

NORTHERN SPOTTED OWLS: INFLUENCE OF PREY BASE AND LANDSCAPE CHARACTER¹

ANDREW B. CAREY, SCOTT P. HORTON, AND BRIAN L. BISWELL
USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington 98502 USA

Abstract. We studied prey populations and the use and composition of home ranges of 47 Northern Spotted Owls (*Strix occidentalis caurina*) over 12 mo in five landscapes in two forest types in southwestern Oregon. We measured 1-yr home ranges of 23 owl pairs, 2-yr home ranges of 13 pairs, and 3-yr home ranges of 3 pairs. The landscapes differed in the degree to which old forest had been fragmented by wildfire and logging. Prey populations were measured at 47 sites in southwestern Oregon. Further data on prey populations were gathered on 14 sites on the Olympic Peninsula in northern Washington, where owls used larger ranges than in Oregon.

Owls in Washington used \approx 1700 ha of old forest annually and primarily one prey species; available prey biomass was 61 g/ha. Owls in Oregon Douglas-fir (*Pseudotsuga menziesii*) forests used 813 ± 133 ha ($0 \pm$ SE) of old forest annually and concentrated on two prey species that had a combined biomass of 244 g/ha. Owls in Oregon mixed-conifer forest used 454 - 84 ha of old forest annually and three primary prey whose availability averaged 338 g/ha. The amount of old forest used by owls studied for 2 yr was 40% greater in the 2nd yr than that used in the 1st yr. No increase in use of old forest was seen in the 3rd yr in Douglas-fir forest; 50% more old forest was used in 3 yr than in the 1st yr in mixed-conifer forest. The most common prey in Washington and Oregon was the northern flying squirrel (*Glaucomys sabrinus*). In areas where the flying squirrel was the primary prey and where predation was intense (as judged by telemetry), flying squirrel populations were depressed. The addition of medium-sized mammal species, especially woodrats (*Neotoma* spp.), to the prey base appeared to reduce markedly the amount of old forest used for foraging.

Owls traversed 85% more Douglas-fir forest and 3 times more mixed-conifer forest in the heavily fragmented areas than in the lightly fragmented areas. Overlap among pairs and separation of birds within pairs in space increased with fragmentation. In the most heavily fragmented landscape, social structure appeared to be abnormal, as judged by the proportion of adult-subadult pairs, instances of adult nomadism, and overlap among the home ranges of pairs. The pattern of fragmentation affected the ability of owls to find concentrations of old forest in the landscapes. Even so, almost all the owls consistently selected old forests for foraging and roosting; only one owl selected a younger type as part of its foraging range. Selection of old forest was significant at three levels: landscape, annual home ranges of pairs, and foraging and roosting sites of individuals. The most important prey species, the northern flying squirrel, was twice as abundant in old forest as in young forest in all areas.

Landscape indices (dominance, contagion, variance in density of old forest) had less predictive ability than indices based on owl home ranges because owls selected areas of concentrated old forest and because patterning was complex, reflecting four processes, each operating at a different scale: physiography, human land ownership (259-ha scale), history of catastrophic fires, and history of small-scale fires and timber harvesting.

Key words: bushy-tailed woodrat, dusky footed woodrat; foraging behavior: Great Horned Owl; habitat selection: home range; landscape ecology, northern flying squirrel; Oregon; Spotted Owl; telemetry; Washington.

INTRODUCTION

Conservation strategies for the Spotted Owl are controversial because of their social, political, and economic impacts (Simberloff 1987) and because the amounts, types, and arrangement of seral stages of coniferous forest required to support viable populations of the threatened

Northern Spotted Owl are not known. There are few original research reports on the ecology of the Northern Spotted Owl; the nature of its dependence on old forest and its response to logging have not been documented well. Forsman et al. (1984) is the most extensive single work. Gutierrez and Carey (1985) provide a summary of ongoing research and the information that had accumulated by 1984. Carey et al. (1990) added information on home ranges, habitat use, and responses to landscapes. Franklin et al. (1990) provided the first estimates

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of the absolute density of Spotted Owls in a landscape, but the effects of spatial arrangement of old growth on Spotted Owls have not yet been investigated (Doak 1989).

Spotted Owls preferentially select old growth for foraging, roosting, and nesting (northern California, Gutierrez et al. 1984; Oregon, Forsman et al. 1984, Carey et al. 1990; Washington, Allen and Brewer 1985) and are scarce in second-growth forests without old-growth components (Forsman et al. 1977, Forsman 1988). In an unreplicated study, Carey et al. (1990) reported a strong negative correlation ($r = -0.83$) between home range sizes of owl pairs and proportion of their range in old growth and concluded that owls strive to maintain a minimum amount of old growth within their ranges, suggesting that owls not only prefer, but require, old growth. There is, however, considerable latitudinal variation in the average amounts of old growth contained within home ranges of pairs of owls: northern California, 769 ha; Oregon, 931 ha; and Washington, 1700 ha (Dawson et al. 1987). Although Dawson et al.'s (1987) figures from Washington were based on limited, unpublished data, they were confirmed by Thomas et al. (1990) who reported median home ranges of 1327 ha for the Washington Cascades and 1853 ha for the Olympic Peninsula.

Forsman et al. (1984) collected 3969 pellets regurgitated by Spotted Owls over 8 yr in nine areas of western Oregon. In Douglas-fir/western hemlock (*Tsuga heterophylla*) forest types, northern flying squirrels averaged 53% of the biomass consumed by owls, 3 times as much as any other prey species. Woodrats were 7-15% of the biomass consumed. In mixed-conifer forests, woodrats averaged 53% of the biomass consumed and flying squirrels were 19% of the biomass. In river valley forests where Douglas-fir was mixed with grand fir (*Abies grandis*) and Oregon white oak (*Quercus garryana*), flying squirrels and woodrats were equally represented in the diet, 29 and 24% of the biomass, respectively. Subsequent studies (2 yr, 1369 pellets; Forsman et al. 1991) revealed that the northern flying squirrel was the primary prey of the Spotted Owl on the western Olympic Peninsula (61% of the biomass) and that bushy-tailed woodrats and flying squirrels were equally represented (39 and 38% of the biomass, respectively) in rocky areas on the eastern Peninsula. This study also revealed that the ratio of flying squirrel to woodrat biomass changed rapidly in the transition zone between the Douglas-fir and mixed-conifer forest types in southwestern Oregon. Numerous smaller studies (published and unpublished) confirm the importance of flying squirrels and woodrats as the primary prey of the Northern Spotted Owl (Thomas et al. 1990). Although the diets of Spotted Owls in western Washington and Oregon have been documented well (Forsman et al. 1984, 1991), the patterns of prey abundance and the influence of prey distribution on habitat use by owls have not been determined.

Six nonexclusive hypotheses have been proposed to explain the requirement of spotted owls for old growth, but only abundance of prey can explain the requirement of Spotted Owls for large areas of old growth (Carey 1985).

This hypothesis predicts that prey abundance (and diversity) and landscape composition should be the major correlates of home range size and the absolute amount of old growth in the range, that latitudinal variation in home range size should reflect prey distribution with changes in home range size being abrupt (reflecting abrupt changes in prey diversity), as opposed to clinal, and that selection of foraging habitat should reflect prey abundance.

Two other hypotheses have additional implications for the effect of spatial arrangement of old growth on Spotted Owls. The predation hypothesis predicts that landscapes dominated by old growth should have lower densities of Great Horned Owls (*Bubo virginianus*; the only predator that has been suggested as having significant impacts on spotted owls) than landscapes in which old growth has been heavily fragmented. Thus, the predation hypothesis predicts that fragmentation of old growth would affect its usefulness to Spotted Owls by increasing predation. Similarly, logging has allowed the Barred Owl (*Strix varia*) to expand its range into that of the Northern Spotted Owl. Barred Owls could compete or hybridize with Spotted Owls (Hamer 1988). The third hypothesis states that habitat requirements for thermoregulation are more restrictive than requirements for foraging; if this is true, then availability of suitable roosting sites could influence the utility of foraging habitat.

Our objectives for this paper are to explore the influence of prey base and landscape character on populations of Northern Spotted Owls. Specifically, for the prey base, we wished to determine: (a) if Spotted Owl home range size and amounts of old growth used are correlated with the diversity and total abundance of the prey base in three forest types: western hemlock forest on the Olympic Peninsula of Washington, Douglas-fir forest in the Oregon Coast Range, and mixed-conifer forest in the Umpqua River Valley and Klamath Mountains of southwestern Oregon; (b) the effects of fragmentation (by wildfire and logging) of old growth on the abundance of prey in the landscape; (c) if patterns of prey abundance reflect the foraging site selection of Spotted Owls; and (d) if prey population sizes in old growth decrease with increasing intensity of owl foraging activity. For owls, we wished to determine the effects of fragmentation on: (a) Spotted Owl foraging: size of area traversed, amounts of old growth used, and selection of habitat types; (b) social behavior amount of overlap among home ranges of owl pairs, the incidence of interactions among adjacent owl pairs, amount of overlap between home ranges within owl pairs, the proportion of owl pairs with subadult members, and incidences of adult nomadism; (c) the incidence and dispersal behavior of unmated, subadult owls; and (d) the abundance of Great Horned Owls (potential predators of Spotted Owls). Fragmentation potentially could influence reproduction of Spotted Owls. Because reproduction of Spotted Owls is sporadic and our study was limited to 3 yr, we cannot address this effect. Similarly, fragmentation could increase negative interactions between Spotted Owls and Barred Owls, but Barred Owls were rare to absent in our study areas and we cannot address this potential effect of fragmentation. Finally, we wished to

