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Source: Journal of Wildlife Management, 71(4):1183-1191. 2007.

Published By: The Wildlife Society-2

DOI: 10.2193/2006-122

URL: <http://www.bioone.org/doi/full/10.2193/2006-122>

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Modeling Foraging Habitat of California Spotted Owls

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ABSTRACT We linked radiotelemetry data from California spotted owls (*Strix occidentalis occidentalis*) with forest inventory data from mixed coniferous forests managed primarily via partial timber harvest practices. We estimated a discrete-choice resource selection function (RSF) based upon 21 choice sets from the forest inventories and nocturnal telemetry locations of radiotagged adult spotted owls occupying 17 home ranges. Nocturnal foraging was strongly associated with forests close to nests and small streams. The combined basal areas of Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and red fir (*Abies magnifica*) and basal area of hardwoods ≥ 20 cm diameter at breast height were positively and unimodally correlated to foraging habitat selection by owls, whereas the relative probability of selection decreased with increasing basal area of ponderosa pine (*Pinus ponderosa*). Opportunistically collected diurnal data indicated that owls roosted in forest stands that contained greater tree densities than those used for foraging. Topographic position, habitat heterogeneity, tree species composition, and forest density also influenced foraging site selection. Because our results indicated that forests can be too dense as well as too open, the study suggests that judiciously applied silvicultural prescriptions may maintain or improve owl foraging habitat. By linking the RSF with forest-inventory data and forest-growth models specific to the region of our study, forest managers can forecast potential consequences of silvicultural options on spotted owl foraging habitat at the level of individuals or that of a population. (JOURNAL OF WILDLIFE MANAGEMENT 71(4):1183–1191; 2007)

DOI: 10.2193/2006-122

KEY WORDS California spotted owl, discrete-choice model, foraging, managed forests, radiotelemetry, resource selection function, *Strix occidentalis occidentalis*.

Thomas et al. (1990) and Verner et al. (1992), in devising conservation strategies for the northern (*Strix occidentalis caurina*) and the California subspecies (*S. o. occidentalis*) of spotted owls, respectively, recommended evaluating spotted owl responses to forestry practices that are less invasive than clearcutting. They hoped that demonstrably beneficial or benign silvicultural prescriptions would be identified. To date, there is little published information that supports reliable comparisons of the short- and long-term effects of such less intensive silvicultural treatments in forests occupied by spotted owls. To our knowledge, only Irwin et al. (2004) developed a habitat assessment model that could forecast the potential effects of thinning small-diameter, shade-tolerant understory trees in mixed coniferous forests occupied by northern spotted owls in Washington's eastern Cascades, USA. Also, Lee and Irwin (2005) linked a forest-growth model with a simple habitat model for evaluating modest reductions in overstory canopy cover of forests occupied by California spotted owls in the Sierra National Forest, California, USA.

Numerous studies compared habitat use by northern spotted owls with availability of seral stages or forest age classes (e.g., Forsman et al. 1984, Glenn et al. 2004). Yet various silvicultural applications of partial harvesting do not change seral stages. Instead, those practices modify stand density, basal area, tree species composition, and tree size-class distribution. Furthermore, seral stages or age classes do not lend well to forecasting future conditions via forest-growth models, which require greater detail. Continuous measures of stand details are required for evaluating

responses by spotted owls to partial-harvest forestry practices (Zabel et al. 1992). Here, we report responses by California spotted owls to variation in forest stand details that resulted largely from previous partial timber harvests in mixed coniferous forests.

We wanted to estimate a resource selection function (RSF) for spotted owls occupying an extensively managed, private industrial forest that was interspersed with less intensively managed and natural federal forests. Resource selection functions (Manly et al. 2002) provide an optimal means of linking spotted owl foraging behavior with their habitat and environmental conditions because RSFs can combine multiple and interacting covariates. Resource selection functions provide reasonable balance between prediction and habitat theory, and thereby have applications in cumulative effects analysis or risk assessment, forest management planning, and population viability analysis (Boyce et al. 1994, Boyce and McDonald 1999). When linked with forest-growth models, spatially explicit harvest-optimizing tools (VanDeusen 2001), and fire-risk models in a Geographic Information System (GIS; McDonald and McDonald 2002), RSFs provide powerful comparative risk assessment and decision-support tools for natural resource managers (Boyce et al. 2002).

We wanted to evaluate nocturnal habitat selection when owls hunt most extensively because we assumed that foraging choices and other nocturnal behaviors, such as territory maintenance, influence lifetime reproductive performance and survival (Newton 1979). We aimed to identify the combinations of vegetative and physical environmental factors that compose foraging habitat. Objectives included estimating a RSF that could 1) include forest stand details so

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as to forecast initial consequences of applications of partial harvesting, 2) forecast long-term effects when linked with forest-growth and other models, 3) promote development of silvicultural prescriptions that may support conservation of California spotted owls, and 4) clarify vegetative and abiotic influences on California spotted owl habitat selection.

