SPOTTED OWL HOME-RANGE AND HABITAT USE IN YOUNG FORESTS OF WESTERN OREGON

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Abstract: To assess spotted owl use of young forests, we studied home-range sizes and habitat-use patterns of 24 adult northern spotted owls (*Strix occidentalis caurina*) on 2 sites in the Oregon Coast Range: the Elliott State Forest (ESF) and state forest lands in the Northern Coast Range (NCR). Conifer forests at ESF were characterized by a mixture of old, mature, and pole-sized conifer, similar to other areas occupied by spotted owls in western Oregon, USA. In contrast, conifer forests at NCR were younger than most other sites occupied by spotted owls in western Oregon and consisted primarily of conifers <80 years old. Broadleaf forest also was abundant (approx 22%) at both ESF and NCR. We used an information–theoretic approach and Akaike's Information Criterion (AIC) to evaluate a priori hypotheses about spotted owl home-range sizes and habitat-use patterns on our study areas. Considering previous knowledge about habitat requirements of the species, we predicted that owls occupying sites with fewer old conifer stands would have larger home ranges and that owls would select the oldest and most structurally diverse forest available for foraging and roosting. Our top model for evaluating home-range sizes indicated that the proportion of older conifer forest within the home range best explained the variability in home-range sizes. Although we found considerable variation in home-range size among owls, home-range sizes at ESF generally were smaller than home-range sizes at NCR, and home ranges at both sites were smaller than those reported for other study areas in western Oregon. Habitat-use patterns also varied widely among owls both within and between sites. Models containing distance to the nest tree, proximity to nearest forest edge, and proximity to nearest broadleaf-forest edge were the most parsimonious models for distinguishing owl locations from random points. On average, owl locations at both study areas were closer to ecotones between broadleaf forest and other cover types and farther from forest–nonforest ecotones than random points. Overall, we did not observe strong selection or avoidance of any cover type, although owls at ESF showed greatest use of older conifer forest while owls at NCR showed greatest use of broadleaf forest. Use of these habitat configurations and cover types by spotted owls had not been well documented prior to our study. The predictive power of our models was not great, however, indicating that factors in addition to those we included in our analysis may have influenced owl habitat-use patterns at our study areas. Based on our results, we recommend that managers at these sites maintain existing old and mature conifer forest, broadleaf forest, broadleaf-forest edges, and forested riparian areas as owl habitat; avoid timber harvest in core use areas; and plan the size of areas managed for spotted owls to reflect actual home-range and core-area sizes for owls in those forests.

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Northern spotted owls generally are associated with mature or late-seral forests in the Pacific Northwest for nesting, roosting, and foraging (Carey et al. 1990, 1992; Forsman 1980; Forsman et al. 1984). Numerous studies have documented selection of old-growth forests by spotted owls for foraging and roosting (see reviews in Thomas et al. 1990). Further, landscape-scale studies have shown that spotted owls select habitats that have a significantly higher proportion of old and mature forest around nest and roost sites than is available on the landscape as a whole (Franklin et al. 2000, Ripple et al. 1991, Swindle et al. 1999). Sites selected for nesting and roosting by spotted owls have a more complex vegetative structure than habitat generally available on the landscape (Forsman et al. 1984, Hershey et al. 1998, Solis 1983) and are comprised of multilayered canopies with high canopy closure and large-diameter trees in the overstory (Call et al. 1992, Solis and Gutiérrez 1990). Foraging habitat is more variable than nesting or roosting habitat (Thomas et al. 1990), although foraging habitat typically is characterized by the multilayered structure found at nest and roost sites (Solis and Gutiérrez 1990).

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Several hypothesized reasons exist for selection of late-seral conifer forest by northern spotted owls. Although differences in prey abundance between older (>400 yr) and younger (30–60 yr) forests do not appear to be a determining factor in spotted owl habitat selection in the Oregon Cascade mountains (Rosenberg and Anthony 1993), late-seral forest may provide a more open forest structure where owls can fly and forage more effectively (Forsman et al. 1984). Additionally, great horned owls (*Bubo virginianus*) may be able to prey more effectively on spotted owls in the younger stands, which great horned owls use more frequently (Forsman et al. 1984). Late-seral forests also may provide protection from weather conditions for roosting and nesting (Forsman et al. 1984, Franklin et al. 2000). Because spotted owls nest almost exclusively in trees and often in cavities, late-seral forests provide the most suitable nest sites (LaHaye and Gutiérrez 1998).

Spotted owls have been known to nest and forage in young forests (Carey and Peeler 1995; Folliard et al. 2000; Gutiérrez et al. 1998); however, information about the structural characteristics of young forests that may be important to spotted owls is lacking, particularly in western Oregon. In addition, the contribution of young-forest habitat to owl nest success, long-term survival, and population stability is unclear. Carey and Peeler (1995) reported that spotted owls in southwest Oregon concentrated foraging in old forest, but selectively used young forest, particularly when dusky-footed woodrats (*Neotoma fuscipes*) were present. In northwest California, where dusky-footed woodrats are the primary prey of spotted owls, Ward et al. (1998) concluded that selection of dusky-footed woodrats over smaller prey species provided an energetic benefit to owls. Additionally, Ward et al. (1998) documented selection of ecotones between late- and early-seral mixed conifer forest where woodrats were most abundant. Folliard et al. (2000) suggested that this matrix of different age and cover types in northwest California may provide a greater abundance and diversity of prey; however, they reported that young forests lacking patches of older trees did not support spotted owls on their study area. Thome et al. (1999) also suggested that owls were using young forests in northwest California because the stands had a diverse species composition and complex structure that provided roost sites and abundant prey. Thome et al. (1999) also reported that the amount of residual trees in the nest stand influenced reproductive success and that residual trees were most important close to the nest site.

Spotted owl surveys on Oregon Department of Forestry (ODF) lands in the 1970s (Forsman et al. 1987) and early 1990s revealed that owls were using young second-growth forest (<80 yr) in the NCR that had not previously been considered habitat for the species. Because this area of the Oregon Coast Range contained little federal land, nonfederal lands were identified in the conservation strategy (Thomas et al. 1990) and draft recovery plan for the northern spotted owl (U.S. Department of the Interior 1992) as important for the species' survival and recovery. Because of the importance of the NCR spotted owl population to the species recovery plan for the region, ODF initiated several studies to better understand the ecology of spotted owls in these young forests and to identify characteristics of the forest types that owls were using. Our objectives were to estimate home-range size, identify core areas within home ranges, and examine habitat associations of radiomarked owls for 2 populations: 1 on NCR and 1 on the ESF in the central Oregon Coast Range. Space-use patterns reflect energy expenditure by owls, and energy expenditure ultimately influences individual fitness (Carey et al. 1992, Ward et al. 1998). We predicted that home-range sizes on our study areas would be larger for owls with less mature and old conifer forest available to them, similar to Carey et al. (1992). We also predicted that owls would select the oldest and most structurally diverse habitat available to them, based on results of other studies of spotted owl habitat use in young forests (Ward et al. 1998, Thome et al. 1999, Folliard et al. 2000). Detailed information on habitat and space use by owls ultimately will be used by ODF to develop silivicultural strategies to provide spotted owl habitat within managed forests in western Oregon.

STUDY AREA

Our study area consisted of the NCR site, which included state forest lands in Clatsop and Tillamook counties, and the ESF in Coos and Douglas counties. Both sites were located in the western hemlock (*Tsuga heterophylla*) zone. Major tree species included Douglas-fir (*Pseudotsuga menziezii*), western hemlock, western red cedar (*Thuja plicata*), red alder (*Alnus rubra*), and bigleaf maple (*Acer macrophyllum*). Mixed and pure hardwood stands were common, particularly in riparian and recently disturbed areas. Much of the region experienced extensive harvest of late-successional forest in the last century, primarily by clearcutting. The climate was maritime with warm, dry summers and mild, wet winters.

The ESF study area encompassed all of the Elliott State Forest (378 km^2) as well as adjacent lands (public and private) that were used by the owls. Average annual rainfall during our study period was 170 cm, and average monthly temperatures ranged from 8 °C in January to 16 °C in July (Oregon Climate Service, Oregon State University, unpublished data). Topography was highly dissected by steep ridges and narrow creek bottoms, and elevations ranged from zero to 633 m. Patches of remnant old forest that escaped fires in the 1860s were present, but most stands were <120 years old (Oregon Department of Forestry 1995). Our ESF site contained more natural regeneration, large trees, and mature forest than NCR. Approximately 25% of the ESF was pole conifer (13–28 cm dbh), 23% was broadleaf, 27% was mature conifer (53–86 cm dbh) or mixed-size conifer (>50% of trees 53–86 cm dbh), 15% was old conifer (>86 cm dbh), and 10% was recent clearcuts or sapling stands (Oregon Department of Forestry 1995).