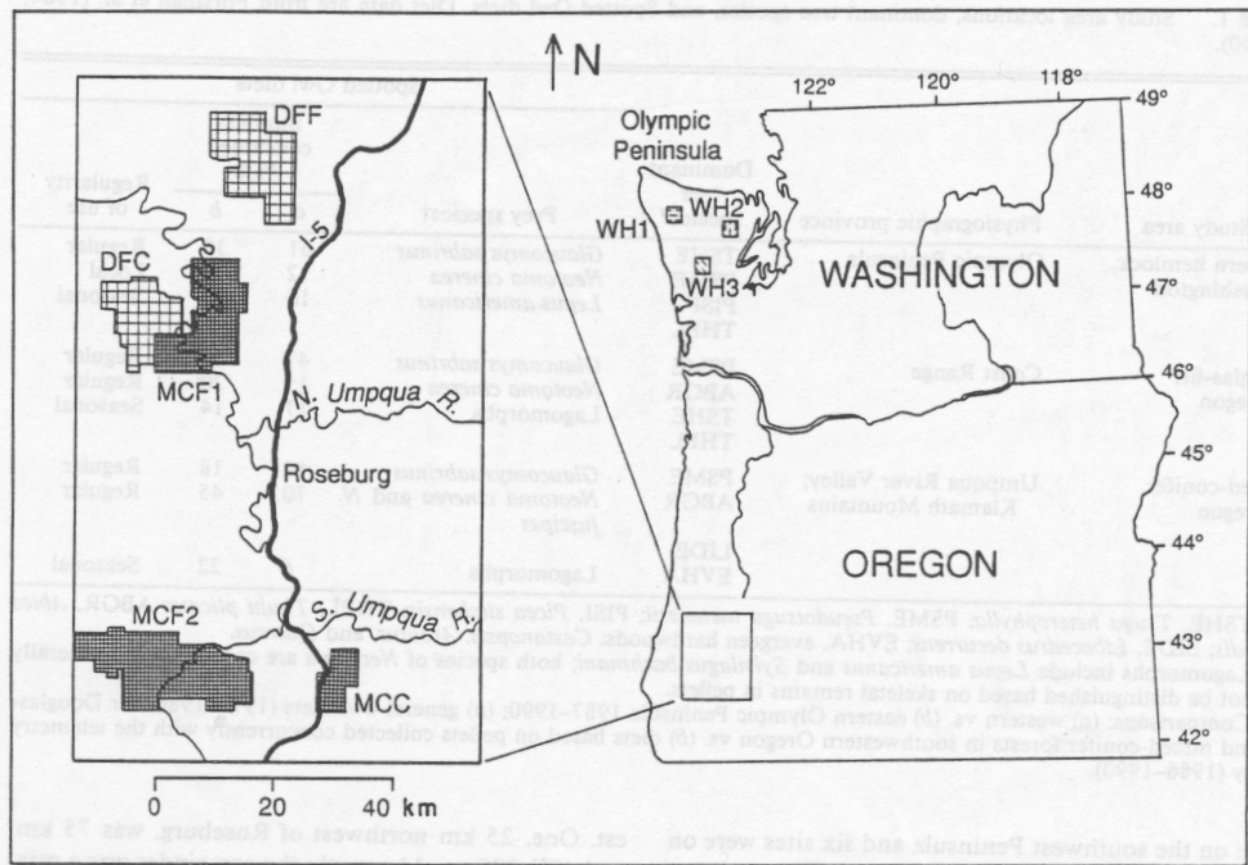


FIG. 1. Locations of study areas in Washington and Oregon, 1985-1989.

determine if Spotted Owl roost sites are more restricted in character and distribution than foraging sites.

STUDY AREAS

We chose study areas in three forest types: western hemlock, Douglas-fir, and mixed-conifer (Fig. 1, Table 1). The types differed not only in plant species composition but also in the species of prey available to the Spotted Owl and relative use of the available prey by the Spotted Owl (Table 1; Forsman et al. 1984, 1991). Forsman et al. (1984) analyzed pellets collected in 6 yr from owls in and around our Coast Range Douglas-fir study areas (1214 pellets) and in mixed-conifer forest 100 km south of our mixed-conifer study areas (651 pellets). Forsman et al. (1991) reported the contents of pellets collected from the owls during our study (96 pellets from the Douglas-fir study areas and 373 pellets from the mixed-conifer study areas) and from owls in western hemlock forests on the Olympic Peninsula (540 pellets on the western peninsula and 340 pellets on the eastern peninsula). We measured prey populations in all three forest types but studied owls only in the Douglas-fir and mixed-conifer types. We used published data on owl home range size and composition in the western hemlock forests in our analyses.

Olympic Peninsula, Washington

The Olympic Peninsula comprises a central core of rugged mountains surrounded by almost level lowlands. The central core and high elevation forests are in Olympic National Park and protected from logging. Midelevation forests are in the Olympic National Forest and are composed of mixtures of old forest and young forest created by clear-cutting, fire, and windstorms. Low elevation forests are owned by private corporations, native American tribes, and Washington State. Mid- to low elevation forests have been highly fragmented by logging; a severe windstorm along the western peninsula in 1921 destroyed large areas of old growth (for example, 2000 ha on one National Forest district). Less than 20% of the original old forest on the peninsula remains (Morrison 1989). We studied rodents on 14 20-ha sites on the Olympic Peninsula. Two sites were on the northeast Peninsula, six sites were on the southwest Peninsula and six sites were on the northwest Peninsula. The western Peninsula sites receive over twice as much precipitation as the eastern Peninsula and southwestern Oregon sites. Summer temperatures are lower and natural regeneration of forest stands is usually caused by windstorms on the western Peninsula sites as opposed to hotter summers and

TABLE 1. Study area locations, dominant tree species, and Spotted Owl diets. Diet data are from Forsman et al. (1984, 1990).

Study area	Physiographic province	Dominant tree species*	Prey species†	Spotted Owl diets		Regularity of use	
				Biomass consumed (%)‡			
				a	b		
Western hemlock, Washington	Olympic Peninsula	TSHE	<i>Glaucomys sabrinus</i>	61	39	Regular	
		PSME	<i>Neotoma cinerea</i>	2	38	Local	
		PISI	<i>Lepus americanus</i>	10	20	Seasonal	
		THPL					
Douglas-fir, Oregon	Coast Range	PSME	<i>Glaucomys sabrinus</i>	47	30	Regular	
		ABGR	<i>Neotoma cinerea</i>	15	20	Regular	
		TSHE	Lagomorphs	17	14	Seasonal	
		THPL					
Mixed-conifer, Oregon	Umpqua River Valley; Klamath Mountains	PSME	<i>Glaucomys sabrinus</i>	14	18	Regular	
		ABGR	<i>Neotoma cinerea</i> and <i>N. fuscipes</i>	70	45	Regular	
		LIDE					
		EVHA	Lagomorphs	6	22	Seasonal	

* TSHE, *Tsuga heterophylla*; PSME, *Pseudotsuga menziesii*; PISI, *Picea sitchensis*; THPL, *Thuja plicata*; ABGR, *Abies grandis*; LIDE, *Libocedrus decurrens*; EVHA, evergreen hardwoods: *Castanopsis*, *Arbutus*, and *Quercus*.

† Lagomorphs include *Lepus americanus* and *Sylvilagus bachmani*; both species of *Neotoma* are consumed but generally cannot be distinguished based on skeletal remains in pellets.

‡ Comparisons: (a) western vs. (b) eastern Olympic Peninsula 1987–1990; (a) general owl diets (1970–1980) for Douglas-fir and mixed-conifer forests in southwestern Oregon vs. (b) diets based on pellets collected concurrently with the telemetry study (1986–1990).

natural regeneration through fire on the eastern peninsula and southwestern Oregon sites. These differences in rainfall, temperature, and type of catastrophic disturbance account for the dominance of western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) on the western Peninsula.

Spotted Owl diets on the Olympic Peninsula consisted predominately of flying squirrels; bushy-tailed woodrats (*Neotoma cinerea*) were consumed only in a few locales and juvenile snowshoe hares (*Lepus americanus*) are preyed upon in the spring and early summer (Table 1; Forsman et al. 1991). Southern red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus* and *P. oreas*) occurred in 20% of owl pellets but constituted < 10% of the biomass consumed by the owls (Forsman et al. 1991). Two species commonly preyed upon by Spotted Owls in Oregon, the dusky-footed woodrat (*N. fuscipes*) and the red tree vole (*Phenacomys longicaudus*), do not occur in Washington.

Southwestern Oregon

We studied five areas near Roseburg, Oregon (Fig. 1) in Douglas-fir and mixed-conifer forests. We established two telemetry study areas in the Douglas-fir forest. One, 25 km northwest of Roseburg, was 75 km² and 40% 300-yr old growth: the remainder was a mixture of clear-cut, pole, and sapling stands (Carey et al. 1990). Based on aerial photographs and cover type maps, we judged the old growth

to be clumped in distribution and we refer to it as Douglas-fir clumped (DFC). The second area was 60 km north of Roseburg and had a history of recent fires (1868, 1939, 1951, 1966; Juday 1977) and timber harvesting. This area was 96 km² and 18% old growth with large amounts of young (35–70 yr), mature (80–100 yr), and mixed-age forests (Carey et al. 1990). We refer to it as Douglas-fir, fragmented (DFF). Flying squirrels predominated in owl diets. Bushy-tailed woodrats were staple prey also, but their importance varies locally. Lagomorphs (snowshoe hares and brush rabbits, *Sylvilagus bachmani*) occurred in the diet in spring and early summer, as in Washington (Table 1; Forsman et al. 1984, 1991). Minor prey included the red tree vole, western redbacked vole (*C. californicus*), and deer mouse (*P. maniculatus*). These averaged 10% of the biomass consumed but composed 50% of the prey ingested in particular years (Forsman et al. 1984, 1991). We chose 11 20-ha, and 8 4-ha, sites, scattered throughout the Douglas-fir telemetry areas, in which to study prey abundance.

We established three telemetry study areas and chose 9 20-ha, and 19 4-ha, sites for studies of prey in the mixed-conifer forest. The mixed-conifer forests are somewhat warmer and drier than the Douglas-fir forests. Fires are more frequent and old-growth forests are characterized by smaller trees and smaller amounts of coarse woody debris than in the Douglas-fir forests (Old-Growth Definition Task Group 1986). Old-growth forests in our 92-km² Umpqua River Valley study area (25 km north of

Roseburg) had been fragmented not only by wildfire and logging but also by grasslands, pastures, and croplands. We refer to it as mixed-conifer, fragmented old growth (MCF1). Gary Miller (*personal communication*) collected 260 pellets from spotted owls during summer in this area; 24% of the biomass consumed by owls was flying squirrel, 44% was woodrat, and 16% was lagomorph. Our two areas south of Roseburg were strongly influenced by Californian biota. The forests resembled those in the valley except that tanoak (*Lithocarpus densiflorus*) is common, and pines (*Pinus ponderosa* and *P. lambertiana*) are present in some stands. One area was 34 km southwest of Roseburg and 173 km²; based on reconnaissance, we classified it as mixed-conifer, fragmented old growth (MCF2). The other area was 34 km southeast of Roseburg and 18 km²; we classified it as mixed-conifer, clumped old growth (MCC). In these mixed-conifer forests, the woodrats (bushy-tailed and dusky-footed) predominated in the Spotted Owl's diet, with the northern flying squirrel still a staple prey. Lagomorphs were seasonally important and minor prey included the red tree vole, western red-backed vole, and deer mouse (Table 1; Forsman et al. 1984, 1991).

METHODS

Locating, capturing, and tracking owls

Within each owl study area, we used call surveys (Forsman 1983) and banding and sighting records of the Roseburg District of the Bureau of Land Management to locate resident Spotted Owls. We placed radio transmitters on 3-7 adjacent pairs of owls per site, depending on the number of owls present and the distances between the owls. Four-year histories (1985-1988) of the owls were prepared from banding and sighting records.