STUDY AREA

Forests in our study area ranged from 700 m to 1,700 m in elevation and were about 50 km east of Chico, California. The forests predominantly contained medium-sized trees: average quadratic mean diameter ranged from 30 cm to 36 cm. The forests were relatively continuous and dense, averaging 1,205 trees/ha, and overstory canopy cover was usually $\geq 40\%$ and averaged nearly 70%. The lands were owned primarily by Sierra Pacific Industries and included some United States Forest Service lands. Forest vegetation was mixed coniferous, dominated by Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), incense cedar (*Libocedrus decurrens*), and occasional sugar pine (*Pinus lambertiana*), and graded into red fir (*Abies magnifica*) at higher elevations. Common hardwood species included California black oak (*Quercus kelloggii*), tanoak (*Lithocarpus densiflorus*), canyon live oak (*Quercus chrysolepis*), and bigleaf maple (*Acer macrophyllum*). Important understory species included Pacific yew (*Taxus brevifolia*), Pacific dogwood (*Cornus nutallii*), California nutmeg (*Torreya californica*), and shrubs such as buckbrush (*Ceanothus* spp.).

The privately managed forests in our study area sustained a variety of past silvicultural treatments, having been managed extensively for wood products for >100 years. A significant portion of the area had been harvested at 10–20-year intervals via overstory removals that included thinning from below (i.e., an upper diam limit). Recent regeneration methods have involved small (7–10 ha) clearcuts, selective harvests, and shelterwood treatments. By incorporating some less intensively managed and natural federal forests, our study area contained a broad range of vegetative and structural conditions, providing a useful template for a retrospective evaluation of factors influencing foraging habitat selection by monitoring radiotagged California spotted owls.

Major prey items included woodrats (*Neotoma* spp.), deer mice (*Peromyscus maniculatus*), red tree voles (*Arborimus longicaudus*), and northern flying squirrels (*Glaucomys sabrinus*), based upon Zabel et al. (1995) and Clark (2002). Pocket gophers (*Thomomys* spp.) are also important to California spotted owls (Munton et al. 2002).

METHODS

We radiotracked spotted owls from April 1999 through March 2004, using standard methods described by Carey et al. (1989), Guetterman et al. (1991), and Millsbaugh and Marzluff (2001). We located and captured owls using accepted procedures (Forsman 1983). Briefly, that involved locating owls by imitating their calls, enticing them with

pet-store mice (*Mus musculus*), and capturing them via noose poles or by hand in early breeding season or summer. We attached tail-mounted transmitters (1999) or backpack harness transmitters (2000–2004) of 7.5–8.0-g mass because there were concerns about the possible effects of previously used 19–24-g backpack-mounted transmitters on owl reproduction and survival (see Paton et al. 1991 and Foster et al. 1992). Although the smaller transmitter packages that we used apparently do not negatively influence spotted owl reproductive success (Irwin et al. 2000) or survival (Loehle et al. 2005), questions linger about the effects on survival from tail-mounted transmitters (Reynolds et al. 2004). We estimated overall and yearly survival via the Kaplan–Meier staggered-entry method and Program MARK (White and Burnham 1999), following Pollock et al. (1989) and Loehle et al. (2005). We recaptured radiotagged owls and fitted them with new transmitters annually. We monitored all birds for nesting attempts and reproductive success.

We mapped the locations of each owl 2–3 nights per week yearlong to provide a reasonably large temporally independent sample (Guetterman et al. 1991). Although weak spatial correlation could influence standard errors but not estimated coefficients (McDonald et al. 2006), we concluded that spatial correlation was nil because spotted owls are capable of traversing much of their home ranges within a 24-hour period (Forsman et al. 1984). We rotated the order of tracking weekly to ensure a range in nocturnal (i.e., 1 hr after sunset to 1 hr before sunrise) sampling times for each bird. We recorded diurnal locations opportunistically. We obtained locations via handheld, 3-element Yagi directional antennae (Wildlife Materials, Inc., Carbondale, IL or Telonics, Mesa, AZ). We used methods similar to those of Glenn et al. (2004) to triangulate owl positions from geo-referenced receiving stations along access roads. The extensive road system helped mitigate many of the well-known radiotracking problems by allowing field personnel to acquire most transmitter signals <200 m from owls. We recorded locations in the field on 1:24,000 topographic maps. If a triangulation polygon was >2 ha, we discarded the location and recorded another sample, usually the same night. We assessed the accuracy of our telemetry system by placing transmitters at geo-referenced locations unknown to radiotracking crews. Average distance to the estimated locations from the true locations was 26 m (SD = 17.1 m, $n = 36$) and the median distance was 17 m.

We obtained habitat data from Sierra Pacific Industries, who inventoried their forests from August 1997 to March 1999, and we inventoried intervening federal timberlands in 2003 in an 80×200 -m grid, resulting in an approximate density of 1 inventory plot/1.6 ha. The company also provided supplemental inventory information to update forest habitat data in 2 areas that were treated via shelterwood-preparatory harvests during our study. After iteratively finding little variation in RSF coefficients from initial analyses of a few habitat variables at 60 m, 80 m, 100 m, and 120 m from geo-referenced variable-radius inventory

plots (40 basal-area factor prism), we assigned habitat values that were ≤ 100 m from telemetry and random locations and within 95% minimum convex polygon home ranges (Hayne 1949, Harvey and Barbour 1965). We estimated home ranges via program BIOTASS (Ecological Software Solutions, Urnasch, Switzerland).