Our NCR study area included 3 distinct areas of rolling foothills (150–400 m) in Clatsop, Tillamook, and Washington counties: Jewell Meadows (293 km^2), Sweethome Creek (67 km^2), and Little Beaver Creek (60 km^2). Average annual rainfall during our study period (216 cm) was greater than at ESF, and average monthly temperatures were slightly cooler than at ESF, ranging from 6 °C in January to 13 °C in July (Oregon Climate Service, Oregon State University, unpublished data). Old conifer forest was not present on the NCR area, and this site was highly fragmented by clearcuts and areas of heavily harvested private land. Much of this land was clearcut in the early 1900s, and some of the regenerated conifer stands were thinned in the 1970s. Approximately 30% of NCR was young mixed-size conifer forest (<50% of trees 53–86 cm dbh), 25% of the area was broadleaf, 30% was pole conifer, and 15% was clearcuts and saplings.

METHODS

Radiotelemetry

Capture, handling techniques, and tail mounting of radiotransmitters (Holohil Systems Ltd. Model RI-2C, Ontario, Canada) followed Forsman (1983) and Guetterman et al. (1991). We attempted to capture and attach radiotransmitters to all adult resident spotted owls on each study area. Both study areas were surveyed intensively for spotted owls from 1992 to 1998 as part of a long-term demographic study (R. G. Anthony, Oregon State University, unpublished data), and we used survey data to identify adult resident owls on both sites. We attached radiotransmitters to 19 adult owls (8 pairs, 3 individuals) at ESF in 1997 and to 12 owls (5 pairs, 2 individuals) at NCR between 1995 and 1998. Most owls at NCR, however, had radiotransmitters attached in 1997. During our study, 16 owls lost radiotransmitters after molting their tail feathers or through radiotransmitter failure. Of these 16 owls, 10 were recaptured and fitted with new radiotransmitters. We monitored most individuals for 12 months, although a number of owls had gaps in monitoring between radiotransmitter loss and recapture (Appendix A).

We monitored owls from the ground using a 2-element yagi antenna and Telonics model TR-2 receivers (Telonics, Inc., Mesa, Arizona, USA). We estimated owl locations by taking compass bearings on the strongest signal from at least 3 different stations within a 1-hr period. Monitoring stations were usually permanent points with known universal transverse mercator (UTM) coordinates estimated with a Global Positioning System (GPS) unit capable of 5–10 m accuracy (Corvallis Microtechnology, Model MC-V, Corvallis, Oregon, USA). When we used temporary stations, we estimated UTM coordinates from 7.5-min U.S. Geological Survey topographic maps. We attempted to locate each owl once per night on alternate nights of the week. Locations were recorded from 1 hr after sunset to 1 hr before sunrise. We rotated the monitoring schedule for individual owls over the course of the week to obtain locations at varying times throughout the night. Additionally, 1 daytime location per week was obtained to identify daytime roost sites.

We used program XYLOG (Dodge and Steiner 1986) to estimate an owl's location and calculate a 95% confidence ellipse based on the standard deviation of bearing intercepts around the mean location. We attempted to obtain triangulations with a small error ellipse (<5.0 ha) around the estimated location. If the error ellipse was >5.0 ha or if we suspected the owl had moved while we obtained bearings, we took additional bearings and estimated the new location. Accuracy of the radiotelemetry system was assessed by placing radiotransmitters at known locations in the field and estimating locations using naive observers. Mean bearing error was 8.34 degrees (SE = 0.75, $n = 12$). Mean distance

Table 1. Models tested using mixed model analysis of variance for identifying factors that may have influenced size of northern spotted owl home ranges in 2 different landscapes in western Oregon, USA, 1995–1998.

Home-range estimation method (Response variable)	Independent variables[a]
Cumulative 95% kernel home range, 100% minimum convex polygon home range, and core-use areas	no effects model
	mature/old[b]
	sex
	study area
	no. locations
	no. weeks monitored
	mature/old, study area
	mature/old, sex
	sex, study area
	mature/old, sex, study area
	mature/old, sex, study area, no. locations, no. weeks monitored
Seasonal 95% kernel home ranges	no effects model
	sex
	study area
	season[c]
	sex, study area
	sex, season
	season, study area
	sex, season, study area

[a] Pair status was included as a random variable in all models because many owls were mated pairs and home-range sizes were not independent.

[b] Mature/old = proportion of older conifer forest (conifer >53 cm dbh) in home-range or core-use area.

[c] Breeding season: 1 Mar–31 Aug. Nonbreeding season: 1 Sep–28 Feb.

of the estimated locations from the true locations was 164 m (SE = 30.59, *n* = 9).

Home-range Analysis

We used a 95% fixed-kernel estimate (Seaman and Powell 1996) calculated using the least-squares cross-validation method in program KERNELHR (Seaman et al. 1997) to delineate each owl's home range. We identified areas of concentrated use (core areas) within home ranges using a "greater than average observation density (>AOD)" contour generated by KERNELHR (i.e., core-use areas had location densities higher than the average density for all locations for that owl; Seaman et al. 1997). We assumed core areas contained critical habitat elements (nest sites, roost sites, frequently used forage sites) and meaningful components contributing to owl survival and reproductive success (Bingham and Noon 1997). The advantage of the >AOD method is that each core area is based on the density of locations within a particular sample and avoids subjective or arbitrary contour selections (Ricca 1999). We also computed 100% minimum convex polygon (MCP; Hayne 1949) home-range estimates using program CALHOME (Kie et al. 1994) for comparison with owl home ranges reported in the literature.

We estimated cumulative, breeding season (1 Mar–31 Aug), and nonbreeding season (1 Sep–28 Feb) home ranges for each owl using all radio-telemetry locations with error polygons ≤5 ha. We estimated home ranges for all owls with >25 locations. We used the term "cumulative" rather than annual for home ranges because several owls were not monitored continually over a full calendar year (Appendix A). Although 4 owls were monitored >1 year, we did not have enough locations in some years to calculate annual home ranges for each year for these owls. Seasonal ranges were estimated for owls that were monitored for at least 3 months during a given season.

We examined factors affecting differences in cumulative home-range (95% kernel and 100% MCP), seasonal home-range (95% kernel), and core-area size among owls by evaluating sets of a priori models (Table 1) using mixed-models analysis of variance (ANOVA; Proc Mixed; SAS Institute 1997). Because most owls monitored were mated pairs and their home ranges were not independent, pair status was included in all models as a random variable while all other variables were fixed. We used AIC for small sample sizes (AIC_c; Burnham and Anderson 1998:51) to rank models and Akaike weights (w_i) to evaluate model likelihood. We also summed Akaike weights across models for each parameter to examine the relative importance of each parameter across all models (Burnham and Anderson 1998:140–141). Our models represented hypotheses based on known information about spotted owl biology. We hypothesized that home-range and core-area sizes might vary between male and female owls, between owls at our 2 study areas, and among owls with different amounts of older conifer forest available to them (Forsman et al. 1984, Carey et al. 1990). Because MCP home-range estimates have been shown to be highly sensitive to sample size (Arthur and Schwartz 1999), we also included number of locations and number of weeks monitored for each owl as model parameters. We included season, sex, and study area parameters in models to examine differences in seasonal home-range sizes because other studies have reported smaller home-range sizes for breeding season than nonbreeding season (Forsman et al. 1984). The amount of variance explained by the top models was estimated as the difference in residual variance between the intercept-only model and the top models using the estimates of residual variance provided by Proc Mixed in SAS.

We also calculated the amount of home-range and core-area overlap between paired owls and among owls occupying adjacent territories to examine how increased habitat fragmentation might contribute to owl space-use patterns. Carey et al. (1992) found that increased home-range size was accompanied by decreased home-range overlap between paired owls and increased overlap among owls occupying neighboring territories.

Habitat-use Analysis

We evaluated a set of a priori models (Table 2) comparing owl locations with random locations for each owl using logistic regression (Rosenberg and McKelvey 1999), AIC_c, and Akaike weights (Burnham and Anderson 1998:124). We summed AIC_c values across owls to identify top models at each study area (Burnham and Anderson 1998:17). We evaluated models for male and female owls separately because most owls were mated pairs and we could not assume that their locations were independent. Similar to the home-range models, we summed Akaike weights across models for each parameter to examine the relative importance of each parameter across all models. To address model-selection uncertainty and because one of our objectives was to assess owl use of different cover types, we used Akaike weights to calculate model-averaged parameter estimates across the entire set of models for each owl (Burnham and Anderson 1998:157). We reported mean values across all owls at each study area.

To facilitate comparison of selection among cover types, we used odds ratios as a measure of selection of a given cover type relative to a reference type, adjusting for all other variables in the model (Rosenberg and McKelvey 1999). To estimate the predictive power of our models, we calculated the maximum-rescaled generalized R^2. This statistic behaves similarly to the linear model R^2. It is based on the likelihood ratio χ^2 and is scaled to account for the discrete dependent variable being <1 (Allison 1999:57). We evaluated the set of models separately for the full set of radiotelemetry locations for male and female owls, as well as for breeding season locations and nonbreeding season locations. We did not have enough roost locations to examine roost and forage habitat use separately.