Owls generally were caught and fitted with transmitters in the spring (the middle of the breeding season). Methods are described by Forsman (1983). Owls were classified as adults (≥ 3 yr) or subadults (1-2 yr) based on plumage (Forsman et al. 1984). We followed telemetry procedures developed during a pilot study in 1986 (Carey et al. 1989, 1990). Procedures included periods of familiarization for each new telemetry technician and study area. These periods consisted of locating Spotted Owls using telemetry followed by locating the owls visually to ascertain the true location and to identify areas in which radio signals might be misleading. Telemetry locations were defined as the center of a polygon formed by 3-4 compass bearings taken from widely separated points. Procedures also included rules for reducing error and periodically visually locating owls after triangulation to ascertain the accuracy of the telemetry procedures; owls were located by telemetry 18 590 times and visually, following telemetry, 2060 times during 1986-1989. Owls were visually located mostly during the day, while roosting. Daytime telemetry procedures were identical to nighttime telemetry procedures; the owls generally roosted in the same stands they foraged in the night before (Carey et al. 1989).

Daytime telemetry and visual locations were conducted systematically, thus covering the full range of areas used by the owls and sampled at night; thus, we feel our estimate of daytime telemetry accuracy applies to nighttime telemetry also. Detailed procedures were reported by Guetterman et al. (1991). For the principal telemetry year (1987-1988), in which we describe habitat use, our procedures resulted in a distance from observers to owls during triangulations of 343 ± 9 m ($O \pm SE$); 95% of triangulation polygons being < 2 ha; and accuracy averaging 68 ± 4 m (difference between polygon centers and actual locations based on 553 triangulations followed by visual locations), despite the rugged terrain in our study areas. Our accuracy was sufficient to assign telemetry locations in stands; therefore we measured vegetation variables only at points where owls were visually located. In highly fragmented areas where stand size was small, the abundance of roads and trails allowed us to confidently determine which stands the owls were using. In all areas, only telemetry locations with polygons < 2 ha were used to determine habitat use.

We located each foraging owl two nights one week, and 3 nights the next week. In addition, we attempted to get one daytime (roost) location every 2 wk. This sampling schedule was designed to maximize the number of independent foraging locations (Carey et al. 1989). Locations were recorded as Universal Transverse Mercator (UTM) coordinates and stored on a microcomputer geographic information system (GIS). Most of the owls were tracked for 12-18 mo; others were followed for 2-3 yr. Data are repeated measures of the response of owls to the landscapes. Measures of movements of the same owls are, thus, nonindependent. While this approach was unavoidable here, it complicates statistical analyses and inferences. We report habitat use and seasonal home range sizes based on one biological year (September 1987-August 1988) to allow calculation of continuous ranges in the nonbreeding season (1 September-28 February) and breeding season (1 March-31 August). Cumulative home ranges are reported for 1-3 yr. Five types of events were recorded: sightings of spotted owls without radios (transient owls, based on banding and resighting records), interactions between Spotted Owls, foraging behavior of Spotted Owls, roosting of Spotted Owls, and the presence of Great Horned Owls. Owls were observed at night near roads and during the day in the forest during attempts to capture resident owls, assess reproductive status, describe roosts, and check the accuracy of telemetric locations. We located all owls equally often (mean 157 ± 1.5 visits/yr); therefore, we report number of observations per owl pair. Telemetry data were examined to determine the number of times adult owls were within 500 m of one another while foraging; we used the center point of the triangulation polygon for calculating the distance between owls. We defined these events as interactions between owls because these owls were generally in the same stand (average stand width was 451 m) and spotted owls generally stay in the same stand while foraging, but move an average of 516 m within a night (Carey et al. 1989).

We described owl perches, roost trees, and the physical

features and vegetation at visually located roost sites. As exploratory analyses, we tested whether the topographic positions of roost sites and the aspects of roost sites and perches differed among seasons (spring, summer, fall, winter) using chi-square tests. We tested whether the proximity of roosts to water differed between summer and other seasons with a *t* test. We used all-possible-subsets regression (Frane 1985) to relate roost heights and cover to weather variables. We described the vertical diversity of vegetative cover at roost sites using the Berger-Parker Index (BPI, Carey et al. 1991 *b*), and compared the BPI of roost sites between old forest and younger stands using a two-tailed *t* test. Percent cover in the four vegetative strata in old forest contrasted with younger stands using Kruskal-Wallis tests. Statistical tests were used as part of the exploratory analyses, not as formal tests of hypotheses.

Prey abundance

During 1985-1989, we captured, marked, and recaptured flying squirrels and woodrats in 14 stands (6 old, dominant trees >250 yr, and 8 young, 40-70 yr old) in western hemlock forests, 11 stands (6 old and 5 young) in Douglas-fir forests, and 9 stands (5 old and 4 young) in mixed-conifer forests. We trapped for 810 nights in spring and fall in Oregon and in fall in Washington, generally using 10 by 10 grids with 40-m spacing and two traps per station. Grid-trapping of woodrats was supplemented in southwestern Oregon by trapping in 27 stands ranging from clear-cuttings to old growth using two parallel lines with 20 m between trap stations, 20 stations per line, and two traps per station for 3-4 nights in the summer. Traplines were placed on streamsides, clearcuts, pole stands, and ridgetops in Douglas-fir and mixed-conifer landscapes. Population sizes on grids were estimated by Chapman's modification of the Petersen-Lincoln index (Menkens and Anderson 1988) or by the minimum number known alive when captures were <10. Densities were estimated by dividing population size by the effective area sampled (trapped area expanded by one-half the mean maximum distance moved between subsequent recaptures). While results from traplines are not directly comparable to results from grids and results using different methods for estimating densities are also not comparable, the estimates should be good indications of relative abundance. Complete details on trapping methods, analysis of heterogeneity, behavior, and time effects on probability of capture, and the applicability of various mark and recapture models are reported by Carey et al. (1991 *a*).

Indices of abundance of small prey (*Peromyscus* spp., *Clethrionomys* spp., and *Microtus* spp.) were obtained using snap-traps set for four nights in two parallel lines with 25 stations per line, 15 m between stations, and two traps per station. These studies were conducted in a subsample of 9 of the stands sampled with grids in southwestern Oregon and in the 14 stands studied on the Olympic Peninsula. Catch per unit effort indices were calculated (Nelson and Clark 1973).

Owl foraging activity in old forest was calculated in owl-years from the proportions of the relocations of owls in a particular stand (proportions from different owls were summed for a stand value). Foraging activity was assumed to reflect predation pressure on prey populations.

Habitat classification

We used 1:12 000 aerial photographs, forest inventory data, and ground reconnaissance to prepare habitat maps for all the 1-km² UTM blocks that included radiotelemetry locations of Spotted Owls. We defined stands as homogeneous units of vegetation based on tree diameter class, canopy closure, and vegetative composition. We classified stands > 4 ha as nonforest, hardwood-riparian, or 1 of 7 stages of coniferous forest development: (1) clearcut (grass, forb, shrub stages); (2) sapling (average tree diameter at breast height, dbh, 2-10 cm); (3) pole (11-20 cm dbh); (4) young (21-50 cm dbh); (5) mature (51-100 cm dbh and even-aged); (6) mixed-age; and (7) old growth (dominant tree dbh > 100 cm, multilayered canopy, large decaying fallen trees, and large standing-dead trees). Mixed-age forests were either old growth with inclusions of young and mature stands <4 ha (mixed-old) or predominately young stands with inclusions of other seral stages (mixed-young). Stand boundaries were digitized using UTM coordinates as reference points. Data were stored in the GIS.

Analysis of movements and tests of selection

Area traversed and habitat selection by individuals.—We calculated annual and seasonal home range sizes using the minimum convex polygon (MCP) method (Hayne 1949) for individuals and their union (sum minus the area of overlap) for pairs, as did Forsman et al. 1984, Gutierrez et al. 1984, Dawson et al. 1987, and Carey et al. 1990. The densities (pairs per square kilometre) of resident pairs were calculated by dividing the sum of the MCP pair home ranges (minus the area of overlap among ranges) by the number of pairs. We felt confident that we discovered all resident pairs; however, unpaired and nonresident individuals may have escaped detection. The MCP home range is an estimate of the area traversed by the owls; henceforth we refer to MCP home ranges as areas traversed. We consider the areas traversed annually by owl pairs to be the best measure of owl response to landscape character (Carey et al. 1990).

For each owl, we tested the hypothesis that use was in proportion to availability, within the area it traversed, for four habitat types: nonforest (including clearcuts); early-seral stages (sapling, pole), mid-seral stages (young, young mixed-age, mature, and hardwood forests), and late-seral stages (old growth and old growth mixed with younger patches of trees, hereinafter referred to as old forest). A chi-square goodness-of-fit test was used to determine where there were significant differences between the expected utilization of habitat types (based on their availability) and the observed

frequency of their usage. When statistically significant differences were found, simultaneous confidence intervals (using Bonferroni's inequality, Byers and Steinhorst 1984) were used to determine which types were avoided (expected usage greater than the 95% confidence interval for observed usage), used in proportion to their occurrence, and selected (expected usage less than the 95% confidence interval for observed usage).