RSF models.—We estimated discrete-choice RSF models to predict foraging habitat selection by spotted owls based upon the sets of forest vegetative features and physical environmental covariates available within individual home ranges. Discrete-choice RSF models (McCracken et al. 1998, Cooper and Millsbaugh 1999, Manly et al. 2002) are appropriate for examining resource selection at the population level when available resources are measured uniquely for each individual; that is, each choice set is distinct. Discrete-choice models also provide the capability of accounting for habitat changes during a study, such as from wildfires or timber harvesting.

We acquired a single random sample of available choices within each choice set, defined as habitat and environmental features available within a home range. Classic discrete-choice models assume that when a choice is made from each of several sets of units, a new random sample of available units is taken (Manly et al. 2002). However, McDonald et al. (2006) showed that a simplified discrete-choice model based upon a single random sample of available units yields valid results. We estimated coefficients for the discrete-choice model by modifying a stratified Cox proportional hazards model in S-PLUS 6 (Insightful Corporation, Seattle, WA), following Manly et al. (2002).

To do so, we compared habitat conditions assigned to telemetry points with those assigned to approximately 3 times as many randomly available points in each choice set, as recommended by a consulting biometrician. For planimetric variables (e.g., elevation, distance to streams), we measured from the geometric centers of telemetry-error polygons and from random coordinate points. We modeled male and female owls separately because we could not be sure that their foraging habitat choices were independent (Glenn et al. 2004). We made no attempt to model separately new birds that replaced those that died or emigrated because we assumed their foraging choices would be independent.

We acquired forest inventory data for stand-density metrics, including basal area by species or species group, quadratic mean diameter, overstory canopy cover, total tree density, and tree density by diameter class (Table 1; West 1983, Long 1985, Lillieholm et al. 1993). Each measure provides a slightly different perspective of variation in stand density. We included physical environmental covariates (elevation, slope, aspect, distance from roads and streams) because we anticipated significant foraging in association with nesting locations, which often are found near lower portions of slopes (Courtney et al. 2004).

We used biological knowledge and local experience to identify covariates for plausible a priori nested models that represented multiple hypotheses that might account for

variation in habitat selection patterns, following Glenn et al. (2004). We used Schwarz' (1978) Bayesian Information Criterion (BIC) for selecting the most parsimonious models, following Shono (2005) and McDonald et al. (2006). Differences in BIC values of ≥ 2 are generally considered to indicate that models are statistically distinguishable (Shono 2005). The literature indicates that nocturnal habitat selection by spotted owls would be associated with convoluted topography, areas in productive vegetation types along riparian zones, specific vegetation composition, forest stands near nest sites, tree density, and forest structures believed to influence populations of the owl's prey (Thomas et al. 1990, Verner et al. 1992, Haufler and Irwin 1994, Courtney et al. 2004, Glenn et al. 2004). Quantifying the effects of such factors should be useful in predicting responses by owls to various silvicultural treatments that modify stand structure and composition (Verner et al. 1992). Information on physical site descriptions could help in determining if it matters to owls where silvicultural treatments occur (e.g., ridges vs. valley bottoms).

Plant communities or tree species relatively near streams should contain a greater abundance of prey via a greater expression of understory vegetation (Carey et al. 1992). For example, woodrats are strongly associated with riparian zones (Anthony et al. 2003), and Haufler and Irwin (1994), Irwin et al. (2000), and Glenn et al. (2004) observed that spotted owls frequently used riparian zones for foraging. Therefore, we postulated that distance from streams would be an important correlate. Woodrat populations probably are influenced by mast- or fruit-producing hardwoods such as oaks (Atsatt and Ingram 1983), so we included basal area of hardwoods as a covariate. We presumed that elevation would be a factor because of a shift in vegetation composition from true firs at higher elevations to Douglas-fir mixed with ponderosa pine and hardwoods at lower elevations, where such mixed forests exhibited greater prey biomass than true-fir vegetation types in southwestern Oregon, USA (Carey et al. 1992).

In addition, we hypothesized that basal area of specific tree species such as Douglas-fir would influence owl foraging behavior because the arboreal red tree vole, an important prey species, feeds principally on needles of Douglas-fir trees (Carey 1991). Further, spotted owls nest most frequently in Douglas-fir trees (Buchanan et al. 1993, Hershey et al. 1998), although in our study area nearly all nests (9 of 11) were in black oak cavities. Spotted owls are considered central-place foragers (Carey and Peeler 1995, Rosenberg and McKelvey 1999), so we hypothesized that distance to nest sites would be an important influence (McDonald and McDonald 2002, Glenn et al. 2004), at least in years when nesting occurs. Although coarse woody debris is also known to be important to spotted owls (Irwin et al. 2000), we were unable to acquire consistent estimates of woody debris. We also did not examine landscape-pattern metrics, such as indices of forest fragmentation, because stands in our study area were relatively continuous and often contained indistinct boundaries. Moreover, except for size of old-forest

Table 1. Definitions of environmental and structural variables used to characterize forest stand conditions used by California spotted owls, California, USA, from 1999 to 2004.