Because forest composition in our study areas was different than many other spotted owl studies, our habitat-use analysis was partially exploratory and contained a relatively large number of a priori models (25 for ESF, 22 for NCR). Spotted owls exhibit central-place movement, meaning that they regularly return to a particular site (nest) within their range (Carey and Peeler 1995, Rosenberg and McKelvey 1999). This behavior is particularly strong during the nesting season when adult owls regularly return to the nest site with prey items. Owls remain near the nest site during the nonbreeding season as well, although they often forage and roost in more distant areas (Forsman et al. 1984). For animals exhibiting central-place behavior, habitat types near the nest point will have a greater probability of use than more distance sites simply as a result of the density to distance relation (Rosenberg and McKelvey 1999).

Table 2. A priori models for habitat selection by northern spotted owls in 2 landscapes in western Oregon, USA, 1995–1998. Models were evaluated using logistic regression.

Study area	Model parameters
Elliott State Forest and Northern Coast Range	
	Distance-p,l[a] mature/old[b], pole[c], (mature/old * distance-l)
	Distance-p,l broad[d], pole, (broad * distance-l)
	Distance-p,l mature/old, pole
	Distance-p,l broad, pole
	Distance-p,l mature/old * distance-l
	Distance-p,l broadedge[e]
	Distance-p,l edge[f]
	Distance-p,l
	Mature/old, pole
Elliott State Forest	
	Distance-p,l mature/old, broad, pole, (mature/old * distance-l)
	Distance-p,l old[g], pole, (old * distance-l)
	Distance-p,l old, pole
	Mature/old, broad, pole
	Old, pole
Northern Coast Range	
	Distance-p,l mature/old, broad, pole, non[h], (mature/old * distance-l)
	Distance-p,l mature/old, broad, pole, non
	Mature/old, broad, pole, non

[a] All models containing distance to the nest (m) were evaluated modeling distance as a linear function and as a third order polynomial (distance + distance^2 + distance^3).

[b] Mature/old: conifer forest >53 cm dbh.

[c] Pole: conifer forest 13–52 cm dbh. Pole was used as a reference for comparing relative use of cover types by owls.

[d] Broad: forest containing >60% broadleaf trees.

[e] Broadedge: distance (m) of radiotelemetry location/random point from nearest broadleaf-forest edge.

[f] Edge: distance (m) of radiotelemetry location/random point from nearest forest (> 13 cm dbh) edge.

[g] Old: conifer forest >83 cm dbh. Models with old were not evaluated for NCR.

[h] Non: nonforested areas and trees <13 cm dbh. Non was not included in ESF models.

We therefore included distance to the nest as a model parameter in some of our models. We modeled distance as linear distance to the nest and also as a third-order polynomial function because we hypothesized that use would decline rapidly with increasing distance from the nest due to the increased energy cost of transporting prey items over long distances. To evaluate whether distance was indeed an important parameter in our habitat-use models, we also included models containing only cover-type parameters.

Based on results of other studies of spotted owls occupying young forests (Carey et al. 1990, Folliard et al. 2000, Thome et al. 1999), we hypothesized that owls would select the oldest and most structurally diverse forest available for foraging and roosting. We also hypothesized, based on the small amount of data collected on spotted owls occupying areas of younger forest, that owls might be selecting broadleaf forest because these forests provided considerable vertical structure and roost sites on our study areas (T. Nierenberg, Oregon State University, unpublished data). Cover types included in models included old conifer (>100 yr, >86 cm dbh), mature/old conifer (>60 yr, >53 cm dbh), pole-sized conifer (<60 yr, 13–53 cm dbh), broadleaf forest (>60% broadleaf, generally red alder and bigleaf maple), and nonforest (trees <13 cm dbh and nonforested areas). Old conifer was very rare on our study sites and was not included as a separate parameter in NCR. Likewise, nonforest was not included in ESF models because it was present only in very small amounts at several owl sites at ESF. We used pole conifer as the reference type in our models for comparing relative use of cover types because it was the only cover type commonly available to all owls. We used a digitized map (PC ARCINFO; Environmental Systems Research Institute 1997) to estimate cover types used by owls. Cover types were identified and typed from 1:12,000 scale aerial photos taken in 1991 and 1996 (Little Beaver site only). We obtained information on harvest activity between 1991 and 1997 from the ODF and used the information to update the habitat map. The minimum mapping unit was approximately 0.15 ha. We visited 81 stands to obtain an estimate for accuracy of stand boundaries and stand classification. Overall classification accuracy for these stands was 84%.

In addition to cover types, we hypothesized that owls might be selecting or avoiding certain forest edges. Franklin et al. (2000) reported that annual survival for spotted owls in northwest California was positively associated with amounts of old forest and the length of edge between owl habitat and other vegetation types. Franklin et al. (2000) also reported a positive association with reproductive output and amount of edge. Although dusky-footed woodrats contributed less to spotted owl diet on our study sites than in northwest California, we included distance of spotted owl locations to nearest high-contrast edge (edge between forest >13 cm dbh and all other cover types) and to nearest broadleaf-forest edge (edge between broadleaf forest and all other cover types) as model parameters because we believed edges might be an important component of habitat selection.

To estimate availability of cover types to owls, we used the maximum distance each owl was detected from the nest to generate a circle around the nest location with radius equal to the maximum distance traveled (Rosenberg and McKelvey 1999). We generated approximately 900–1,100 random locations within the circle for each owl to represent available habitat and used the cover-type map to assign cover types, measure distance to the nest point, and measure distance to forest edge types for each random point. In a few cases, the farthest 1–2 points traveled fell outside the digitized map. In these cases, we used the largest circle size that fell within the boundary of the map or used the farthest radiotelemetry point within the map extent. We do not believe that truncating the amount of available habitat at the map extent biased our estimates of available habitat for these owls. As part of a region-wide demographic modeling project (R. G. Anthony, E. D. Forsman, W. J. Ripple; Oregon State University, U.S. Department of Agriculture Forest Service; unpublished data), habitat composition was measured around current and historic owl nests at ESF ($n = 25$) and NCR ($n = 13$) at 3 spatial scales (600 m, 1,500 m, and 2,400 m radius circles around nest sites; Table 3). At both sites, percent late-seral conifer (>75cm dbh) and mid-seral conifer and broadleaf (25–75cm dbh) were greater in the 600-m circles than the 1,500- or 2,400-m circles. Differences in percent composition between the 1,500- and 2,400-m circles, however, were minimal (<1%) at both sites, and sites that were truncated at the map extent were all >2,800-m radius circles.

RESULTS

We successfully tracked 15 owls (9 male, 6 female) at ESF and 9 owls (4 male, 5 female) at NCR between October 1995 and August 1998.

Table 3. Estimates of mean proportion of 3 cover types around spotted owl nest sites for 2 populations in western Oregon, USA: Elliot State Forest (ESF) and Northern Coast Range (NCR). Cover types were measured using a digitized vegetation map derived from 1:12,000-scale aerial photos.

	Circle radius (m)					
	600		1,500		2,400	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
ESF (n = 24 owl nests)						
Nonforest	0.183	0.019	0.254	0.018	0.262	0.014
Mid-seral conifer[a] and broadleaf	0.614	0.035	0.561	0.023	0.562	0.022
Late-seral[b] conifer	0.186	0.031	0.184	0.020	0.173	0.020
NCR (n = 13 owl nests)						
Nonforest	0.155	0.012	0.234	0.013	0.242	0.011
Mid-seral conifer and broadleaf	0.807	0.013	0.745	0.013	0.741	0.011
Late-seral conifer	0.022	0.050	0.110	0.002	0.009	0.001

[a] Mid-seral conifer: 25–50 cm dbh.

[b] Late-seral conifer: >50 cm dbh.

Number of locations per owl ranged from 30 to 261 ($\bar{x}$ = 81.6, SE = 9.58).

Cumulative Home-range Size

The ANOVA model that best described the variation in 95% fixed kernel home-range sizes for our 2 study areas included only the proportion of older conifer forest in the home range (Table 4). The Akaike weight for this model (w = 0.53) was considerably higher than for the next best model (proportion of older conifer forest and study area: w = 0.12). The proportion of variance explained by this model relative to the no-effects model was 0.41. Summed Akaike weights by variable indicated that the older conifer forest variable had a much greater relative contribution to model fit (0.78) than the next highest variable (study area: 0.23). Although the relation was not strong (r = –0.36, P = 0.08; Fig. 2A), we observed a general trend toward smaller home-range sizes with greater proportions of older conifer forest.