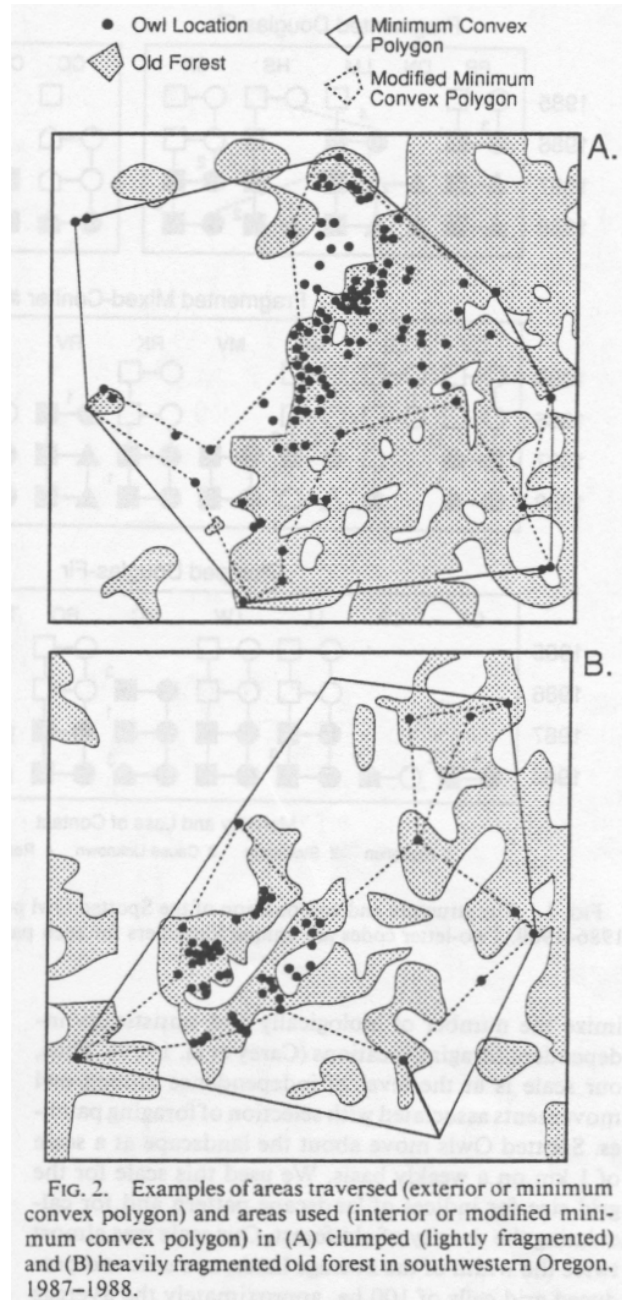
Area used and population selection of habitat types.—The modified minimum convex polygon (MMCP) method (Harvey and Barbour 1965) delineates areas actually used by the owls more precisely than does the MCP method (Carey et al. 1989): henceforth we will refer to MMCP ranges as areas used. Fig. 2 illustrates the difference between areas traversed and used in clumped and fragmented landscapes. We tested for habitat selection at the population level (for each of the five landscapes) by comparing average percentages of the areas used by pairs in 1987-1988 that were old forest to percentages of the landscapes that were old forest using a paired *t* test. We calculated the amounts of old forest in the areas used by pairs that were tracked ≥ 2 yr, beginning with the first telemetry year, then cumulatively by season. We used a paired *t* test to determine if owl pairs used significantly more old forest in 2 yr than they did in 1 yr.

To determine if habitat use differed from that expected from a uniform territorial spacing, we placed a grid over each landscape habitat type map. The size of the grid cells was proportional to the average area used in that landscape. We calculated the mean proportion of old forest in the cells and compared that mean to the mean proportion of old forest in the areas used with a paired *t* test. To explore further the influence of landscape character on owl use of space we calculated the amount of overlap (union divided by sum) between members of pairs and among adjacent pairs for both areas traversed and areas used.

Selection of individual stands.—We wished to determine if owls selected particular stands for foraging in habitat types that were generally avoided (nonforest and early seral stages). For each landscape, we combined all owl locations and used the MMCP method to delineate the landscape boundaries. We tested for individual stand selection (percent use of stand greater than expected based on the percent of the MMCP landscape occupied by the stand) using the Poisson parameter test ($P < .05$; Dowdy and Wearden 1983).

Spatial pattern

Choice of scale is critical to analysis of landscape patterning (O'Neill et al. 1988b). We chose as our scale 1 km, approximately the mean distance moved by owls between successive nighttime telemetry locations. Our radiotelemetry sampling scheme was designed to maximize the number of biologically and statistically independent foraging locations (Carey et al. 1989). Thus, our



scale is at the level of independence among owl movements associated with selection of foraging patches. Spotted Owls move about the landscape at a scale of 1 km on a weekly basis. We used this scale for the grid size for indices of landscape pattern and for calculating the density of old forest. Our scale was almost twice the width of the average landscape unit and produced grid cells of 100 ha, approximately the average size of stands of the owls' selected habitat and almost twice the average stand size.

Pattern indexes.—We calculated the three indices (dominance, contagion, fractal dimension) suggested by

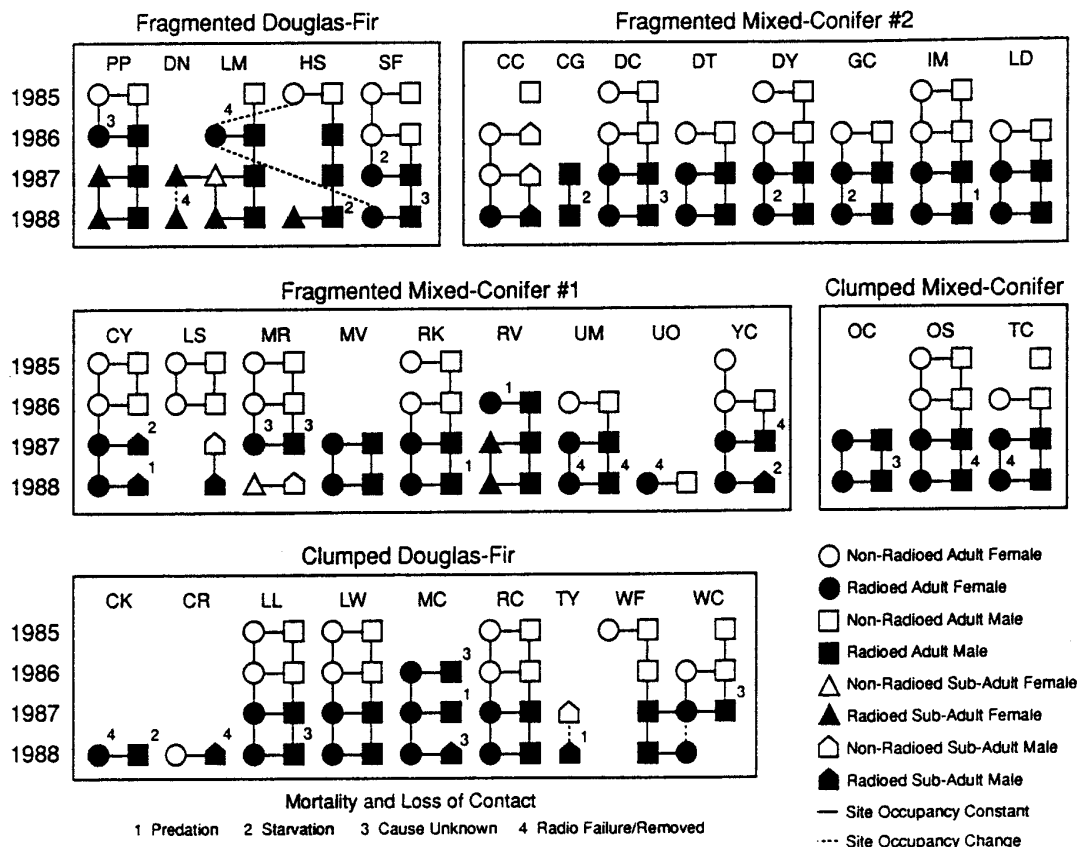


FIG. 3. The structure and composition of the Spotted Owl populations studied in five landscapes in southwestern Oregon, 1986-1989. Two-letter codes are unique identifiers for each pair of owls.

O'Neill et al. (1988a), the proportion of the MMCP landscape that was preferred habitat, the variance of the density of preferred habitat, and mean stand area and mean stand width (calculated from 60 km of systematically placed transects in each landscape).

Biological index.—Based on previous work (Carey et al. 1990), we assumed that (1) areas traversed reflect the responses of Spotted Owls to the landscapes they inhabit; (2) owls select home ranges that have a greater than average concentration of old forest; (3) owls attempt to maintain at least a certain amount (800-1000 ha in Douglas-fir forest) of old forest in the areas they traverse; (4) area traversed reflects the proportion of the area that is old forest; (5) areas traversed represent what is available to the owls and that owls traverse only what is necessary to meet their life requirements; and (6) the MMCP home range best delineates the areas actually used by the owls. Given these assumptions, we developed an index of how well the pattern of abundance of old forest met the habitat-area requirements of the owl. This index is the ratio of the amount of old forest in the area used to the area traversed to meet life requirements. This is a biological index (BIOX) to the degree of fragmentation of old forest.

Predicting home range characteristics.—Measures of

landscape pattern were examined for invariance and correlations. Redundant variables ($r > 0.90$, $P < .05$) were identified and the simplest (most easily measured) chosen for analysis. We determined which measures of spatial pattern were good predictors of area traversed and area of old forest used by all-possible-subsets regression with the Mallows' C_p criterion (Frane 1985). Only regressions significant at $P < .01$ were accepted. Only variables with coefficients significantly different from zero ($P < .05$) were retained in the equations. We analyzed the data at three levels: across all pairs, by forest type (Douglas-fir vs. mixed-conifer), and by mean values for pairs within landscapes. Arcsine square root transformations were used for ratio values and \log_{10} transformations were used for area values in the analysis of individual observations (pair values).

In all cases where values are presented with estimates of variation, the information shown is mean \pm 1 SE.

RESULTS

Characteristics of Spotted Owl populations

Population composition.—Radio transmitters were placed on 54 adult (26 females, 28 males) and 13 (5 females, 8 males) subadult owls during 1986-1988 (Fig. 3). No

TABLE 2. Observed properties of populations of Spotted Owls in five landscapes in southwestern Oregon, 1986–1988.

Area*	No. pairs (N)	1987–1988 data†					1986–1988 data‡				
		Area traversed (km ²)		Overlap		Density (pairs/km ²)	Range length (km)‡		Adult pairs		Great Horned Owls (No./pair)
		\bar{X}	SE	A (%)	B (%)		\bar{X}	SE	N	PN	
MCC	3	533	58	1	75	0.190	2.9	0.4	8	1.00	9.0
MCF1	5	1675	352	11	47	0.066	5.3	1.7	21	0.71	5.0
MCF2	6	1796	261	6	47	0.059	5.5	1.4	21	0.86	6.8
DFC	5	1569	463	13	54	0.071	4.7	1.6	18	0.89	1.4
DFF	4	2908	595	26	28	0.046	7.2	3.1	10	0.50	7.5

* MCC = mixed-conifer, clumped, Klamath Mountains old forest; MCF1 = mixed-conifer, fragmented, Umpqua River Valley, old forest; MCF2 = mixed-conifer, fragmented, Klamath Mountains old forest; DFC = Douglas-fir, clumped, Coast Range old forest; DFF = Douglas-fir, fragmented, Coast Range old forest.

† Area traversed (minimum convex polygon home range), percent overlap among pairs (A) and between members of pairs (B), and densities are for the 1987–1988 annual pair home ranges.

‡ Range lengths are the lengths of the major axes of areas traversed by individuals.

§ Proportion of pairs composed of two adult birds, PN (vs. one adult and one subadult) and the number of Great Horned Owl detections per Spotted Owl pair are based on 1986–1988 data.

young were fledged by radio-tagged owls during the principal telemetry year (1988), although 22% of the females were sedentary early in the breeding season, which is behavior typical of birds attempting to nest. But, these females made nocturnal excursions from their “nest groves” prior to expected hatching dates that indicated nesting was unsuccessful.

