.e., is it used primarily for foraging if not for nesting and roosting?).

Therefore, we modeled habitat selection by California spotted owls as a function of land ownership to evaluate the potential contribution of private land to owl conservation in the Sierra Nevada. Specifically, we examined whether owls selected public land with a higher probability than private land.

STUDY AREA

Our study area was 3,188 km^2 in the approximate center of the Sierra Nevada, California. The topography was

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[1]*E-mail: Perry.williams@colostate.edu*
[2]*Present address: Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO 80523, USA*
[3]*Present address: Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 226 Russell Labs, 1630 Linden Drive, Madison, WI 53706, USA*

mountainous and bisected by steep river drainages. Elevations ranged from 233 m to 3,041 m. The study area had a Mediterranean climate with hot, dry summers and cold, wet winters. Vegetation at lower elevations was dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), and California black oak (*Quercus kelloggii*), and at higher elevations by California red fir (*A. magnifica*; Küchler 1977). Vegetation was influenced by land ownership, aspect, climate, fire, logging, livestock grazing, edaphic conditions, and elevation (Laymon 1988, Bias and Gutiérrez 1992, Verner et al. 1992, Skinner and Chang 1996). These influences resulted in a diverse pattern of forest types. National forests (public land) comprised 2,363 km^2 (74%) of the study area and were managed according to the Sierra Nevada Framework (U.S. Forest Service 2004). Private land comprised 825 km^2 of our study area. Industrial private timber companies were the largest private-land owners (88%), and were required to manage their land in accordance with the California Forest Practices Act (California Forest Practices Rules 2010 Title 14, California Code of Regulations Ch. 4, 4.5, and 10) but not specifically for California spotted owls. The spatial arrangement of private lands within the study area varied, but was often arranged in a checkerboard distribution (Bias and Gutiérrez 1992).

METHODS

Owl Population Description and Sample Selection

We selected our sample of owls randomly from among a subset of all known owl territories in the study area. Our subset included the owl territories that met the following 4 criteria. First, owl territories could not have had tree harvest within their hypothetical home range within the past 5 years or during our study. Second, territories had to be located in areas with a high ratio of public to private land (i.e., <50% private land). Third, owl territories had to have sufficient suitable habitat to allow for a harvest treatment of up to 121 ha and still retain enough (121 ha) suitable habitat for owl management (242 ha total). Fourth, owls could not be captured and radiomarked if they were part of demographic studies in the region. We developed these 4 constraints because this sample of owls was also used to examine the effects of fuel reduction treatments on owls in a separate study. The first and second criteria allowed us to avoid recent or concurrent timber harvest in the territory of owls, which could confound the results. The third criterion ensured that we only included territories that contained enough suitable habitat for owls after the planned harvest occurred. Finally, the forth criterion ensured that we did not interfere with other research studies in the area by radiomarking owls (i.e., potential to confound estimates of vital rates; Paton et al. 1991).

The fact that we avoided territories with a high ratio of private to public land meant we had the potential to bias our inference because we were interested in comparing relative use between these 2 ownership categories. For example, theoretically, when eliminating those territories that had a high proportion of private land, we could have inadvertently been selecting owl home ranges whose center was public but whose periphery was private because the closest 300 acres (121 ha) surrounding an owl's nest or roost site were designated as a protected habitat area by the U.S. Forest Service. Thus, with all home ranges centered on public land, one might predict that private land would be on the periphery of home ranges. If private lands were on the periphery of home ranges, owls would show disproportionate use of public land because they are central place foragers (Carey and Peeler 1995, Rosenberg and McKelvey 1999). To address this issue we did the following: first, we only made inference to the territories in our study site that met these criteria; second, within each territory we examined the ratio of public to private land to determine whether this ratio changed from the center of the owl's territory to the periphery of their territory. We did this because we wanted to know what proportion of private land was available to owls, and if the availability changed as a function of the distance from the center of an owl territory to its periphery. We examined how this ratio changed as a function of distance by first identifying the geographic center of each owl's recorded telemetry locations. We then created a circle for each owl with the center of the circle at the geometric center of telemetry locations, and radius extending from the center to the owl's furthest telemetry location. We then generated a grid of systematic points spaced every 50 m within each circle and identified the land ownership at each point. Using these land-ownership identifications, we calculated the proportion of points that were public. Finally, we examined how this proportion changed as a function of increasing distance from the center of the circles.