Variable	Definition and unit	Abbreviation
Vegetation covariates		
Basal area (BA)	Cross-sectional area of all stems in a stand measured at breast height (m ² /ha)	BASAL
Douglas-fir BA	Basal area occupied by Douglas-fir trees >12.7 cm dbh	BASALDFIR
Ponderosa pine BA	Basal area occupied by ponderosa pines >12.7 cm dbh	BASALPP
White fir BA	Basal area occupied by white fir trees >12.7 cm dbh	BASALWfir
Fir basal BA	Combined basal areas of Douglas-, red, and white fir trees	BASALFIR
Hardwood BA	Basal area occupied by hardwood species, in 2 groups: 12.7–20 cm dbh (small); >20 cm dbh (large)	BASALHDW
Canopy cover	Proportion of ground (%) covered by forest tree crowns	CANCOV
Quadratic \bar{x} diam	Diam of tree corresponding to average basal area of a stand of trees (cm)	QMD
Trees/ha	Total no. of trees/ha >12.7 cm dbh in a stand	TPH
Size class	Density of green trees of specified size (e.g., GREEN13 is density of trees \geq 13 cm dbh; GREEN66 is density of trees \geq 66 cm dbh)	GREENxx
Small-tree density	Density (no./ha) of green trees 12.7–25 cm dbh	SMALL
Large snags	No. of snags \geq 66 cm dbh and >1.8 m tall	SNAG
Abiotic covariates		
Distance to streams	Distance (m) from telemetry or random point to nearest permanent stream	DWATER
Elevation	Elevation (m) of point above \bar{x} sea level	ELEV
Roads	Distance (m) to nearest traveled road	ROAD
Nest	Distance (m) to nesting site	NEST

patches, Meyer et al. (1998) were unable to detect important statistical effects of fragmentation indices on territory selection or occupancy by northern spotted owls in western Oregon.

There are enormous possible combinations of variables in models that could include >20 covariates, their nonlinear transforms, and possible interactions. Therefore, we limited the number of models that we examined by proceeding in stages and by employing BIC to optimize the number of covariates that could be supported by the data. The order of including truly independent variables doesn't affect the outcome (T. McDonald, WEST, Inc., personal communication), so we arbitrarily initiated the modeling process by identifying the 5 top models that included up to 6 continuous planimetric or physical environmental covariates, including their quadratic and natural-log transforms. A single (i.e., unpaired) owl at one location had no nest, so we used median values from other home ranges to represent nest distance for telemetry and random points there. Aspect was modeled by trigonometric functions (Stage 1976).

We then selected the top 5 models among those that included the several habitat factors and their quadratic and natural-log transforms. We considered basal area, percent overstory canopy cover, total tree density, and quadratic mean diameter in separate models because they were correlated. We added the density of small (12.5–25.0 cm dbh; Table 1) and large (>66 cm dbh) trees to the models that contained overall stand-density covariates because Irwin et al. (2004) found a negative correlation between small-diameter trees and reproduction and site occupancy of northern spotted owls in mixed coniferous forests in Washington, and because numerous studies demonstrated a close association between northern spotted owls and large trees (Thomas et al. 1990). After that, we constructed 25 models that integrated the best 5 models with planimetric

variables with the top 5 habitat-only models. We selected the top 10 models among those combinations for further consideration.

After we observed that basal area was the strongest tree-density covariate, we subdivided total basal area into component basal areas of hardwoods and specific coniferous species to represent variation in composition. We further divided basal area of hardwoods into 2 size classes (12.5–19.9 cm and \geq 20 cm dbh). Because of similarities in foliage structure among some coniferous trees, we combined the basal areas of Douglas-fir, white fir, and red fir. We considered basal area of ponderosa pine individually because pure pine stands are used only rarely by California spotted owls (Gutiérrez et al. 1992). We also considered several extra models that included suspected interactions between planimetric variables and vegetation covariates because McDonald and McDonald (2002) found that use of tree size classes by a northern spotted owl pair in western Oregon varied with proximity to streams. In our study area, widely scattered large trees were often retained in fuel breaks along roads adjacent to some ridge-tops. We suspected such open areas would be little used by the owls (Zabel et al. 1995), yet such large trees would be expected to attract owls in other configurations. We report here the top 7 models; we did not consider all other models as competing models based upon BIC scores.

Finally, we presumed that habitat selection might vary between nesting and non-nesting seasons because Call et al. (1992) found that California spotted owls used different habitats in those seasons. We tested for a seasonal effect using *t*-tests to compare coefficients of covariates in the final RSF model when reestimated for nesting (1 Feb–30 Sep) and non-nesting (1 Oct–31 Jan) seasons.