Transmitters were placed on subadults only if they roosted with adults of the opposite sex that did not have adult mates during the breeding season. The percentage of pairs that were adult (i.e., made up of two adults vs. one adult and one subadult) ranged from 100% in the clumped mixed-conifer landscape to 50% in the fragmented Douglas-fir landscape. Populations in clumped old-forest landscapes had higher percentages of adult pairs than populations in the respective fragmented landscapes (Table 2). We observed 45 independent instances of subadult owls associating with adult owls. As far as we could determine, none of these was a subadult with its parent. There was no detectable seasonality to the associations. In eight instances, the associations were between adult females and subadult males and lasted 1–24 wk; 6 of the 7 females involved were paired with adult males at the time. Two subadult males were associated with one adult female. The other instances were short (observed only on 1 d). During the breeding season, one subadult male attempted to copulate with a female that had an adult mate. Another subadult male had successive (within one breeding season), long (2 and 6 mo) associations with two adult females, the first with a single adult, the second with a paired adult. This subadult was found near the adult female and her mate on one occasion and with two adult females (both paired with adult males) on another occasion. Four subadult females paired with adult males; one subadult male paired with an adult female: one pair was formed by two subadults.

Spacing.—The home ranges of 23 pairs were studied during the principal telemetry year (Table 2). We located these owls 6640 times, averaging 289 ± 8.8 relocations per pair and 144 ± 4.7 relocations per bird. Density of resident pairs was highest in the MCC landscape (0.190 pairs/km²) and lowest in the DFF landscape (0.046 pairs/km²). Areas traversed ranged from an average of 533 ± 58 ha in the MCC to 2908 ± 595 ha in the DFF. Overlap among home ranges of pairs was minimal (1%) in the MCC, low in the MCF1, MCF2, and DFC, and highest in the DFF (26%). Overlap between members of pairs was highest in the MCC (75%) and lowest in the DFF (28%).

Over 24 mo, 128 instances of resident owls of different pairs foraging within 500 m of one another were recorded; no agonistic encounters were observed. There was no detectable difference in the rate of male-male, female-female, and male-female contacts. There was no detectable seasonality in the rate of contacts, except that contacts were low in December and January, reflecting an increased separation of members of pairs prior to the breeding season. The rate of contact averaged 56 ± 3.2 contacts per month among the 23 pairs, with contacts dropping to 12 per month in December and January. Five multiple contacts (3–4 birds in the same area) were recorded in the Douglas-fir study areas. One stand in the DFF was used by six individual owls at one time or another.

Movements out of home ranges.—Two adult females formed new pair bonds. One (WC in the DFC, Fig. 2), shifted her range 1.5 km north to join a single, resident, adult male after her mate died. The other (HS-LM-SF in the DFF) changed mates and home ranges 3 times in 4 yr (Fig. 2). She was banded as an adult in the study area in July 1985. In the winter of 1986, she moved 30 km north of the study area, where her radio transmitter failed. She was found back in the DFF in the spring of 1988.

TABLE 3. Areas over which subadult Spotted Owls roamed in southwestern Oregon in 1987–1988.

Owl	Time tracked (mo)	Area (km ²)	Range length* (km)
DN♀	11	204	25
TY♂	9	34	16
MC♂	5	36	11
CR♂	3	26	9

* Length of the major axes of areas traversed by individuals.

We do not know if she had a mate in 1987. Another adult female (MV in the MCFI) was nomadic. She left her home range in early August and roamed over 38 km² in 6 wk (7 km south of her normal range) but returned to her home range and mate. We observed the dissolution of one pair (CK in the DFC; following heavy clear-cutting in their range (no other range was so strongly affected). The owls moved 5 km each (in different directions). We followed the female for 3 mo and removed her radio; the male died after 6 mo. The female roamed over 44 km², the male over 14 km².

Movements of subadults.—Four subadults were followed during and after associations (roosting with a potential mate during the breeding season) with single, resident adults. They roamed over areas 26 to 204 km² and did not return to the adult (Table 3). Two (MC, TY; Fig. 1) moved into heavily fragmented landscapes (MCFI and the area west of DFC). There they foraged in second-growth, young (10–50 cm diameter trees) forests throughout the summer; they died in the fall, apparently from starvation since they were emaciated when found dead. The area used by TY (Bottle Creek in the MCF) also was occasionally used by another subadult male (LS) and regularly by a paired subadult female (RV). One adult female (MV) visited the area during her nomadism. One subadult (CRM) moved east of the DFC. One (DN) moved south of the DFF into predominantly second-growth forest mixed with farmland. She ranged widely for a year before settling; when last located, she was with a subadult male.

Roosts.—We measured 1007 roost sites of 62 Spotted Owls from May 1986 to November 1989 (485 in Douglas-fir forests and 522 in mixed-conifer forests). Most (86–88%) were in old forest, 109 (11%) were in midseral stands, and 12 (1%) were in regenerating (clearcut, sapling, or pole stands) or nonforested areas. Douglas-fir was the dominant or codominant species in the canopy at 94% of the roost sites. Midstories were most often dominated by Douglas-fir (68% of the 640 sites with a midstory) followed by western hemlock (26%), Pacific madrone (*Arbutus menziesii*, 22%), western redcedar (*Thuja plicata*, 14%), bigleaf maple (*Acer macrophyllum*, 14%), and grand fir (12%). Multilay-

ered vegetation was present at most roost sites. Overstory cover was usually sparse (the modal cover class was 6–12%), mid- to understory cover was dense (2448%), and shrub cover was usually >48%. Vertical diversity of vegetation at roosts did not differ significantly between old forest (BPI = 2.3 ± 0.02, N = 630) and younger stands (BPI = 2.2 ± 0.05, N = 104; $t = 1.91$, $df = 732$, $P = .06$).

Slopes around roost sites were very steep and averaged 49 ± 1%. The steepness was typical of the area and its small standard error reflects the large sample size for roosts. Roost sites were evenly distributed among upper (36%), mid- (28%), and lower (36%) slopes, but the owls roosted more frequently than expected on upper and midslopes in the spring, fall, and winter, and on lower slopes in the summer ($\chi^2 = 25.97$, $df = 4$, $P < .01$). Owls roosted more frequently than expected on north, northeast, and east aspects and less frequently on south and southwest aspects in the summer and more frequently on south and southwest aspects in the spring and fall ($\chi^2 = 26.25$, $df = 14$, $P < .05$); there was no strong preference in winter. We estimated the proximity of 378 roosts to water; summer roosts (N = 157) averaged 74 ± 7 m from water (which creates a cool microclimate) and were significantly closer to water than winter roosts (99 ± 5 m, N = 221; $t = 2.68$, $df = 306.6$, $P < .01$).

Owls roosted in 21 species of trees and tall shrubs, but 90% of the roosts were in nine common canopy and midstory trees: Douglas-fir, 46%; western hemlock, 13%; western redcedar, 9%; incense-cedar, 5%; bigleaf maple, 5%; grand fir, 4%; giant chinkapin (*Castanopsis chrysophylla*, 3%); Pacific madrone, 2%; and canyon live oak (*Quercus chrysolepsis*, 2%). Roost trees averaged 61 ± 2 cm dbh and 26 ± 1 m tall. Roosts were protected by 69 ± 1% overhead cover and 36 ± 1% lateral cover. Lateral and overhead protection were weakly correlated with the severity of precipitation and with the interaction of precipitation and wind speed ($P < .05$, maximum $r = 0.17$ for lateral cover vs. precipitation). Lateral and overhead cover were weakly correlated ($r = 0.30$, $P < .01$). Only 2% of the variability in the sum of lateral and overhead cover could be explained by regression ($F = 14.88$, $df = 1, 654$, $P < .01$). The interaction of precipitation and wind was the only variable retained in the regression and its coefficient was low (coefficient = 0.06, $t = 3.86$, $P < .01$). Perch heights varied from on the ground or fallen trees (rarely) to 78 m, averaging 13.7 ± 0.4 m. Temperature explained only 10% of the variance in perch height ($R^2 = 0.10$, $F = 93.90$, $df = 1, 880$, $P < .01$). Temperature was inversely related to perch height (regression coefficient = -1.05, $t = -9.69$, $P < .01$). Other variables did not explain any significant additional variance. We found no evidence that roost sites were more restricted in distribution than foraging sites, and the weak correlation with climatic variables suggests that thermoregulation is not a major factor affecting owl habitat use in southwestern Oregon.

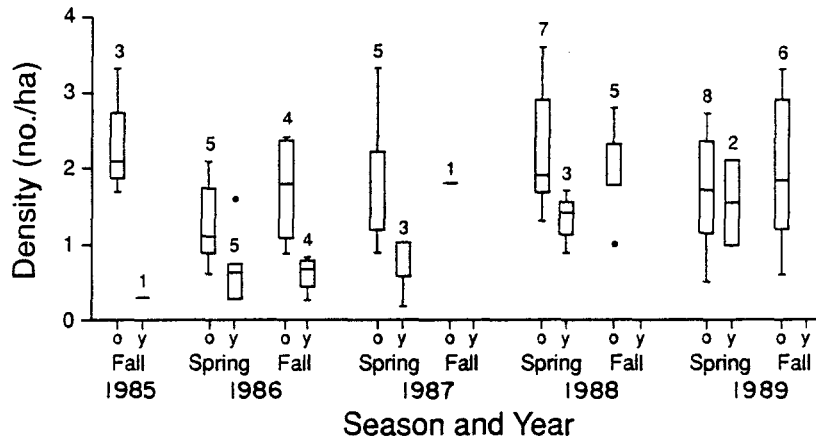


FIG. 4. Box and whisker plots (mean, range, and interquartile range) of fall and spring northern flying squirrel density in old forest (o) and managed, young forest (y) in southwestern Oregon, 1985-1989. Number of stands sampled is shown above each plot.

Great Horned Owls.—Great Horned Owls were found in the vicinity of the Spotted Owls on 130 occasions. The rate at which we encountered Great Horned Owls near Spotted Owls was highest in the MCC and lowest in the DFC (Table 2), contrary to the pattern predicted by the owl predation hypothesis.

Prey abundance

Flying squirrels.—Average densities, over years and seasons, did not differ between mixed-conifer and Douglas-fir forests ($t = 0.95$, $df = 8$, $P > .05$ for old forest; $t = 1.08$, $df = 4$, $P > .05$ for young forest) and were 1.9 ± 0.1 flying squirrels/ha in old forest ($N = 8$ trap periods) and 0.9 ± 0.2 flying squirrels/ha in managed, young forest ($N = 6$ trap periods), a twofold difference in density. Flying squirrel densities in old forest were consistently higher than densities in managed, young forest (paired $t = 3.13$, $df = 5$, $P < .05$, Fig. 4). Densities on the Olympic Peninsula were low and averaged 0.5 ± 0.2 flying squirrels/ha in old forest and 0.2 ± 0.4 flying squirrels/ha in managed, young stands (paired $t = 2.79$, $df = 2$, $.10 > P > .05$) over 3 yr.