From our population of territories that met our sampling criteria, we randomly selected 12 owl territories representing 24 owls (12 pairs). At each of the 12 territories, we surveyed for owls following the methods described by Forsman (1983). We determined their sex by vocal characteristics (Forsman et al. 1984), their age by plumage characteristics (Forsman 1981), and their pair status by behavioral associations (Franklin et al. 1996). We attempted to capture all owls and outfit them with a backpack very high frequency radiotransmitter (Model RI-2C; Holohil Systems Ltd., Carp, ON, Canada) attached with a Teflon®-coated harness, a U.S. Geological Survey locking aluminum band, and a uniquely colored plastic band and tab (Franklin et al. 1996). To locate radiomarked owls we triangulated on radio signals and recorded the compass direction to the strongest radio signal detected at ≥3 monitoring stations spaced >160 m apart within 30 min. We only used locations that had confidence ellipses <5 ha for analysis. We used telemetry locations collected one-half hour before sunset to one-half hour after sunrise (Williams et al. 2011).

Modeling Resource Use by Owls

We examined habitat use using the exponential form of the resource selection function (RSF): $w_j = \exp\{\beta_1 x_{1j} + \ldots + \beta_k x_{kj}\}$, where w_j was the relative probability of selection at location j and $x_{1j},\ldots,x_{kj}$ were covariates we measured at each telemetry location for models with β_0, …, β_k estimated parameters. For the RSF, we excluded the estimated parameter β_0 (Manly et al. 2002). We estimated our parameter values and selected our model for our RSF using generalized linear mixed-effects regression models (GLMM). In our GLMM we assumed a binomial distribution of the response variable and a logit link. Our response variable was whether the location was a nighttime telemetry location (i.e., used) or a randomly selected location (i.e., available). We selected our random locations from within the minimum bounding circle (i.e., the smallest circle that enclosed every point) around all of each owl's radiotelemetry locations (for the purposes of this study, we termed this an owl's home range). The mean minimum bounding circle was 3,775 ha (SD = 4,725 ha). We used a systematic grid of samples, with 1 location every 50 m within each owl's home range. The number of available locations depended on the size of the territory and ranged from 1,043 to 64,977 locations. We examined the effect the number of available points we used had on our parameter estimates by inspecting trace plots of the parameter value against available sample size to ensure each parameter converged.

Because our main objective was to examine the relative land-ownership use by owls we considered a covariate that identified land ownership at each location as public or private. We used land-ownership data from the Placer and Eldorado County Assessor offices, interfaced with owl location data using a Geographical Information System (ArcMAP Version 10.1), to estimate whether a location was on public or private land. In addition to land ownership, we also considered distance from a location to the center of the owl's observed activity. We did this because we thought the probability an owl would use a location would decline for locations further from the center of their observed activity. Rosenberg and McKelvey (1999) showed that nesting spotted owls exhibited this behavior. Specifically, in their study, owls selected forage locations near their nest tree with higher probability than more distant locations. Because owls in our study did not nest, and because they used multiple roosts, we selected the geometric center of the nighttime telemetry locations as the center from which to measure distance to locations. We considered distance functions up to a third-order polynomial in our model suite. Lastly, we considered owls a random effect, and thus, the intercept of our model was able to change for each owl. Thus, our most general GLMM was

$$Y_{ij} \sim \text{Binomial}\,(1, p_{ij})$$

$$\text{logit}\,(p_{ij}) = \beta_0 + \beta_1(\text{owner}_{ij}) + \beta_2(\text{dist}_{ij}) + \beta_3(\text{dist}^2_{ij}) + \beta_4(\text{dist}^3_{ij}) + a_i$$

$$a_i \sim N\,(0, \sigma^2_a)$$

where p_{ij} was the probability that the ith owl would use the jth location; owner = 0 for private land and owner = 1 for public land; dist_{ij} was the distance between each location and the ith home-range center; a_i was a random effect for each owl that had a normal distribution with mean 0, and variance σ^2_a.

To examine the hypothesis that the ownership was correlated with location selection by owls, we created 8 models. Four of the 8 models included the ownership variable, and the other 4 models did not (Table 1). Each set of 4 models consisted of a model with no distance function, a linear distance function, a quadratic distance function, and a third-order polynomial for the distance function (Table 1). We estimated the parameters and model fit using the lme4 package in Program R (function:glmer). We compared our models using the approximated Akaike's Information Criterion (AIC). We selected the model with the lowest AIC value to use in our RSF.