Model validation.—We tested predictive capabilities of the final model by using a process similar to the *k*-fold cross-

Table 2. Dates and numbers of telemetry locations for California spotted owl resource selection function (RSF) analysis, California, USA, from 1999 to 2004. Choice sets involve availability of resources within home ranges of individual owls, usually a pair of owls at each site. Additional choice sets occurred for home ranges that sustained timber harvesting during the study, representing use and availability of resources before and after harvesting.

Location ^a	Date and yr of data					Total	Choice sets
	Apr 1999– Mar 2000	Apr 2000– Mar 2001	Apr 2001– Mar 2002	Apr 2002– Mar 2003	Apr 2003– Mar 2004		
Boundary	81	132	185	109	101	608	2
Butte	0	46	0	56	0	102	0
Cedar	0	53	156	153	118	480	2
Coldhill ^b	87	132	176	156	143	694	4
Garland	0	40	83	0	0	123	1
Ike Dye	0	134	142	155	132	563	2
Inskip	78	118	16	78	111	401	2
Lovelock	72	155	0	0	0	227	2
Platt	111	134	185	111	137	678	2
Powellton ^b	35	124	161	2	118	440	4
Total	464	1,068	1,104	820	860	4,316	21

^a Two other owl home ranges that involved 8 and 16 telemetry locations were excluded from analyses.

^b Two additional choice sets resulted from selective timber harvesting midway through the study.

validation described in Boyce et al. (2002). For cross-validation, we iteratively excluded each choice set, reestimated the final model from the remaining choice sets, and predicted telemetry locations of the excluded choice set. To do so, we regressed the observed number of telemetry locations in the excluded choice sets against the sample-size-adjusted predicted number of telemetry locations in each of 20 equal-sized bins of relative probabilities, scaled to 1.0 by dividing by the largest value. Following Howlin et al. (2004), we concluded that a model had good predictive abilities if the slope of the regression was >0.0 and not statistically different from 1.0; moderate if the slope was >0.0 but the 95% confidence interval did not contain 1.0; and poor if the slope was not different from 0.0.

RESULTS

We recorded 4,316 telemetry points from 17 owls (Table 2), from which we excluded 744 daytime locations and 209 locations from a few birds for which we could not estimate home ranges because they emigrated early in the study. We also excluded 102 locations from one area (Butte) because the owls there traveled extensively, did not occupy a distinct home range, and did not nest. We tracked a single owl at one home range (Garland), but pairs of owls produced young in 8 nesting territories prior to or during the study. We observed no nesting attempts during the study at 2 of the territories (Cedar Creek and Inskip). We developed 2 additional choice sets for each of 2 locations where partial timber harvesting occurred midterm in the study (Coldhill and Powellton; Table 2) to represent used and available conditions before and after harvesting. We excluded data collected during the harvesting at those home ranges. This protocol resulted in 3,078 nocturnal telemetry locations, 11,303 random locations, and 21 choice sets for estimating discrete-choice RSF models.

Several covariates differed ($P < 0.05$) in univariate comparisons among random, telemetry, and roosting locations (Table 3). We found only limited use in stands

with <12 m²/ha or in those with >70 m²/ha. Radiotagged owls hunted for prey in stands that contained an average of 1,160 trees/ha, and home ranges contained stands with 14 large green trees/ha on average, whereas owls foraged in stands with 17 such trees/ha. Compared to random locations, nocturnal telemetry locations were closer to nests and small streams at lower elevations in stands that contained more total basal area, more basal area in Douglas-fir trees, and more large-diameter trees (Table 3). At irregularly collected daytime locations, when owls would be expected to be roosting, telemetry points were even closer to nests and near streams in stands with greater tree densities, more basal area, more overstory canopy cover, more large trees, and less basal area of ponderosa pine. Such

Table 3. Average and standard error for habitat and environmental conditions at roosting, foraging, and random locations, based upon 4,316 telemetry points and 18,815 random landscape locations within California spotted owl home ranges^a, California, USA, from 1999 to 2004.

Variable ^a	Roosting		Foraging		Random	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
BASAL (m ² /ha)	49.6	1.0	43.5	1.0	40.1	0.5
BASALDFIR	16.6	0.6	13.5	0.4	9.9	0.2
BASALWFIR	10.4	0.5	10.1	0.2	12.0	0.1
BASALPP	6.4	0.5	7.8	0.2	7.1	0.2
BASALHDW _{SMALL}	2.2	0.2	2.4	0.2	2.4	0.2
BASALHDW _{LARGE}	8.4	0.2	8.1	0.5	7.8	0.3
CANCOV (%)	75.0	1.0	69.0	1.0	67.0	2.0
TPH (no./ha)	1,345	72	1,160	48	1,205	27
GREEN66 (no./ha)	20.0	1.0	17.3	0.5	13.8	0.3
SNAG (no./ha)	3.0	0.3	3.8	0.3	3.5	1.2
SMALL (no./ha)	275	11	261	10	270	5
QMD (cm)	39.6	0.3	36.0	0.2	33.2	0.2
ASPECT(°)	207	3	205	2	203	1
ROAD (m)	126	3	117	1	114	1
ELEV (m)	1,004	6	1,020	3	1,050	3
NEST (m)	1,154	67	1,286	26	2,340	16
DWATER (m)	130	5	137	3	175	2
SLOPE (°)	5.0	0.8	5.0	0.1	5.0	0.1

^a Definitions of variables are provided in Table 1.