Cumulative home-range estimates (95% fixed kernel) ranged from 246 to 3,014 ha ($\bar{x}$ = 1031 ± 124.6 ha, n = 24). Home-range sizes were larger at

Table 4. Analysis of variance models than best explained variance in home-range size, core-use area size, and seasonal range size for northern spotted owls in Elliott State Forest and Northern Coast Range study areas, Oregon, USA, 1995–1998. Lower Akaike's Information Criterion (AIC_c) values indicate more parsimonious models. Akaike weights (w_i) are the proportional likelihood of the models.

	Model parameters	AIC_c[a]	ΔAIC_c	w_i	Proportion of variance explained by model[d]
95% fixed kernel home range	Mature/old[b]	374.9	0	0.53	0.41
	Mature/old, study area	377.9	3.0	0.12	
	Mature/old, sex	378.1	3.2	0.11	
	No effects model	378.9	4.0	0.07	
100% minimum convex polygon home range	Study area	395.0	0	0.80	0.07
	Study area, mature/old	401.2	6.2	0.04	
	Study area, sex	401.7	6.7	0.2	
	No effects model	402.0	7.0	0.02	
Core-use area	Mature/old	271.9	0	0.65	0.30
	Mature/old, study area	274.1	3.2	0.13	
	Mature/old, sex	274.3	3.4	0.12	
	No effects model	278.5	6.6	0.02	
Seasonal range	Season[c]	611.2	0	0.53	0.25
	Season, study area	613.2	2.0	0.19	
	Season, sex	613.7	2.5	0.15	
	No effects model	616.9	5.7	0.03	

[a] Pair status was included as a random variable in all models because many owls were mated pairs and home-range sizes were not independent.

[b] Mature/old = proportion of home-range or core-use area that was mature/old conifer (>53cm dbh).

[c] Season = Breeding season (1 Mar–31 Aug). Nonbreeding season (1 Sep–28 Feb).

[d] Model variance was estimated as the difference in residual variance between the no effects model and the top model.

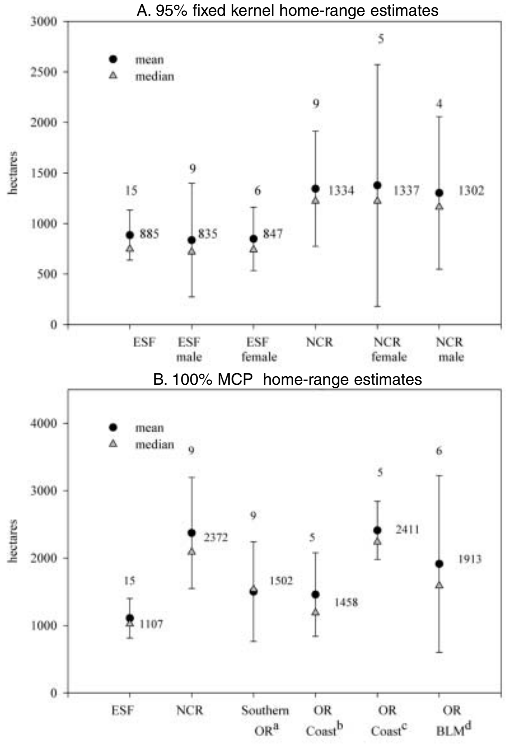

Fig. 1. (A) Ninety-five percent fixed kernel and (B) 100% minimum convex polygon (MCP) home-range estimates for spotted owls on the Elliott State Forest (ESF; 1997) and Northern Coast Range (NCR; 1995–1998) study areas, Oregon, USA. Estimates of 100% MCP home ranges from other studies are included for comparison with our study. Error bars represent 95% confidence intervals around means. Numbers of owls monitored are listed above error bars.

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[a] Carey et al. (1990).

[b] Thomas et al. (1990). Thrailkill and Meslow study: 1987–1988 home-range estimate.

[c] Thomas et al. (1990). Thrailkill and Meslow study: 1988–1989 home-range estimate.

[d] Forsman et al. (1984). Home-range estimates for owls in Central Oregon Coast Range.

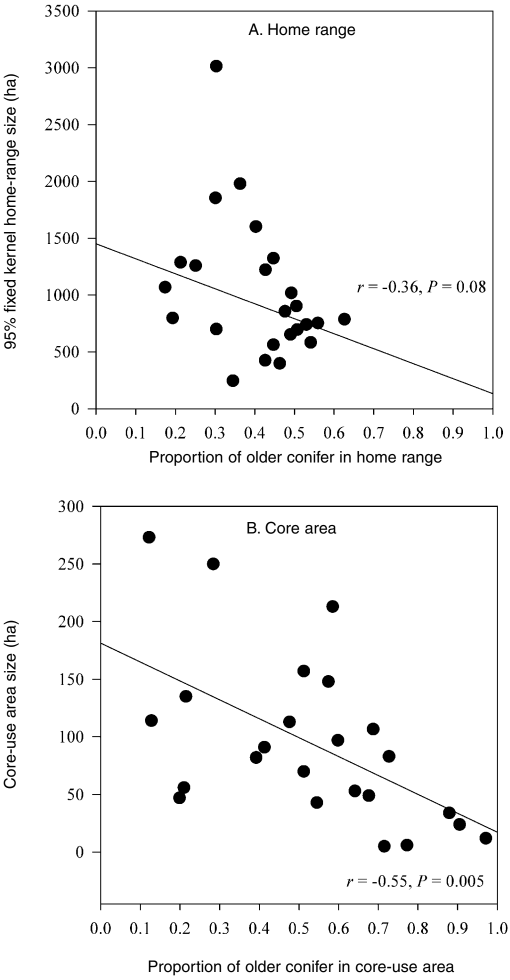

Fig. 2. Relation between spotted owl (A) home-range and (B) core-area sizes and proportion of range that was older conifer forest (>53 cm dbh) for 24 owls at Elliott State Forest (1997) and Northern Coast Range (1995–1998) study areas, Oregon, USA.

NCR ($\bar{x}$ = 1,344 ha, SE = 247.0, n = 9) than at ESF ($\bar{x}$ = 842 ha, SE = 114.7, n =15), although 95% confidence intervals (CIs) overlapped considerably (Fig. 1A). Home ranges at ESF had a higher proportion of mature and old conifer forest ($\bar{x}$ = 0.46 [95% CI: 0.41 to 0.51], SE = 0.24, n = 15) than owl ranges at NCR ($\bar{x}$ = 0.32 [95 % CI: 0.23 to 0.41], SE = 0.04, n = 9).

In contrast to the kernel home-range estimates, the model that best explained the differences in 100% MCP home-range sizes contained only the study-area parameter (Table 4). The study-area model was 13 times more likely (w = 0.80) than the next best model (sex, older: w = 0.06), although the proportion of variance explained by this model (0.07) was quite low. We found that differences in length of monitoring periods or number of locations obtained for individual owls had little effect on either 100% MCP or 95% fixed kernel estimates. One hundred percent MCP home-range estimates (Fig. 1B) were smaller for ESF ($\bar{x}$ = 1,108 ha [95% CI: 815.2 to 1,400.8], SE = 136.5, n = 15) than NCR ($\bar{x}$ = 2,214 ha [95% CI: 1,387.9 to 3,037.1], SE = 356.9, n = 9). Similarly, estimates were smaller for ESF and larger for NCR than for 100% MCP estimates recorded elsewhere in western Oregon (range = 1,465–2,451 ha; Fig. 1B).

Core Areas

The ANOVA model that best explained the variability in core-area size was the same as for the kernel home-range estimates and included proportion of older conifer forest within the core area (w = 0.65; Table 4). This model was 5 times as likely as the next best model, which contained proportion of older conifer forest and study-area variables. Amount of variance explained by this model was 0.30. Relative contribution of variables to model fit was also similar to the kernel home-range estimates, with the summed Akaike weights by variable being considerably greater for proportion of older forest (0.95) than for the next highest variable (study area: 0.18). The relation between core-area size and proportion of older conifer was stronger (r = –0.55, P = 0.005) than for home-range size and proportion of older conifer in the home range (r = –0.36, P = 0.08; Fig. 2B).

Core areas were extremely variable, ranging from 5 to 273 ha. Mean cumulative core-area size was 94 ha (SE = 14.9, n = 24). One female owl at ESF had a very small core area (5 ha). Although we monitored her in both breeding and nonbreeding seasons and occasionally located her far from the nest tree area in winter, 40% of locations for this owl were within the 5-ha core area. Core-area sizes were comparable between ESF ($\bar{x}$ = 87 ha, SE = 6, n = 15) and NCR ($\bar{x}$ = 100 ha, SE = 5, n = 9) with considerable overlap of 95% confidence intervals (ESF: 45.46 to 128.69, NCR: 45.21 to 154.79). Core-area sizes for male ($\bar{x}$ = 94 ha [95% CI: 52.3 to 135.7], SE = 19, n =13) and female ($\bar{x}$ = 95 ha [95% CI: 41.1 to 148.9], SE = 24, n = 11) owls were similar as well. As with home-range size, the proportion of older conifer forest within the core area was greater at ESF ($\bar{x}$ = 0.625, SE = 0.056, n = 15) than at NCR ($\bar{x}$ = 0.374, SE = 0.073, n = 9), with minimal overlap of 95% confidence intervals (ESF: 0.506 to 0.744, NCR: 0.205 to 0.543).