Moderate-to-high foraging activity (>0.3 owl-years within 1 km of the center of the trap grid) appeared to depress flying squirrel populations (Fig. 5). Populations on two trap grids that contained owl nest sites (in 1986) showed marked depression, but the population of Riverview did not show a significant influence from the owl pair that nested there in 1989 (Fig. 6C). Flying squirrel populations in the young stands (Fig. 7) seemed to increase with time, suggesting a response to trapping (for example, to the copious bait in the traps) or to nearby forest management activities (immigration of individuals displaced by timber harvesting or from populations that increased in response to installation of nest boxes).

Flying squirrel densities in old forests with bushy-tailed woodrat populations (2.04 ± 0.4 flying squirrels/ha, $N = 4$)

did not differ significantly from densities in old forests without bushy-tailed woodrat populations (1.4 ± 0.3 flying squirrels/ha, $N = 7$). Patterns of abundance over time within stands showed no correlation between bushy-tailed woodrat abundance and northern flying squirrel abundance, despite their use of similar den sites that may be limited in availability (Carey 1991).

Woodrats.—No woodrats were caught during 2 yr on 14 sites on the Olympic Peninsula even though woodrats are easily trapped when present (personal observations). Bushy-tailed woodrats were caught at 25 of the 47 sites in southwestern Oregon. Densities averaged from 0 to $1.08 \pm$

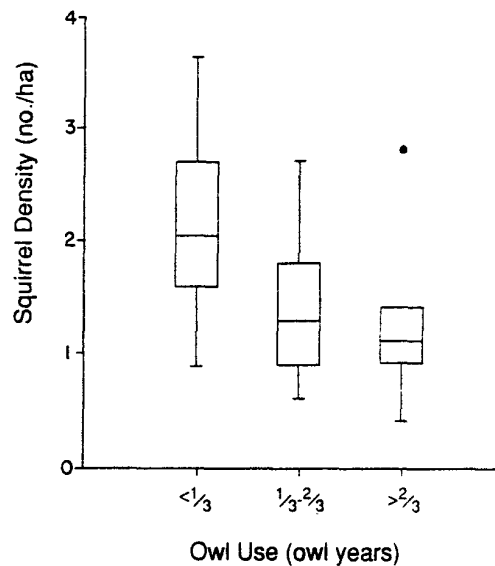


FIG. 5. Box and whisker plots (mean, range, and interquartile range) of foraging activity of Spotted Owls vs. densities of northern flying squirrels in southwestern Oregon, 1986-1988.

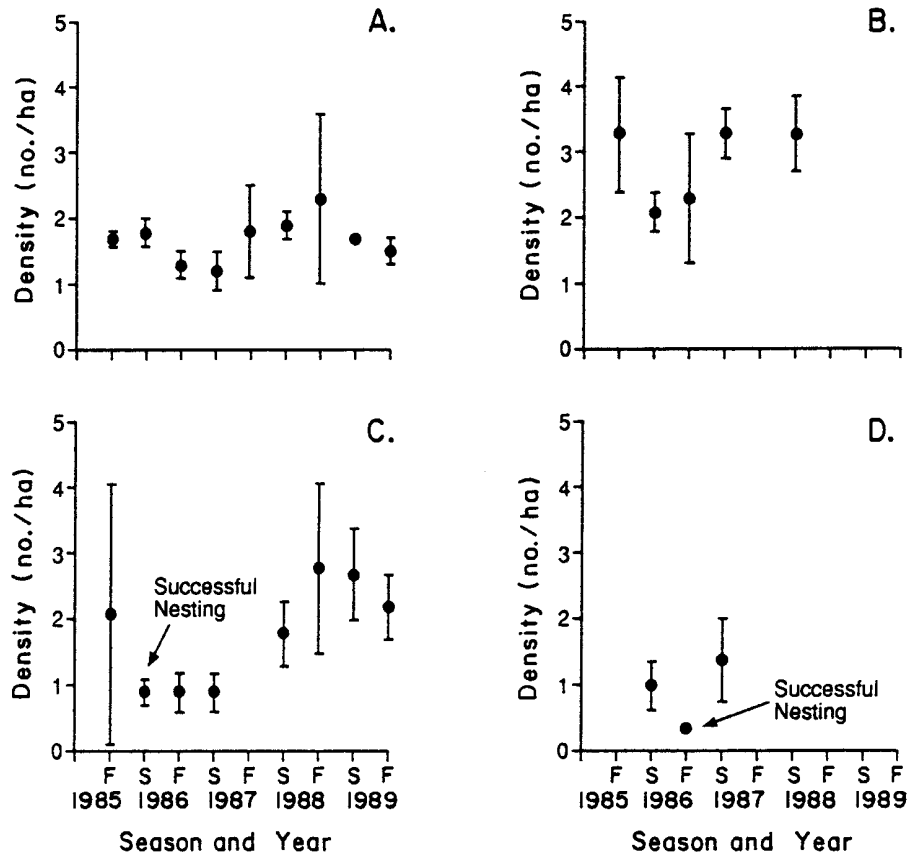


FIG. 6. Seasonal (F, fall; S, spring) and annual variability in northern flying squirrel densities (means and 95% confidence intervals) in four old-forest stands in southwestern Oregon, 1985–1989. Miner Creek (A) and Camas Creek (B) had low predation pressure; Riverview (C) and Cherry Creek5 (D) were around or near nest groves of Spotted Owls and had high predation pressure.

0.51 bushy-tailed woodrats/ha per habitat type (Table 4). In the Douglas-fir forest, bushy-tailed woodrats were most common in closed-canopy forest along streams. Bushy-tailed woodrats did not use upland sites every year or every season within a year (Table 5). In the mixed-conifer forest, bushy-tailed woodrats were abundant in old growth, the rocky site, pole stands, and especially near streams (Table 4). Dusky-footed woodrats were caught at 16 of the 47 sites in Oregon. Densities averaged from 0 to 1.42 ± 1.42 dusky-footed woodrats/ha per habitat type. Dusky-footed woodrats were rare in Douglas-fir forest but common in mixed-conifer sawlog stands, old growth, pole stands, and especially along streams (Table 4).

Occupancy of mixed-conifer sites (20 of 28 sites) by woodrats was more consistent than in the Douglas-fir sites (12 of 19 sites); few dusky-footed woodrats were on Douglas-fir sites and bushy-tailed woodrats were present only in some years (Table 5). Both species of woodrats were most abundant in mixed-conifer forest along streams and occurred in relatively high densities in pole stands (Table 4). The abundances of both species were positively correlated with total vegetative cover < 6 m (Spearman rank correlation,

$r_s = 1.0$, $P = .0$, $N = 5$ for dusky-footed woodrats and $r_s = 0.88$, $P < .05$, $N = 9$ for bushy-tailed woodrats). In 8 of the 13 sites of such preferred habitat, dusky-footed woodrats outnumbered bushy-tailed woodrats. Only in the rocky site and the Douglas-fir streamside sites were the bushy-tailed woodrats abundant and more numerous than dusky-footed woodrats. In mixed-conifer forests, the two species were found together in 5 of 8 old-growth sites, 3 of the 6 pole sites, and in one streamside site; the abundances of the two species were negatively correlated ($r_s = -0.52$, $P < .05$).

The two species of woodrats differed in population structure. Bushy-tailed woodrats occurred in small social groups averaging 1.0 ± 0.2 males and 2.3 ± 0.3 females per site, for an average biomass per occupied site of 876 g. Dusky-footed woodrats occurred in larger groups, averaging 2.8 ± 0.3 males and 3.3 ± 0.7 females per site for an average biomass per occupied site of 1548 g, almost twice that of the bushy-tailed woodrats.

Biomass of medium-sized prey.—Biomass of flying squirrels and woodrats was 61 g/ha in old western hemlock forest, 244 g/ha in old Douglas-fir forest, and 388 g/ha in old mixed-conifer forest, a ratio of $\approx 1:4:6$.

Average area of old forest used for foraging by Spotted Owls showed a shift of the ratio: 4:2:1. Area of old forest used by Spotted Owls decreased with increasing biomass of prey (Fig. 8).

Small mammals.—The numbers of small mammals in old forests were nearly equal in Washington and Oregon (Table 6). Mean relative biomass in old forests was 188 g/ 100 trap nights in Washington and 204 g/ 100 trap nights in Oregon. Previous studies in southwestern Oregon found no difference in abundance of small mammals between young and old forest (Carey 1989).

Spotted Owl ranges

Areas traversed varied with both forest type and degree of fragmentation of old forest. Areas traversed were similar in composition to their respective landscapes. Areas of old forest used were similar among landscapes within forest types. The average amount of old forest used in Douglas-fir forest was twice the average in mixed-conifer forest. The average amount of old forest used in 2 yr was 40% greater than that used in 1 yr.

Areas traversed by pairs.—Areas traversed by pairs varied fivefold among the five landscapes, reflecting effects of both forest type (mixed-conifer vs. Douglas-fir. $F = 12.24$, $df = 1$, $P < .01$) and fragmentation (light vs. heavy, $F = 18.66$, $df = 1$, $P < .01$; Table 2). The areas traversed in landscapes classified as “clumped old growth,” were 52% (MCC) and 67% (DFC) old forest. Despite the predominance of old forest in the DFC, the areas traversed there were 3 times as large as in the MCC. Areas traversed in the fragmented landscapes were 33-44% old forest and 1.6 times as large in the DFF as in the fragmented, mixed-conifer landscapes. The differences in percent old forest between the landscapes (defined by 1-km² UTM blocks; Table 7) and the areas traversed averaged 1-8% in four of the landscapes and 30% in the DFC. Among landscapes the difference was near zero ($t = 1.6$, $df = 4$, $.10 > P > .05$). Range lengths were 2.9-7.2 km and reflected home range size.

In Douglas-fir study areas, owls in fragmented old forest traversed twice the area traversed in clumped old forest, yet the areas traversed contained 937 ± 172 ha (DFC) and 1013 ± 153 ha (DFF) of old forest, nearly equal amounts. Areas traversed in mixed-conifer landscapes contained 263 ± 19 ha (MCC), 524 ± 107 ha (MCF1), and 824 ± 207 ha (MCF2) of old forest (averaging 537 ± 162 ha), just 52% of the old forest in the Douglas-fir ranges. Areas traversed in fragmented mixed-conifer landscapes were 3.3 times as large and incorporated 2.6 times as much old forest as in the clumped mixed-conifer landscape.