Table 4. Coefficients and standard errors for top discrete-choice models for estimating relative probability of a California spotted owl selecting a point in the landscape for nocturnal foraging that was characterized by the covariates, California, USA, from 1999 to 2004. The notation e^{-x} means number of decimal places to left of coefficient or standard error.

Model rank	1		2		3		4		5	
BIC ^a	205,029.2		205,035.2		205,035.6		205,035.8		205,036.7	
Covariate ^b	Coeff.	SE	Coeff.	SE	Coeff.	SE	Coeff.	SE	Coeff.	SE
NEST	$5.28e^{-4}$	$2.22e^{-5}$	$5.28e^{-4}$	$2.22e^{-5}$	$5.26e^{-4}$	$2.22e^{-5}$	$5.25e^{-4}$	$2.22e^{-5}$	$5.29e^{-4}$	$2.23e^{-5}$
NEST ²	$-3.06e^{-8}$	$3.31e^{-9}$	$-3.07e^{-8}$	$3.32e^{-9}$	$-3.06e^{-8}$	$3.31e^{-9}$	$-3.05e^{-8}$	$3.31e^{-9}$	$-3.08e^{-8}$	$3.31e^{-9}$
DWATER	$7.72e^{-4}$	$1.68e^{-4}$	$7.92e^{-4}$	$1.69e^{-4}$	$8.09e^{-4}$	$1.69e^{-4}$	$7.93e^{-4}$	$1.68e^{-4}$	$7.51e^{-4}$	$1.69e^{-4}$
DWATER ²	$-1.58e^{-6}$	$2.75e^{-7}$	$-1.60e^{-6}$	$2.75e^{-7}$	$-1.63e^{-6}$	$2.75e^{-7}$	$-1.61e^{-6}$	$2.75e^{-7}$	$-1.56e^{-6}$	$2.75e^{-7}$
BASALFIR	$1.54e^{-3}$	$3.07e^{-4}$	$1.57e^{-3}$	$3.07e^{-4}$	$1.68e^{-3}$	$3.05e^{-4}$	$1.65e^{-3}$	$3.05e^{-4}$		
BASALFIR ²	$-3.88e^{-6}$	$1.20e^{-6}$	$-3.98e^{-6}$	$1.20e^{-6}$	$-4.31e^{-6}$	$1.20e^{-6}$				
BASALPP	$-2.18e^{-3}$	$1.80e^{-4}$	$-2.77e^{-3}$	$3.55e^{-6}$	$2.81e^{-3}$	$3.54e^{-4}$	$-2.19e^{-3}$	$1.80e^{-4}$		
BASALPP ²			$2.87e^{-6}$	$1.47e^{-6}$	$2.95e^{-6}$	$1.47e^{-6}$				
BASALDF									$1.14e^{-3}$	$3.69e^{-4}$
BASALDF ²									$-3.26e^{-3}$	$1.68e^{-4}$
BASALHDW _{Large}	$8.34e^{-4}$	$3.78e^{-4}$	$8.17e^{-4}$	$3.78e^{-4}$	$-1.36e^{-4}$	$1.64e^{-4}$	$-1.77e^{-4}$	$1.68e^{-4}$	$9.15e^{-4}$	$3.78e^{-4}$
BASALHDW _{Large} ²	$-5.05e^{-6}$	$1.81e^{-6}$	$-4.98e^{-6}$	$1.81e^{-6}$					$-5.39e^{-6}$	$1.81e^{-6}$
BASALHDW _{SMALL}							$3.97e^{-4}$	$3.04e^{-4}$		
BASALHDW _{SMALL} ²										
BASALWF									$2.52e^{-3}$	$4.96e^{-4}$
BASALWF ²									$-8.75e^{-6}$	$2.46e^{-6}$

^a We calculated Bayesian Information Criterion (BIC) as $-2\log\text{-likelihood} + k \times \log n$, where n is the sum of telemetry and random points.

^b Definitions of variables are provided in Table 1.

locations also were further from roads, which largely were placed higher on slopes or on ridges.

RSF models.—Abiotic environmental factors, primarily including distance to nest, distance to water, and elevation were strongly associated with spotted owl foraging habitat selection. The number of nocturnal telemetry locations declined rapidly and nonlinearly with increasing distance from nests and streams, although the relations were nearly linear over the range of distance values in the study area. Forest habitats near first- and second-order streams were more likely to be used for foraging by spotted owls than those near larger streams. Foraging habitat selection was not strongly associated with roads, slope, and aspect. Distance to roads and elevation entered models only as interactions with vegetation covariates.