Home-range and Core-area Overlap

We calculated mean home-range and core-area overlap between individual owls of mated pairs that were monitored during both breeding and nonbreeding seasons to estimate amount of shared area. Home-range overlap of mated pairs was 54% (SE = 4.54, n = 16). Overlap was higher at ESF ($\bar{x}$ = 61.5% [95% CI: 44.5 to 78.5], SE = 20.4, n = 8) than at NCR ($\bar{x}$ = 46.9% [95% CI: 35.9 to 57.8], SE = 13.1, n = 8). Similarly, amount of core-area overlap was greater at ESF ($\bar{x}$ = 76.5% [95% CI: 55.01 to 97.99], SE = 25.7, n = 8) than at NCR ($\bar{x}$ = 28.1% [95% CI: 6.44 to 56.57], SE = 29.9, n = 8).

We also examined home-range overlap among owls that occupied adjacent territories for 3 territories at NCR and 6 territories at ESF. Overlap was higher at NCR ($\bar{x}$ = 14.89% [95% CI: 6.66 to 25.59], SE = 4.3) than at ESF ($\bar{x}$ = 6.67% [95% CI: 2.05 to 11.32], SE = 2.16). Core areas did not overlap at any adjacent owl territories.

Seasonal Home-range Size

The model that best explained variation in seasonal ranges contained only the variable for season (Table 4). The model containing season and study area was competitive with the top model (ΔAIC_c = 2.0), although its Akaike weight was low (w = 0.19) relative to the top model (w = 0.53). Summed Akaike weights by variable indicated that season (0.924) had greater relative importance than either study area (0.359) or sex (0.305). Amount of variance explained by the top model was 0.25.

We estimated sizes of breeding season home ranges using data from 15 spotted owls at ESF and from 7 owls at NCR. Sizes of nonbreeding season home ranges were estimated using data from 13 spotted owls at ESF and from 8 spotted owls at NCR. Overall, owls had larger home ranges during the nonbreeding season ($\bar{x}$ = 1,239 ha [95% CI: 957.9 to 1,520.1], SE = 134, n = 24) than during the breeding season ($\bar{x}$ = 898 ha [95% CI: 589.9 to 1,206.4], SE = 147.3, n = 24). Similar to cumulative home-range estimates, breeding-season home ranges were larger and more variable at NCR ($\bar{x}$ = 1,199 ha [95% CI: 371.8 to 2,025.6], SE = 337.9, n = 7) than at ESF ($\bar{x}$ = 736 ha [95% CI: 462.1 to 1,010.5], SE = 125.9, n = 13); however, nonbreeding-season home ranges were similar between NCR ($\bar{x}$ = 1,280 ha [95% CI: 659.6 to 1,900.6], SE = 262.4, n = 8) and ESF ($\bar{x}$ = 1,209 ha [95% CI: 891.1 to 1,527.0], SE = 142.6, n = 11).

Habitat Use

Amount of each cover type available to owls varied widely among individual owls and between study areas. Pole conifer comprised approximately 23% of available habitat for owls at both NCR and ESF. Owls at NCR had slightly more nonforest (18%) and broadleaf (28%) available than owls at ESF (nonforest: 14%; broadleaf: 22%). Owls at ESF had more mature/old forest ($\bar{x}$ = 42%) available than owls at NCR ($\bar{x}$ = 30%). In addition, 18% of habitat available to owls at ESF was old forest with large trees (>83 cm dbh) and multi-

Table 5. Akaike's Information Criteria (AIC_c) values for top habitat-use models ($\Delta AIC_c < 5.0$) differentiating spotted owl radiotelemetry locations from random locations in Elliott State Forest (ESF) and Northern Coast Range (NCR) study sites, Oregon, USA, 1995–1998. Lower ΔAIC_c values indicate more parsimonious models. If no model was <5.0 ΔAIC_c units from the top model, we included the next most competitive model for comparison. Twenty-eight models were originally evaluated for ESF and 23 models were evaluated for NCR.

		AIC_c values for individual owls												R^{2a}	
Model	K	Owl 1	Owl 2	Owl 3	Owl 4	Owl 5	Owl 6	Owl 7	Owl 8	Owl 9	ΣAIC_c	ΔAIC_c	w_i	Mean	SE
ESF overall															
Male owls (No. locations)		98	75	29	85	75	67	107	83	36					
Distance-p[b] edge	3	465.77	468.44	251.15	557.17	451.63	332.82	554.86	469.79	193.34	3,744.96	0.00	0.98	0.20	0.04
Distance-p (mature/old*distance-l[c])	5	464.96	471.99	246.89	547.11	454.47	331.54	577.53	464.21	194.69	3,753.38	8.42	0.01	0.20	0.04
Female owls (No. locations)		27	57	94	55	77	19								
Distance-p edge	3	235.72	360.10	541.04	333.04	303.14	155.29				1,928.32	0.00	0.67	0.27	0.27
Distance-p broadedge	3	236.11	357.05	544.16	336.46	299.17	157.06				1,930.02	1.70	0.29	0.06	0.06
ESF breeding season (1 Mar–31 Aug)															
Male owls		76	49	29	55	48	50	71	47						
Distance-p broadedge	3	375.06	294.78	250.46	371.60	318.59	269.50	403.57	262.23		2,545.80	0.00	0.99	0.29	0.04
Distance-l edge	5	372.18	292.45	256.69	388.28	319.15	270.08	389.91	267.34		2,556.08	10.28	0.01	0.27	0.04
Female owls		23	32	65	30	58									
Distance-p broadedge	3	203.65	234.43	418.17	228.60	196.36					1,281.20	0.00	0.61	0.28	0.09
Distance-p edge	3	201.75	233.22	412.80	229.45	204.91					1,282.12	0.92	0.38	0.29	0.09
ESF nonbreeding season (1 Sep–28 Feb)															
Male owls		22	30	27	36	36									
Distance-p edge	3	186.89	280.65	228.81	282.16	295.45					1,273.95	0.00	0.62	0.12	0.03
Distance-p broadedge	3	180.88	281.58	229.53	288.86	295.61					1,276.46	2.51	0.18	0.12	0.03
Distance-p (old*distance-l) old pole	5	187.52	280.86	230.17	290.74	288.23					1,277.52	3.57	0.10	0.13	0.03
Female owls		25	29	25											
Distance-p edge	3	197.96	234.61	168.17							600.74	0.00	0.31	0.25	0.05
Distance-p	4	197.06	233.33	170.37							600.76	0.03	0.30	0.24	0.05
Distance-p broadedge	3	195.33	233.98	171.46							600.78	0.05	0.30	0.25	0.04
Distance-p (old*distance-l) old pole	5	193.57	236.07	173.82							603.46	2.72	0.08	0.26	0.04
NCR overall															
Male owls		82	262	48	102										
Distance-p broadedge	5	541.14	916.31	350.40	361.30						2,169.16	0.00	0.87	0.32	0.11
Distance-p edge	5	536.61	916.27	352.52	367.58						2,172.98	3.81	0.13	0.32	0.11
Female owls		75	107	47	69	54									
Distance-p broadedge	5	467.40	596.73	301.33	428.62	363.14					2,157.21	0.00	0.99	0.24	0.04
Distance-p mature/old pole broad non	8	476.52	590.46	300.06	436.95	363.86					2,167.84	10.63	0.00	0.25	0.04
NCR breeding season															
Male owls		76	164	39											
Distance-p broadedge	5	306.10	586.46	238.82							1,131.38	0.00	0.63	0.43	0.15
Distance-p edge	5	304.45	586.08	242.06							1,132.59	1.21	0.34	0.43	0.15

(continued on next page)

Table 5. continued.

Model	K	AIC$_c$ values for individual owls									ΣAIC$_c$	ΔAIC$_c$	w_i	R^{2a}	
		Owl 1	Owl 2	Owl 3	Owl 4	Owl 5	Owl 6	Owl 7	Owl 8	Owl 9				Mean	SE
Female owls		33	65	54	31										
Distance-p broadedge	5	276.72	408.96	301.33	173.96						1,160.97	0.00	0.99	0.30	0.07
Distance-p edge	5	280.14	408.21	300.71	183.33						1,172.39	11.43	0.00	0.29	0.07
NCR nonbreeding season															
Male owls		43	98	33											
Distance-p broadedge	5	346.88	577.59	274.90							1,199.37	0.00	0.30	0.15	0.03
Distance-l broadedge	3	345.87	576.91	276.86							1,199.64	0.27	0.26	0.13	0.04
Distance-l edge	3	343.99	576.84	279.19							1,200.02	0.65	0.22	0.13	0.04
Distance-p edge	5	344.92	577.55	277.58							1,200.05	0.69	0.21	0.15	0.03
Female owls		42	38	33	42										
Distance-p edge	5	283.41	297.63	272.53	318.15						1,171.73	0.00	0.94	0.19	0.04
Distance-p mature/old pole broad non	8	289.63	320.97	265.86	301.02						1,177.48	5.75	0.05	0.21	0.03

[a] Maximum rescaled generalized R^2.