RESULTS

We collected 1,339 nighttime telemetry locations (range = 41–209 locations/owl) distributed among 14 data sets obtained from 13 radiomarked owls (1 owl was considered as 2 separate samples because it dispersed to a new (non-overlapping) territory after its mate died and, therefore had access to a different landscape comprising a different proportion of private land). Thus, our sample of owls for home-range analysis consisted of 4 pairs, 4 single female owls, and 2 single male owls. We recorded 156,297 systematic, available locations within the bounded home ranges of owls. Of foraging locations and random locations, 19% ($n = 256$) and 26% ($n = 41{,}152$), respectively, were on private land. The maximum difference in the ratio of public:

Table 1. Generalized linear mixed models developed to examine the functional relationship between California spotted owl resource selection and land ownership in the Sierra Nevada, California, USA, during 2006, and the model selection results. We used generalized linear mixed models to obtain our parameter estimates for our resource selection function and for Akaike's Information Criterion (AIC) estimates. The model was: $\text{logit}\,(p_{ij}) = \boldsymbol{x}^T_{ij}\boldsymbol{\beta} + a_i$, where p_{ij} was the relative probability of use for the ith owl and jth location, and $\boldsymbol{x}^T_{ij}\boldsymbol{\beta}$ were the 8 models below, and a_i was a random effect for each owl.

Model ($\boldsymbol{x}^T_{ij}\boldsymbol{\beta}$)	No. fixed effects parameters	ΔAIC
$\beta_0 + \beta_1(\text{dist}) + \beta_2(\text{dist}^2) + \beta_3(\text{dist}^3) + \beta_4(\text{public})$	5	0.00
$\beta_0 + \beta_1(\text{dist}) + \beta_2(\text{dist}^2) + \beta_3(\text{dist}^3)$	4	1.67
$\beta_0 + \beta_1(\text{dist}) + \beta_2(\text{public})$	3	15.60
$\beta_0 + \beta_1(\text{dist})$	2	17.38
$\beta_0 + \beta_1(\text{dist}) + \beta_2(\text{dist}^2) + \beta_3(\text{public})$	4	17.50
$\beta_0 + \beta_1(\text{dist}) + \beta_2(\text{dist}^2)$	3	19.36
$\beta_0 + \beta_1(\text{public})$	2	179.30
β_0	1	183.57

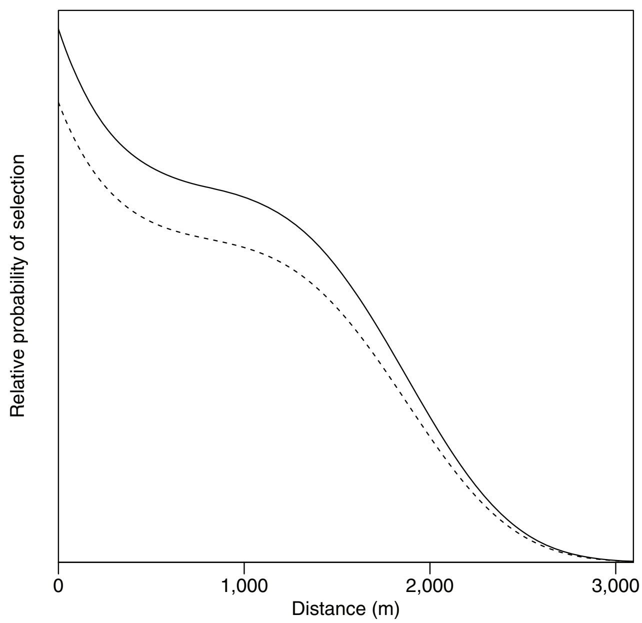

Figure 1. Estimated resource selection function for a population of California spotted owls in the central Sierra Nevada, California, USA, during the summer of 2006. The solid line is the estimated function for public land, and the dashed line is for private land. Distance from center is the distance from the geometric center of owl use locations.

private land from between 0 m and 1,000 m of the geometric center (approx. 315 ha; 79% public) and 0–5,000 m of the geometric center (approx. 7,850 ha; 74% public) was 5%.