The best models (Table 4) indicated that stands more likely to be chosen for foraging included those with intermediate values of the combined basal areas of the 3 fir species and greater basal area of large-diameter hardwoods. We found evidence to support a unimodal relation between relative probability of use and the sum of basal areas of the 3 fir species (Fig. 1). The relative probability of use declined within increasing basal area of ponderosa pine. Overstory canopy cover was not contained among the top models. Except for hardwoods, variables representing tree density by size class and snags were not important. Green trees >66 cm diameter at breast height were important in 2 models as an interaction with elevation, although these models were not competitive based upon BIC scores.

When we partitioned data between nesting and non-nesting seasons and reestimated the final RSF, we did not find that owls used different habitat conditions between nesting and non-nesting seasons. We found only that the apparent influence of distance to nests differed, as expected.

The association with NEST was lower ($P = 0.023$) in the non-nesting season; the coefficient for NEST in the non-nesting season was $2.54e^{-4}$ (SE = $1.97e^{-5}$) compared to $5.38e^{-4}$ (SE = $1.97e^{-5}$) for the nesting season.

Model validation.—Coefficients for model parameters varied over low to modest ranges when we iteratively excluded individual choice sets, and we reestimated the best model from remaining data. As a result, we judged the final model reasonably robust. Of the model validation runs, 18 showed good (13) or moderate (5) correspondence for predicting telemetry points of the excluded choice sets, and 3 choice sets indicated no statistical relationship. The 3 poor validation runs involved choice sets based upon data from 3 male owls that successively occupied the Powellton area before and after harvesting, a choice set for the female at Powellton after harvesting, and a choice set that involved 2 male owls at Inskip. In the Powellton case, owls nested only in 1999 and we observed no nesting attempts at Inskip. Further, of the 5 excluded choice sets for which the final model showed moderate correlations, we did not observe nesting or nest success was very low, suggesting that NEST may have had less influence at those locations. Based upon those observations and because we found that NEST had reduced or nil effects in the non-nesting season, we reran the model validations on those 8 choice sets without NEST in the model. In doing so, all correlations except one improved to “good” (i.e., the correlation’s 95% CI overlapped 1.0); the correlation for the Coldhill female telemetry locations after harvesting remained moderate at 0.649 (SE = 0.12).

DISCUSSION

The RSF results met our goals for integrating details of forest stand density and composition with abiotic environ-

Table 4. Extended.

6		7	
205,037.2		205,043.8	
Coeff.	SE	Coeff.	SE
$5.28e^{-4}$	$2.22e^{-5}$	$5.25e^{-4}$	$2.22e^{-5}$
$-3.06e^{-8}$	$3.31e^{-9}$	$-3.05e^{-8}$	$3.32e^{-9}$
$7.77e^{-4}$	$1.68e^{-4}$	$7.92e^{-4}$	$1.68e^{-4}$
$-1.58e^{-6}$	$2.75e^{-4}$	$-1.61e^{-6}$	$2.75e^{-7}$
$1.55e^{-3}$	$3.07e^{-4}$	$1.66e^{-3}$	$3.05e^{-4}$
$-3.89e^{-6}$	$1.10e^{-6}$	$-4.27e^{-6}$	$1.20e^{-6}$
$-2.17e^{-3}$	$1.80e^{-4}$	$-2.19e^{-3}$	$1.80e^{-4}$
$7.89e^{-4}$	$3.80e^{-4}$	$-1.61e^{-4}$	$1.68e^{-4}$
$-5.05e^{-6}$	$1.81e^{-6}$		
$3.99e^{-4}$	$4.03e^{-4}$	$-2.08e^{-4}$	$5.65e^{-4}$
		$3.97e^{-6}$	$3.08e^{-6}$

mental descriptors of foraging habitat for California spotted owls. The probability of a California spotted owl selecting a stand for nocturnal foraging was most strongly associated with moderately dense forest stands in close proximity to nest sites, usually in lower slope positions adjacent to small streams. Those associations probably occurred because densities of the owls' prey likely were more abundant in the riparian zones or moist forests. Dusky-footed woodrats (*Neotoma fuscipes*), important prey items, are riparian associates in forests of the Pacific Northwest (Anthony et al. 2003) and are most abundant in riparian zones in mixed conifer forests in western Oregon (Carey et al. 1999). We also found that large hardwoods were associated with spotted owl foraging, as did Glenn et al. (2004) in western Oregon. Carey et al. (1992), working in western Oregon and Block et al. (2005), working in Arizona, USA, noted that spotted owl prey exhibit greater densities in plant communities that have a greater expression of understory hardwood shrubs and herbaceous species. Call et al. (1992) also found that California spotted owls frequently hunted for woodrats and other prey in hardwood-dominated riparian zones.

We also found that coniferous tree species composition and density were strongly correlated to the relative probability of foraging in forest stands by California spotted owls. For example, basal area of ponderosa pine exerted negative effects on the estimated relative probability of use, whereas combined basal areas of Douglas-fir, white fir, and red fir had unimodal effects on the estimated relative probability of use (Fig. 1). Thus, maintaining 35–55 m²/ha of basal area in Douglas-fir, white fir, or red fir should support optimal foraging habitat for California spotted owls. That basal area range is also supported by data in Gutiérrez et al. (1992).