[b] Distance from nest(m) + distance from nest^2 + distance from nest^3

[c] Linear distance from nest (m).

layered canopies characteristic of "typical" spotted owl habitat, while old forest at NCR was minimal (<5%). Although NCR contained extensive tracts (>1,000 ha patches) of young mixed-sized conifer (>50% of trees <53 cm dbh) and large patches of broadleaf forest (>250 ha), mean patch size for stands of mature/old conifer was smaller (2.6 ha) than at ESF (8.8 ha). Although sites at ESF contained relatively large patches of broadleaf (>200 ha), these stands tended to be narrower riparian corridors than broadleaf stands at NCR.

Models that best described overall habitat-use patterns varied widely among individual owls at both study areas (Table 5). Models containing distance from the nest performed better than models with only cover types, and the polynomial distance from the nest function performed better than the linear distance function. However, when we examined results across owls at each study area, the top models for male and female owls were similar at ESF and NCR and contained distance from the nest and variables describing distance to forest edge. At ESF, distance to forest–nonforest edge was included in the top model for both male and female owls, while distance to broadleaf-forest edge was included in the best model for male and female owls at NCR. At ESF, the model containing distance from the nest and distance to nearest broadleaf-forest edge was a competitive model (ΔAIC_c = 1.70) for female owls, and the model containing distance from the nest and distance to nearest forest–nonforest edge was somewhat competitive (ΔAIC_c = 3.81) for male owls at NCR. Models containing cover-type parameters ranked considerably lower (all $\Delta AIC_c > 5.0$) than the top models. Overall, we found a negative relation between spotted owl locations and distance to broadleaf-forest edge and a positive relation between spotted owl locations and nonforest edge; however, individual owls varied widely.

Akaike weights summed across models for individual parameters and averaged across owls indicated that distance to the nest (polynomial) had the highest relative importance at ESF ($\bar{x}$ = 0.65, SE = 0.083, n = 15) and NCR ($\bar{x}$ = 0.76, SE = 0.102, n = 9). Cover type was a close second at ESF ($\bar{x}$ = 0.62, SE = 0.081, n = 15), while distance-to-edge variables ($\bar{x}$ = 0.53, SE = 0.137, n = 9) were more important than cover type ($\bar{x}$ = 0.46, SE = 0.134, n = 9) at NCR. Although the top models at ESF included distance-to-edge variables, their contribution to model fit was lower ($\bar{x}$ = 0.28, SE = 0.076, n = 15) than other variables. Predictive power of our models as indicated by mean generalized R^2 values (Allison 1999;

Table 5) was not great (range = 0.20–0.32), suggesting that other factors in addition to the variables we measured may have influenced spotted owl habitat-use patterns observed on our study areas.

When we examined habitat associations separately for breeding and nonbreeding seasons, top models for both seasons were relatively similar at both study areas to top models for the full data sets (Table 5). Although the top models varied widely among individual owls, the model containing distance from the nest and distance to broadleaf-forest edge was the top model for male and female owls at both study areas during the breeding season. The model containing distance from nest and distance to forest–nonforest edge was a competitive model for male owls at NCR ($\Delta AIC_c = 1.21$) and for female owls at ESF ($\Delta AIC_c = 0.92$). As with the full data set, we observed a negative relation with distance to broadleaf-forest edge.

For the nonbreeding season, the top model for male and female owls at ESF and female owls at NCR was the model containing distance from nest and distance to forest–nonforest edge. For male owls at NCR, the top model contained the distance to broadleaf-forest edge rather than forest–nonforest edge, although all the models containing edge parameters were competitive (all $\Delta AIC_c < 0.70$). Models containing cover-type variables were more competitive for the nonbreeding season analysis than for breeding season or for both seasons combined. At ESF, the model containing old conifer, pole conifer, and an interaction between old conifer and distance from the nest ranked relatively high for both male ($\Delta AIC_c = 2.72$) and female ($\Delta AIC_c = 2.72$) owls. At NCR, the model containing mature/old conifer, pole conifer, broadleaf forest, and nonforest was the highest ranking model (ΔAIC_c = 5.75) with cover-type parameters for female owls. Predictive power of models as indicated by generalized R^2 values was similar for breeding-season models (range = 0.24–0.44) and the full data set, but was considerably lower for nonbreeding-season models (range = 0.10–0.26).

Although distance to the nest was the most important variable in the habitat-use models, individual owls varied greatly in the mean distance traveled from the nest tree (Fig. 3). Overall, mean distance traveled from the nest was greater at NCR ($\bar{x}$ = 1,658 m, SE = 157.9, $n = 9$) than at ESF ($\bar{x}$ = 1,191 m, SE = 110.3, $n = 15$). The difference between the study areas in distance traveled was greater during the breeding season (NCR: $\bar{x}$ = 1,577 m; ESF: $\bar{x}$ = 1,014 m) than in the nonbreeding season (NCR: $\bar{x}$ = 1,819 m; ESF: $\bar{x}$ = 1,434 m). As expected, owls at both sites were located close to the nest tree more often during the breeding season than the nonbreeding season, and female owls were located closer to the nest tree than male owls during breeding season (Fig. 3). Although owls regularly returned to nest sites, we often located them far from nest trees. Approximately 20% of locations were >2,000 m from the nest.

Distance to both forest–nonforest and broadleaf-forest edge were important factors in habitat selection for owls on our study areas, possibly more important than cover type itself. As indicated by the large confidence intervals (Fig. 4), individual owls varied greatly in their proximity to edges. On average, radiotelemetry locations for owls were closer to broadleaf-forest edges and farther from forest–nonforest edges than random points (Fig. 4). However, locations for some individual owls were farther from broadleaf edges and closer to nonforest edges, suggesting that individual owls were utilizing habitat differently.

Although distance-to-habitat-edge models outperformed cover-type models, cover-type variables were components of competitive models for habitat use for individual owls, particularly at ESF. Model-averaged parameter estimates indicated that owls at ESF selected old (odds ratio: 1.12), mature/old (odds ratio: 1.24), and broadleaf (odds ratio: 1.04) forest more often than pole conifer (Table 6). At NCR, owls selected broadleaf forest (1.60) most strongly, but also selected mature/old conifer forest (1.21; Table 6). Nonforest was used about as often as pole conifer (odds ratio: 1.01). Owls at ESF showed higher selection for mature/old habitat relative to old forest overall and during the breeding season. However, during the nonbreeding season, owls showed stronger selection for old conifer (odds ratio: 1.40). At NCR, owls consistently showed strongest selection for broadleaf forest relative to pole conifer. As with model fit, parameter estimates varied greatly among individual owls, indicating a high degree of variability in habitat-selection patterns among individual owls.

DISCUSSION

Home Range

In Oregon, annual home-range size for spotted owls varies among individual owls, physiographic provinces, and from year to year (Thomas et al. 1990). In our study, mean and median home-range sizes (100% MCP) for owls at ESF were slightly smaller than home-range sizes reported