Our model with the lowest approximated AIC included the owner variable, and all 3 distance variables (Table 1). This model indicated that our sample of owls were more likely to select public land than private land (Table 1). The RSF with the estimated parameters from our top model was:

$$w_j = \exp\{0.15\,(\text{owner}_j) - 2.06\,(\text{dist}_j) + 4.35\,(\text{dist}_j^2) - 3.46\,(\text{dist}_j^3)\}$$

where 0.15 was the increase in the log relative probability of use for public land, and −2.06, 4.35, and −3.46 described the change in log relative probability of use for one standard deviation change in distance from the center of the territory (1 SD = approx. 2,000 m; Fig. 1). None of the confidence intervals for the parameter estimates overlapped 0 (Table 2). The distance function included in the model indicated that owls selected locations near the center of their home range with higher probability than more distant locations (Fig. 1).

Table 2. Parameter estimates and their associated 95% confidence intervals for our top model estimating resource selection by California spotted owls in the central Sierra Nevada, California, USA, during summer 2006.

Fixed effects	Estimate	Lower 95% CI	Upper 95% CI
public	0.15	0.10	0.20
dist	−2.06	−2.69	−1.42
dist^2	4.35	2.30	6.39
dist^3	−3.46	−5.08	−1.83

These values were estimated using a generalized linear mixed model, and were used for the parameter estimates in the resource selection function.

The estimate of the variance of the population of owls for the random intercept (i.e., σ_a^2) was 0.57.

DISCUSSION

As is the case with all studies using model-based inference, our inference is to the population whose observable characteristics of habitat use are similar to our observed sample. We selected our sample over a large geographical area (3,188 km^2) randomly from a subset of owls based on the specific inclusion criteria listed in the methods. Thus, our sampling procedure increased the probability that our sample was representative of the owls in our study area that fit these criteria.

We examined the functional relationship between owl foraging use and land ownership. Both public and private land in the central Sierra Nevada have experienced a complex history of logging, which has resulted in a highly heterogeneous landscape on both public and private land (Bias and Gutiérrez 1992). This history has created uncertainty about habitat relationships of spotted owls in the Sierra Nevada (Verner et al. 1992). One of these uncertainties was the use of private lands by spotted owls. We found that, although owl home ranges overlapped a large amount of private land, they used private land disproportionately less than they did public land. Thus, our findings supported previous observations that owls will forage on private land, but, at least in the central Sierra Nevada, it was used less than public land.

Although, land ownership alone did not influence habitat selection by owls, there were several potential explanations for our results of differential use of public and private land. First, the distribution of public and private land within the home ranges of owls we studied could have influenced owl use patterns. If private lands were found primarily on the periphery of home ranges, we would expect owls to use it less because owls are central place foragers and more likely to use areas near their nest for foraging (Carey and Peeler 1995, Rosenberg and McKelvey 1999). This was not the case because the proportion of private land only varied by about 5% from the geometric center of an owl's home range to its periphery. Second, it was possible that either vegetation composition or structure or both could have been different between public and private land. Many studies have shown that spotted owls are habitat specialists that use late-successional forest stands with complex structure and composition disproportionately to its availability (Gutiérrez et al. 1995). A greater amount of these forest types was likely found on public land because of conservation requirements and other constraints on land management placed on national forest managers (Collins et al. 2010). Laymon (1988) and Bias and Gutiérrez (1992) reported that private lands within our study area were more heavily logged than public lands, with both large trees and dead or dying trees removed during logging operations. Bias and Gutiérrez (1992) further noted that the number of possible nest trees, basal area of old-growth trees, mean height of old-growth trees, number of possible nests in old-growth trees, and basal area of snags were different between public and private land.

Therefore, differences in land use by California spotted owls might have reflected differences in vegetation and/or structure available to these radiomarked owls. When one considers that habitat heterogeneity is positively correlated with owl home-range size in the central Sierra Nevada (Williams et al. 2011), it is not surprising that owl home ranges in the central Sierra Nevada contain a mix of public and private lands because of the intermixed distribution of these ownerships. Yet, the owl's disproportionate use of private lands suggests that private land is not of as high value to the owls as public land.

MANAGEMENT IMPLICATIONS

Our results suggest privately owned land is not equivalent to publicly owned land as a contributor to spotted owl conservation in the central Sierra Nevada. Hence, conservation strategies should rely primarily on public land management. Moreover, timber harvest and management actions that reduce the amount of suitable owl habitat in potential home ranges that have a high proportion of private land should be minimized. We also suggest that managers of private land consider timber harvest strategies that, at minimum, maintain foraging habitat because owls will use a broader array of habitats and structure for foraging than they do for nesting and roosting.

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