We emphasized foraging habitat, assuming that it confers greater overall reproductive success. Yet survival could be

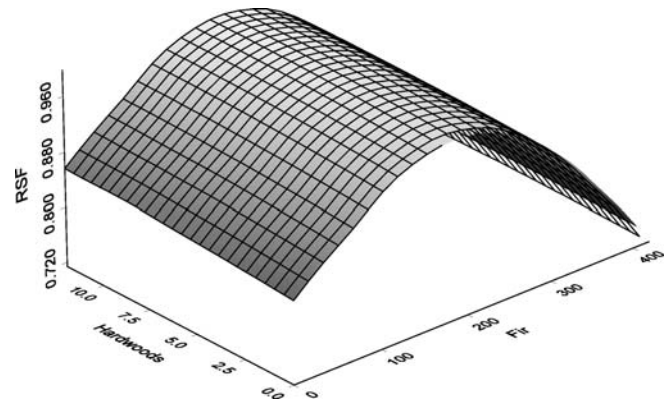


Figure 1. Association between combined basal areas (m²/ha) of Douglas-fir, red fir, and white fir (Basal fir) and basal area of large hardwoods (>20 cm dbh) with the relative probability of a location being selected by a California spotted owl near Chico, California, USA, from 1999 to 2004. We held all other variables in the best model (Table 4) constant at average values. RSF = resource selection function.

constrained by other factors (Franklin et al. 2000), such as dense stands that help spotted owls avoid predators or provide respite from inclement weather. Indeed, we found that forest stands associated with daytime roosts were denser and contained greater basal area (especially Douglas-fir) and overstory canopy cover than for nocturnal locations. That suggests optimal habitat conditions likely involve heterogeneous mixtures of forest stands with differing composition and densities, as indicated for northern spotted owls (Franklin et al. 2000, Zabel et al. 2003).

The final RSF exhibited good predictive capabilities, after accounting for non-nesting owls that apparently foraged in areas beyond nest sites. Although consistency in model validation regressions among choice sets is comforting, it could be related more to similarity among territories than to similarity in patterns of habitat selection. However, we included a broad range of conditions in the study, including some blocks of unmanaged old-growth forests, which unquestionably provide good habitats. Foraging habitat selection was initially poorly predicted in the choice set for the 2 male owls at Inskip, which included a large block of old-growth forest. However, the final RSF predicted foraging habitat selection by 4 female owls that successively used the Inskip territory rather well and did so for the 2 males there when we excluded NEST. Further, the model accorded reasonably well with foraging use by 4 owls after partial harvesting modified habitat conditions in 2 areas.

Although RSFs probe basic determinants of habitat selection, or those factors that likely affect fitness, habitat conditions identified by our modeling cannot necessarily be considered definitive indicators of population requirements. Reproductive output by the owl pairs in our study was relatively low (0.25 fledglings/yr), and Kaplan–Meier annual survival rate averaged 0.723, perhaps a response to low total amounts of habitat. However, we found considerable variation in survival rate estimates among years based upon Program MARK (0.51–0.93) and correspondingly wide 95% confidence intervals (0.28–0.99), probably a reflection

of small sample sizes. We obtained the lowest survival estimate (0.51) the year (1999) that we employed tail-mounted transmitters, which may have a negative influence on survival (Reynolds et al. 2004). Also, most published studies of spotted owl demography have been unable to account for a large amount of variation in vital rates based upon measures of habitat categories (e.g., Blakesley et al. 2001, Olson et al. 2004, but see Dugger et al. 2005). Yet, because we emphasized foraging habitat, we believe the RSF incorporates factors that likely are important in controlling population performance (Boyce and McDonald 1999).

MANAGEMENT IMPLICATIONS

The California spotted owl is protected by an interim conservation strategy that involves a dynamic reserve system and a shifting habitat mosaic implemented via silvicultural treatments at the scale of individual owl territories (Franklin et al. 2004). That strategy requires comparative risk assessments because silvicultural treatments may degrade habitats for spotted owls in the short term (Irwin and Thomas 2002). Where pertinent inventory data are available, our RSF model can be used for such comparative risk assessments of short- and long-term effects of forest fuels treatments or other silvicultural prescriptions. In so doing, the model should be used in conjunction with fire-risk models and local forest-growth models in a GIS, following McDonald and McDonald (2002).

ACKNOWLEDGMENTS

We are grateful for numerous financial and logistic contributions by Sierra Pacific Industries. The American Forest Resource Council and the National Council for Air and Stream Improvement also provided financial support. We thank C. Loehle for providing estimates of survival rates, K. Livezey and J. Dunk for constructive comments on an early draft, and T. McDonald for statistical advice. We also thank R. J. Gutiérrez, J. Ganey, and an anonymous referee for valuable criticisms.

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Associate Editor: Block.