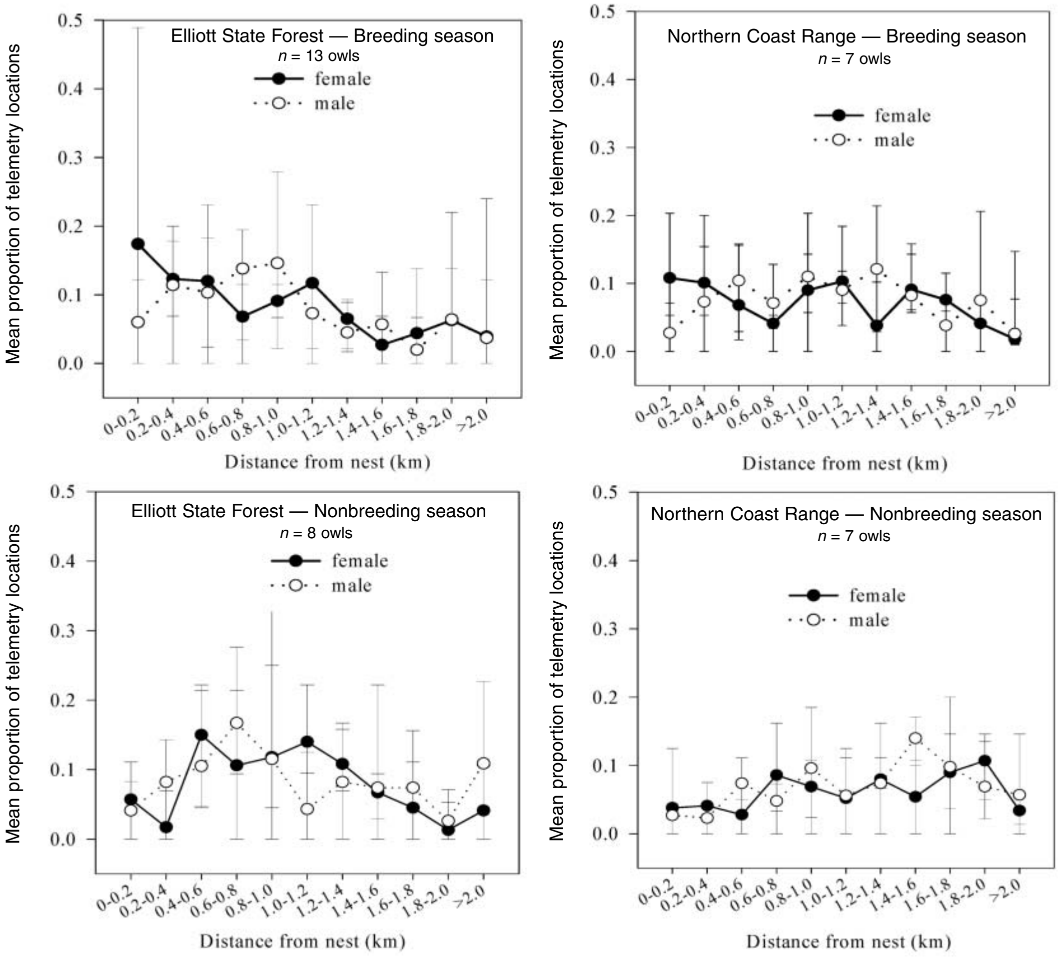

Fig. 3. Mean proportion of spotted owl radiotelemetry locations at increasing distances from the nest during breeding (1 Mar–31 Aug) and nonbreeding (1 Sep–28 Feb) seasons at Elliott State Forest and Northern Coast Range study areas, Oregon, USA, 1995–1998. Mean proportion of locations in each 200-m increment >2.0 km were assigned to the last category. Error bars represent minimum and maximum values. Number of estimated locations for each owl ranged from 30 to 261.

elsewhere in the Oregon Coast ranges, while those at NCR were larger. Our results were consistent with our initial prediction that owls with less mature/old conifer forest available would have larger home ranges. Patterns we observed were more similar to those reported for spotted owls in fragmented forests in southwest Oregon (Carey et al. 1992) than for those occupying young mixed-conifer forest in northwest California (Zabel et al. 1995). Carey et al. (1992) reported that the proportion of late-seral forest in owl home ranges varied less than home-range size in Douglas-fir forests where northern flying squirrels (*Glaucomys sabrinus*) were the primary prey. In contrast, Zabel et al. (1995) reported that spotted owls that consumed more woodrats had smaller home ranges and the relation between home-range size and proportion of late-seral forest was weak. Our home-range results also were consistent with results reported by Swindle et al. (1999), who found that spotted owl nests in the western Oregon Cascades tended to be centered in clumps of old forest and that the amount of old forest within owl territories decreased as distance from the nest increased. Because owls cannot expand their home ranges indefinitely without impairing their ability to survive and reproduce, the lower proportion of mature/old conifer forest we observed in home ranges at NCR may reflect the lower availability of this cover type at NCR.

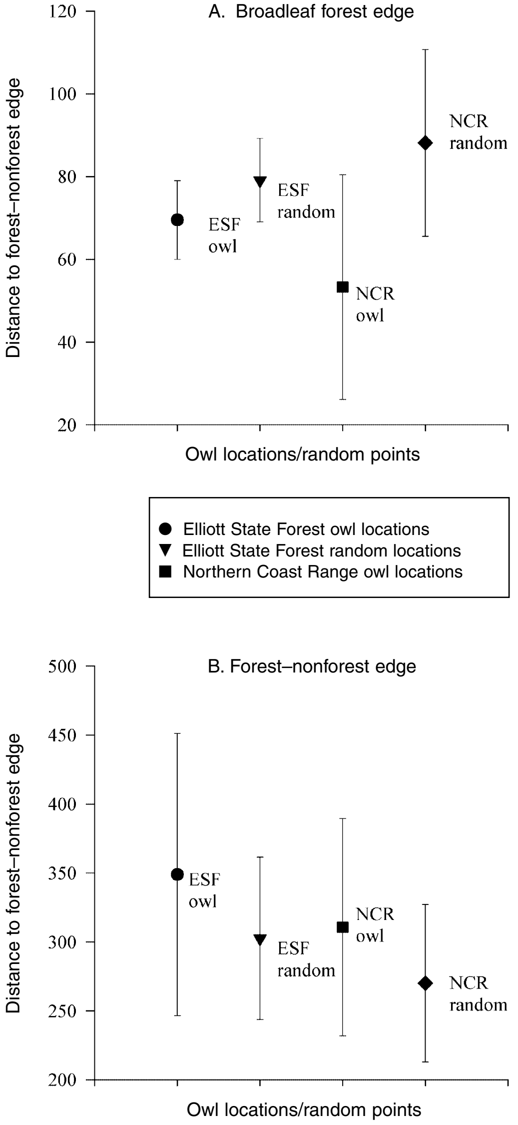

Fig. 4. Average distance to (A) broadleaf-forest edge and (B) forest–nonforest edge for spotted owl radiotelemetry locations and random points recorded at the Elliott State Forest (ESF; 1997) and Northern Coast Range (NCR; 1995–1998) study areas, Oregon, USA. Error bars represent 95% confidence intervals around means.

Vegetation differences between NCR and ESF also appeared to influence the amount of home-range overlap, both between individuals in a mated pair and among owls occupying adjacent territories. The ESF area had greater home-range and core-area overlap between paired owls, while the NCR area had greater overlap among adjacent owl territories. Amount of overlap at ESF was comparable to results reported by Forsman et al. (1984) for paired owls (68%, range = 40–93%) and among adjacent sites (12%, range = 3–25%) in the western Cascades. Our results also were consistent with Carey et al. (1992), who reported that overlap between members of pairs decreased and overlap among owls in neighboring territories increased with increasing home-range size. Carey et al. (1992) proposed that increased home-range size and the subsequent changes in overlap patterns may indicate poor quality or declining habitat which may result in increased adult dispersal and nomadism. Furthermore, Carey and Peeler (1995) reported that as home ranges became very large, spacing among social units based on long-distance calls broke down.

Consequently, home-range patterns we observed at NCR add to existing concerns about the health of this population. Demography of spotted owl populations on NCR and ESF indicated that the NCR population was not self-sustaining between 1990 and 1999 (Franklin et al. 1999). Adult survival rates and fecundity were lower at NCR than at ESF and most other spotted owl study areas in the region-wide analysis (Franklin et al. 1999). Adult survival rates and fecundity at ESF were similar to other study areas, while the juvenile survival rate was higher (Franklin et al. 1999). Because the home-range patterns we observed appear to correspond with measures of fitness, our results suggest that the patterns of home-range size and amount of home-range overlap may provide surrogate measures for evaluating the quality of habitat for spotted owls.

In northwest California, researchers (Folliard et al. 2000, Thome et al. 1999, Ward et al. 1998, Zabel et al. 1995) have identified several factors that appear to allow owls to survive in young managed forests with less late-seral conifer habitat than most other forests occupied by owls. Ward et al. (1998) concluded that selection of large prey species (dusky-footed woodrats) provided an energetic benefit to spotted owls over other prey species and reported that owls selected conifer–hardwood edge sites for foraging where dusky-footed woodrats were more abundant. In the same area, Zabel et al. (1995) reported reduced home-range sizes where owls consumed more woodrats, indicating that owls may be able to meet their energy requirements by using prey-rich edge sites. Thome et al. (1999) also suggested that spotted owls that chose younger stands may have benefited from higher woodrat densities, and Folliard et al. (2000) reported that nest

Table 6. Average parameter estimates and odds ratios from logistic regression analysis of spotted owl habitat selection in Elliott State Forest (ESF; 1997) and Northern Coast Range (NCR) Study Areas (1995–1998), Oregon, USA. Odds ratios indicate use of each cover type relative to pole conifer (13–53 cm dbh) forest. Old forest was not included in NCR models and nonforest was not included in ESF models.