Areas traversed by individuals, and the means of areas traversed within landscapes, were similar between the breeding and nonbreeding seasons ($t = 2.04$, $df = 40$, $P > .01$ for individuals; $t = 1.56$, $df = 4$, $P > .05$ for landscape means; Table 8). Male and female winter ranges did not differ in size ($t = 1.09$, $df = 20$, $P > .05$).

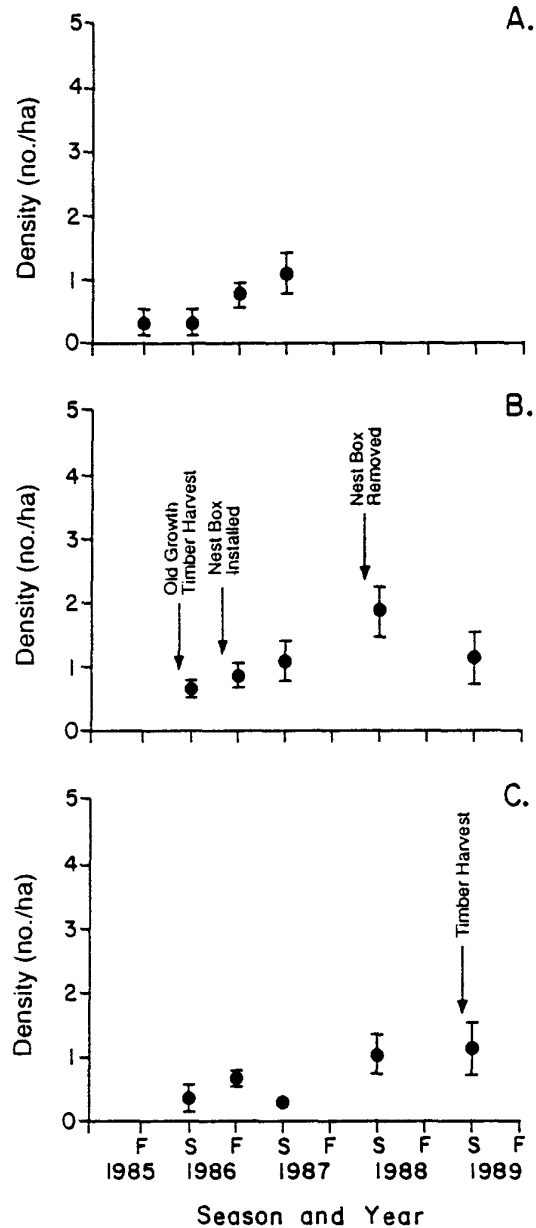


FIG. 7. Seasonal and annual variability in northern flying squirrel densities (means and 95% confidence intervals) in three young, managed stands in southwestern Oregon, 1985–1989. Little Wolf Creek (A) had no adjacent disturbance; Bear Creek (B) had nearby old forest harvested and nest boxes added; Ward Creek (C) had nearby timber harvest.

Female summer ranges were larger (by 40%) than those of males ($t = 2.18$, $df = 20$, $.01 < P < .05$), opposite of what would be expected in successfully breeding pairs (females remain on their nests until the young are fledged). Proportions of home ranges in old forest were similar between seasons ($t = 1.77$, $df = 4$, $P > .05$).

Areas used by pairs.—Areas used were 70 ± 5% of the areas traversed, ranging from 59% in the DFF to

TABLE 4. Woodrat density (individuals/ha) in two biotic regions and various habitat types (means \pm 1 SE).

Forest type*	Habitat type	No. stands	Species†		Total
			NECI	NEFU	
Olympics					
WH	Old, sawlog, streamside	14	0	0	0
Southwestern Oregon					
DF/MC	Ridgetops	3	0	0	0
DF	Managed sawlog	5	0.02 \pm 0.01	0	0.02
DF	Old growth	6	0.04 \pm 0.02	0	0.04
MC	Clearcuts	3	0.08 \pm 0.08	0	0.08
MC	Managed sawlog	5	0	0.40 \pm 0.40	0.40
DF	Streamside sawlog	6	0.46 \pm 0.19	0.04 \pm 0.04	0.50
MC	Old growth	8	0.20 \pm 0.80	0.43 \pm 0.13	0.64
MC	Rocky	1	0.59 \pm 0.57	0.06 \pm 0.06	0.65
MC	Managed pole	6	0.46 \pm 0.20	1.07 \pm 0.48	1.53
MC	Streamside sawlog	3	1.08 \pm 0.51	1.42 \pm 1.42	2.50

* WH—Western Hemlock; DF—Douglas-fir; MC—mixed conifer.

† NECI—*Neotoma cinerea*; NEFU—*Neotoma fuscipes*.

89% in the MCC. Amount of old forest in the areas used did not differ significantly within forest type (Douglas-fir: $t = 0.84$, $df = 7$, $P > .05$; mixed-conifer: $F = 1.98$; $df = 2, 11$; $P > .05$; Table 9). But the amount of old forest used in Douglas-fir forest (813 ± 133 ha) was almost twice that in mixed-conifer forest (454 ± 84 ha: $t = 2.43$, $df = 21$, $P < .05$). Overlap among areas used by pairs was high in the DFF (23%) but low in the MCC (< 1%), MCF1 (9%), MCF2 (2%), and DFC (8%).

Cumulative amounts of old forest used.—Nine pairs in mixed-conifer forest and four pairs in Douglas-fir forest were tracked for > 2 yr. Median values for old

forest used seemed to reach an asymptote in the 3rd yr; however, sample sizes were small in the 3rd yr (Fig. 9). The average percent increase in old forest used was slight during the second breeding season (Douglas-fir, 4%; mixed-conifer, 9%) and marked during the second nonbreeding season (Douglas-fir, 40%, paired $t = 5.04$, $df = 3$, $P < .01$; mixed-conifer, 43%, paired $t = 4.89$, $df = 8$, $P < .01$). The average cumulative amount of old forest used was lower in the third breeding season (and in the used by owls averaged 1.5 times as much old forest as third nonbreeding season) in the Douglas-fir forest, an artifact of decreasing sample size (number of owl pairs).

TABLE 5. Numbers of individual bushy-tailed woodrats captured in trapping grids in stands sampled three or more seasons in southwestern Oregon during the fall and spring, 1985–1988.

Stand	Forest stage*	Forest type†	Number of individuals							
			F 1985	S 1986	F 1986	S 1987	F 1987	S 1988	F 1988	S 1989
Miner	O	D	0	0	1	0	1	2	3	0
Peterson	O	D		0	0	0		0	0	0
Cherry4	O	D		1	3	0				
Cherry5	O	D	3	2	0	0				
Camas	X	D	0	0	0	0	0			
Westpet	X	D		0		0		0		0
Riverview	O	M	4	7	3	4		6	6	1
Lost	O	M						14	10	4
Wolf	Y	D	0	2	0	0				
Middle	Y	D	0	0	1	1				
Witte	Y	D	0	0	0	0	0	0		
Witte	Y	D	0	0	0	1	0	0		
Bearc	Y	M		0	0	0	0			0
Bearw	Y	M		0		0	0	0		
Wardc	Y	M		0	0	0	0	0		
Wardw	Y	M		0		0	0	0	0	0

* Forest stages: O—old growth; X—mixed age; Y—young, small sawlog.

† Forest types: D—Douglas-fir; M—mixed-conifer.

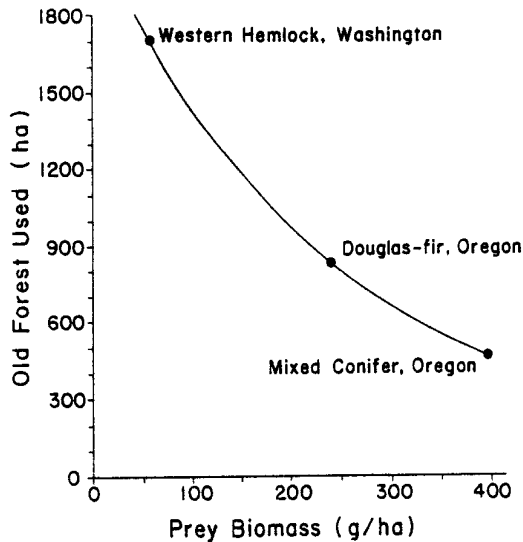


FIG. 8. The effect of prey biomass on areas of old forest used by Spotted Owls in mixed-conifer forest in Oregon, Douglas-fir forest in Oregon, and western hemlock forest in Washington.

The increase was 50% in the mixed-conifer forest in the third nonbreeding season. The pairs in Douglas-fir forest used 982 ± 172 ha of old forest over 2 yr; those in mixed-conifer forest used 647 ± 91 ha.

Habitat selection

Old forest was the only habitat type selected out of proportion to its availability by 46 of 47 owls. Areas were generally available in the landscapes. One owl selectively foraged in young forest. Nine of 577 stands of habitat types that were generally avoided were selected for foraging more than would be expected based on their area.

Individual owls.—Old growth was selected for foraging by 83% of the owls and used in proportion to availability by the remaining 17% (Table 10). Mixed-old stands were selected by 9% of the owls and used proportionately by 66% of the owls. Midseral stages were used proportionately or avoided, with one exception. One owl selectively foraged in young, streamside forest, which constituted 24% of its range. Early seral stages were avoided by 57-68% of the owls. When use and availability

were compared for four habitat types, mid-seral stages were avoided by 50% of the owls in mixed-conifer forest and 77% of the owls in Douglas-fir forest.

Four of the eight owls that used old growth in proportion to availability selected mixed-old stands, which were much more abundant than old growth in their ranges. None of the owls that were neutral (use proportional to availability) towards old growth selected earlier seral stages. All spent 45-77% of their time in old forest (Table 11).

Landscape level.—Across the five landscapes, the mean percentage of the areas used that was old forest averaged 1.5 times the percentage of old forest in the gross landscape (Tables 7 and 12, $t = 5.95$, $df = 4$, $P < .01$), indicating that the areas used encompassed more old forest than would be expected through random placement of ranges. Areas used contained more old forest than did similarly sized, systematically placed squares (Table 9; $t = 2.50$, $df = 4$, $P < .05$), indicating that owl ranges contained more old growth than would be expected as a result of range placement as an ideal consequence of territorial interactions. No other forest type was selected for at the population level.

Use of early seral stands.—Owls were located at least once in 22% of the nonforested and 36% of the early seral stands. Four of 249 nonforested stands and 5 of 328 early seral stands were selected. The sizes of these selected stands were 4-22 ha; numbers of locations in the stands were 3-6 (with expectations of 0-3). One clearcut and 2 pole stands in MCF1, 1 clearcut and 1 pole stand in the MCF2, and 2 clearcut, 1 sapling, and 1 pole stand in DFC were selected. In contrast, we located owls in 53% of the midseral stands and 61% of the old forest stands. Selection of patches within stands was suggested by the pattern of locations with stands.