		ESF						NCR					
	Parameter	n	$\bar{x}^a$ parameter estimate	SE	Lower CI	Upper CI	Odds ratio	n	$\bar{x}$ parameter estimate	SE	Lower CI	Upper CI	Odds ratio
All locations	Old	15	0.1113	0.0738	–0.0469	0.2695	1.12	9					
	Mature/old		0.2186	0.1824	–0.1728	0.6100	1.24		0.1916	0.1756	–0.2134	0.5966	1.21
	Broadleaf		0.0416	0.1328	–0.2433	0.3265	1.04		0.4539	0.1795	0.401	0.8677	1.60
	Nonhabitat		0.0115	0.1183	–0.2613	0.2829	1.01						
Breeding season	Old	13	0.0364	0.0166	0.0003	0.0725	1.04	7					
	Mature/old		0.1741	0.1745	–0.2058	0.5510	1.19		0.0554	0.0629	–0.0986	0.2094	1.05
	Broadleaf		0.1663	0.0891	–0.0277	0.3603	1.18		0.2698	0.1499	–0.0970	0.6366	1.31
	Nonhabitat		0.0004	0.0169	–0.0409	0.0417	1.00						
Nonbreeding season	Old	8	0.3345	0.1714	–0.0705	0.0690	1.40	7					
	Mature/old		0.0737	0.0581	–0.0633	0.2107	1.08		–0.0280	0.1706	–0.4455	0.3895	0.97
	Broadleaf		–0.0300	0.0657	–0.1850	0.1250	0.97		0.2528	0.2012	–0.2395	0.9451	1.30
	Nonhabitat		–0.3088	0.3419	–1.1450	0.5277	0.73						

[a] Model-weighted parameter estimates averaged across all owls at each study area.

landscapes contained a greater amount of edge than random sites.

Owl habitat on our study areas was comprised of fragmented Douglas-fir forests rather than the mixed-conifer forest found in northwest California. Northern flying squirrels were generally considered to be the primary prey species of spotted owls in our study area (Forsman et al. 1984). Woodrats were generally less abundant in Oregon than in California (Carey et al. 1999); however, they were still a component of owl diets on our study areas, particularly at ESF. Pellet analysis (A. Ellingson, Oregon State University, unpublished data) indicated that bushy-tailed woodrats (*Neotoma cinerea*) and rabbits (unidentified *Leporid* spp.) were a greater component of owl diets at ESF (35.5% and 13.9%, respectively; n = 318 pellets) than at NCR (13.0% and 4.0%, respectively; n = 206 pellets). Furthermore, bushy-tailed woodrats were a higher proportion (35.5%) of the diet than northern flying squirrels (30.2%) at ESF, while at NCR, flying squirrels (57.5%) were the largest component of owl diets. Energetic benefits derived from the availability of 2 large prey species to owls may have contributed to the smaller home-range sizes observed at ESF.

Habitat Use

Our habitat-selection models provided some new information about habitats selected by spotted owls in young forests in the Oregon Coast Ranges. Distance to forest-edge types appeared to have a stronger influence on habitat use by owls at both ESF and NCR than cover type. Although owls usually were associated with broadleaf edges, owls generally were located farther from forest–nonforest edges than random points. Most forest–nonforest edges on our study areas were associated with clearcuts, while most broadleaf forests on our study areas were associated with riparian areas and contained a large amount of older conifer–broadleaf edge. At ESF, bushy-tailed woodrats were likely to be abundant in these riparian areas (Carey et al. 1999). Broadleaf trees at both sites also added to structural diversity of forest stands and provided roost sites. Although red alder dominated most broadleaf stands, bigleaf maple was present in many stands, particularly at NCR. At ESF, myrtlewood (*Umbellularia californica*) also was a common component of both broadleaf and conifer stands. Because myrtlewood is an understory species, it was not identified in our habitat classification scheme. However, it added considerable structural diversity in forest stands at ESF, providing additional canopy layers and supporting abundant epiphyte populations. We frequently observed owls roosting in myrtlewood trees, particularly on warm summer days.

Even though spotted owls in our study varied widely in the mean distance that they traveled from the nest, all of the top habitat-selection models included distance of owl locations from the nest tree. This indicated that spotted owls on our study areas selected cover types at least partially based on proximity to the nest. If our models had failed to include distance to the nest, selection may have been confounded with availability, and the likely consequence would have been to detect selection of cover types close to the nest while discounting more distant cover types (Rosenberg and McKelvey 1999). Rosenberg and McKelvey (1999) demonstrated that this bias can be extreme when a cover type is correlated with distance to the nest as is common in species such as spotted owls that select nesting sites at a landscape scale (Ripple et al. 1997, Swindle et al. 1999). Because our models accounted for both cover type and distance to the nest, our estimators of selection reflected what cover types owls at NCR and ESF were selecting for foraging and roosting, given where they chose to locate their nests.

Rosenberg and McKelvey (1999) emphasized the importance of evaluating nest-site selection independent of foraging/roost-site selection to understand the biological basis of the patterns detected in habitat-use models for central-place foragers because selection criteria for the central place (nest) may differ from the habitat requirements for foraging habitat. Although we did not conduct a detailed analysis of nest-tree selection in our study, nest sites for owls at NCR and ESF generally were located within mature/old conifer forest or along conifer–broadleaf edges associated with riparian areas. Nest trees typically were large conifers (85%), but some nests also were in bigleaf maple trees at both areas and 1 nest was located in a red alder tree at NCR (A. Ellingson, Oregon State University, unpublished data). Characteristics of nest sites in our study including presence of broadleaf forest and broadleaf-forest edges were similar to those observed by Folliard et al. (2000) in northwest California, but differed somewhat from results of other studies in western Oregon. Hershey et al. (1998) and Swindle et al. (1999) both found that nests were associated with higher proportions of old forest than found on the landscape overall.

We found that selection for mature/old conifer forest was not as strong as for other studies. In part, this may have resulted from including distance to nest as a variable in our models. However, most studies on habitat selection of northern spotted owls have shown strong selection for late-seral forests and avoidance of young forests and clearcuts (Carey et al. 1990, Forsman 1980, Forsman et al. 1984, Solis 1983). Among 10 radiotelemetry studies of spotted owl habitat use in Oregon and Washington conducted between 1975 and 1990 (reviewed in Thomas et al. 1990), late seral was the only forest type that owls used consistently more than expected for roosting and foraging.

Individual owls on our study areas varied greatly in habitat-use patterns and appeared to be utilizing different strategies for surviving in younger forests. Furthermore, the low predictive power of our models suggests that factors in addition to those we included in our models influenced spotted owl habitat-use patterns on our study areas. At ESF, amount of mature/old conifer was relatively similar to most other areas with spotted owls in the Oregon Coast Ranges, and cover types were distributed relatively evenly across our entire study area. Patch sizes of mature/old conifer, pole conifer, and nonforest were similar throughout the forest while broadleaf forest was restricted to relatively narrow riparian zones. In contrast, forest at NCR was generally younger than most other sites with spotted owls in the Oregon Coast Ranges and contained much larger tracts of nonforest, pole conifer, and broadleaf forest.

Cover-type use patterns at ESF were relatively similar to other studies in that some owls selected remnant patches of old forest within their ranges; however, a number of owls did not. Likewise, individual owls at ESF also varied in selection and avoidance of broadleaf forest. On the other hand, most owls at NCR showed stronger selection for broadleaf forest than for mature/old conifer forest, although some individuals selected mature/old conifer and some avoided broadleaf forest.

MANAGEMENT IMPLICATIONS

We identified some habitat-use patterns of spotted owls in young forests that will be useful in management of spotted owls and their habitat in the Oregon Coast Ranges. In addition, observed home-range sizes and home-range overlap indicated that the quality of habitat available to spotted owls at NCR is poorer than habitat at ESF. In areas of western Oregon where spotted owls occupy sites with little or no old conifer forest, we recommend that managers retain existing old and mature conifer forest, broadleaf forest, broadleaf-forest edges, and forested riparian areas as owl habitat. Older forest appears to be most important close to the nest. Consequently, we recommend that timber harvest in core areas be avoided. In addition, because our results indicated that owls occupying areas with less mature/old conifer had larger home ranges, we recommend that the size of areas managed for spotted owls reflect actual home-range and core-area sizes for owls in those forests (e.g., ESF = 1,000 ha; NCR = 1,500 ha).

The status of the owl population in the northern Oregon Coast Range is in question. We therefore recommend that ODF maintain areas of forest that have documented use by owls. State forests in Oregon have considerably less old forest than other areas where spotted owls are more densely populated and the NCR population is isolated from other owl populations. Because the low quality of habitat may limit northern spotted owl abundance, all existing owl territories at NCR should be maintained until researchers and managers have a greater understanding of the factors that affect this population.

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Appendix A. Timetable for collection of radiotelemetry locations for individual northern spotted owls on the Elliott State Forest (ESF) and Northern Coast Range (NCR) study areas, Oregon, USA. Lines indicate periods when locations were gathered. Gaps indicate periods when owls were not monitored.