Landscape and home range characteristics

Across landscapes, forest type (with attendant differences in prey biomass) was the only predictor of the amount of old forest used: the pattern of abundance of old forest in the landscapes had no discernible effect. Areas traversed reflected primarily the amount of old forest used and, secondarily, relative abundance (percent of the area traversed) of old forest. Within the Douglas-fir forest a type, areas traversed reflected primarily the relative abund-

TABLE 6. No. captures per 100 trap nights for *Peromyscus* spp., *Clethrionomys* spp., and *Microtus oregoni* in old forests on the Olympic Peninsula of Washington and in southwestern Oregon, 1988-1989 (means \pm 1 SE).

	N*	<i>Peromyscus</i> †	<i>Clethrionomys</i> ‡	<i>Microtus</i>	Total
Washington	7	6.2 \pm 1.3	2.6 \pm 1.0	0.9 \pm 0.1	9.7
Oregon	8	1.6 \pm 0.2	7.6 \pm 0.0	...	9.2

* Number of stands sampled.

† *P. maniculatus* in Oregon; *P. oreas* and *P. maniculatus* in Washington.

‡ *C. californicus* in Oregon; *C. gapperi* in Washington.

TABLE 7. Composition (% of area) of five landscapes inhabited by Spotted Owls in southwestern Oregon, 1987–1988, subdivided at two different levels of resolution.

Landscapes*, divided into 10 habitat types						Landscapes*, divided into 4 habitat types					
Habitat type	MCC	MCF1	MCF2	DFC	DFF	Habitat type	MCC	MCF1	MCF2	DFC	DFF
Coniferous forest											
Old growth	20	23	23	26	14	Old	44	32	45	37	30
Mixed-old	24	9	22	11	16						
Mixed-young	5	5	6	2	17	Sawlog	27	34	13	22	40
Mature	2	2	1	3	2						
Young	20	23	6	16	18						
Pole	16	9	9	15	8	Regeneration	24	15	27	29	15
Sapling	8	6	18	14	7						
Clearcut	2	3	12	8	4	Nonforest	4	18	14	12	14
Nonforest	2	15	2	4	10						
Hardwood forest	0	4	0	1	3						

* MCC—mixed-conifer clumped old forest; MCF1—mixed-conifer (Umpqua River Valley) fragmented old forest; MCF2—mixed-conifer (Klamath) fragmented old forest; DFC—Douglas-fir clumped old forest; DFF—Douglas-fir fragmented old forest.

ance of old forest. In the mixed-conifer forest type, however, areas traversed seemed to reflect the pattern of abundance of old forest. Thus, after accounting for major differences in prey biomass (controlling for forest type), the degree and pattern of fragmentation of old forest has significant effects on the areas traversed by owls to meet their needs.

Composition of landscapes and areas used by owls.—Gross (UTM-block) landscapes were 62–330 km² and 30–45% old forest (Table 7). Landscapes defined by the MMCP encompassing all owl locations were 40 ± 4% (29–52%) smaller and had slightly higher percentages of old forest (33–55%, averaging 45 ± 4%; Table 12) than gross landscapes. Areas used by Spotted Owls were 35–73% old forest. The percentages of old forest in the areas used was significantly greater than in the gross landscapes ($t = 5.95$, $df = 4$, $P < .01$) but not significantly different from the MMCP landscape ($t = 1.75$, $df = 4$, $.05 < P < .10$).

Landscape indices.—None of the landscape indices (dominance, contagion, variance in density of old forest) was correlated with the proportion of the gross landscape that was old forest; however, the variance in density of old forest showed a significant

correlation with the proportion of the MMCP landscape that was old forest. Dominance and contagion were highly correlated (Table 13). Contagion was also correlated with the mean BIOX ($r = 0.84$, $P = .08$).

None of the landscape indices was correlated with either areas traversed or areas used by Spotted Owl pairs. All were correlated with the proportions of the areas traversed and areas used that were old forest, but none as highly as BIOX. Old forest used and old forest traversed and percent of areas used and percent of areas traversed that were old forest were highly correlated (Table 14).

Predicting the amount of old forest used.—Forest type was the only predictor of the amount of old forest used ($R^2 = 0.31$, $F = 9.39$, $df = 1, 21$; $t = 3.06$, $P < .01$ for the coefficient of regression). Deletion of one outlier raised the R^2 to 0.48 ($F = 18.40$, $df = 1, 20$; $t = 4.29$, $P < .001$). Forest type (and the attendant effects of prey abundance) thus appeared to be the prime determinant of the amount of old forest required by the owls. Landscape pattern had no discernible effect on the amount of old forest used.

Predicting the area traversed.—At the landscape level, the area traversed was not correlated with any of the landscape indices; it was correlated with the mean amount of old forest used ($r = 0.88$, $N = 5$, $P < .05$). The

TABLE 8. Areas traversed (ha) by season by Spotted Owls in five landscapes in southwestern Oregon, 1987–1988.

Area	Individual				Pair			
	Summer		Winter		Summer		Winter	
	\bar{X}	1 SE	\bar{X}	1 SE	\bar{X}	1 SE	\bar{X}	1 SE
MCC	388	28	322	31	456	48	385	54
MCF1	892	218	816	131	1520	383	1115	300
MCF2	773	110	1139	159	1093	176	1542	215
DFC	735	192	908	159	1150	406	1315	284
DFF	1150	233	1703	339	1757	465	3332*	628

* Based on two pairs with complete winter data; not significantly larger than the annual estimates of home range based on four pairs, two of which lost a mate during the year.

TABLE 9. Home-range-sized squares compared to modified minimum convex polygon (MMCP) home ranges (areas traversed), southwestern Oregon, 1987–1988.

Area	Area of square		MMCP home range (ha)		Square old forest (ha)		MMCP old forest (ha)		Square (% old)	MMCP (% old)
	(ha)	<i>N</i>	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE		
MCC	500	11	472	43	212	22	240	22	45	53
MCF1	1200	12	1154	235	376	53	368	67	32	35
MCF2	1200	21	1208	272	509	37	633	182	43	52
DFC	1200	14	1018	160	428	71	713	69	36	73
DFE	1800	6	1721	413	597	176	938	260	34	52

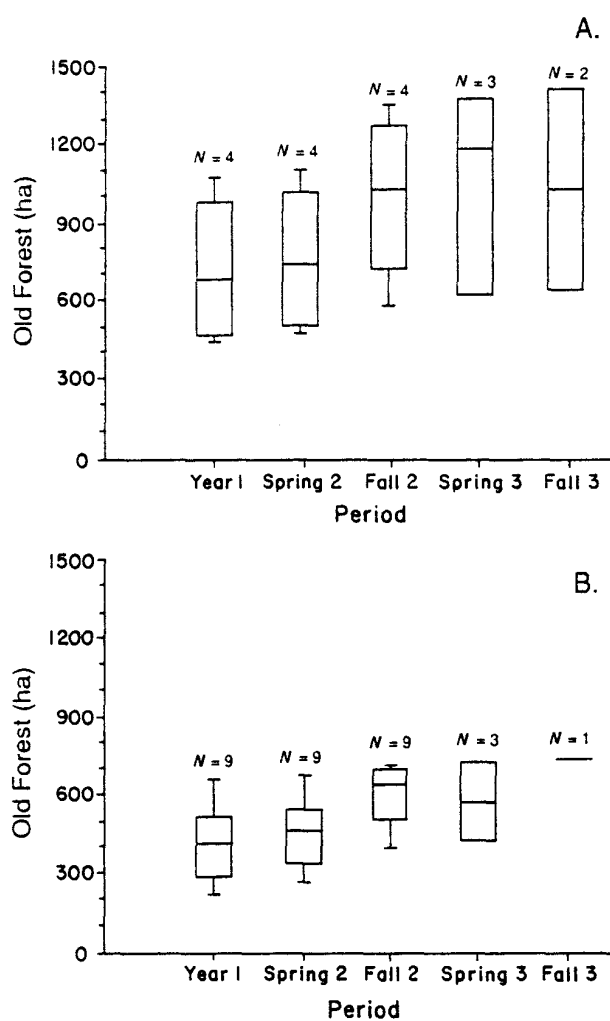


FIG. 9. Cumulative amounts of old forest used by pairs of Spotted Owls during 1987–1989, beginning with the amount used in the 1st yr of study and by season thereafter in (A) the Douglas-fir biotic region and (B) the mixed-conifer biotic region. Sample sizes (*N* = number of pairs) are given above each box and whisker plot, which shows mean, range, and interquartile range.

amount of old forest used and the proportion of the area traversed that was old forest accounted for 98% of the variance in the area traversed ($F = 46.36$, $df = 2, 2$, $P < .05$). The proportion of the area traversed that was old forest contributed 21% to the R^2 and was negatively correlated with the size of the area traversed ($r = -0.47$). The amount of old forest used contributed 76% to the R^2 and was positively correlated with the area traversed ($r = 0.88$). Across forest types, 93% of the variance in area traversed ($N = 23$) could be accounted for by the amount of old forest used and the proportion of the area traversed that was old forest ($F = 63.48$, $df = 2, 20$, $P < .01$). The area contributed 66% to the R^2 , the proportion 31%.

When the area of old forest used and BIOX were used as independent variables ($r = 0.20$, $P > .05$, Table 14), $R^2 = 0.98$ ($F = 532.61$, $df = 2, 20$, $P = .01$). BIOX explained more variance (contribution to the R^2 was 43%) than contagion,

TABLE 10. Percentages of 47 Spotted Owls avoiding, proportionately using, and selecting nine habitat types in southwestern Oregon, 1987–1988 (expected use greater than, within, and less than the 95% confidence intervals for observed use, respectively).*

Habitat type	Percentages†		
	Avoided	Proportional	Selected
Coniferous forest			
Clearcut	60	21	0
Sapling	68	28	0
Pole	57	34	0
Young	40	51	2
Mature	17	26	0
Mixed-young	23	19	0
Mixed-old	17	66	9
Old growth	0	17	83
Hardwood forest	9	23	0
Nonforest	23	11	0

* Chi-square goodness-of-fit tests ($P < .05$) and calculation of confidence intervals with correction for multiple comparisons were used to test use vs. availability.

† Percentages do not always sum to 100 because not all habitat types were found in all owl home ranges.

TABLE 11. Habitat selection (time allocation) by eight Spotted Owls that used old-growth forest in proportion to its availability in southwestern Oregon, 1987–1988. Chi-square goodness-of-fit tests and confidence intervals adjusted for multiple comparisons were used to determine if owls avoided (A) or selected (*) types ($P < .05$) or used the type in proportion to its availability (N; $P > .05$). Mean percent use (and availability) values are shown for old forests.

Owl	Nonforest	Stage of forest development				
		Early stages	Middle stages	Mixed-old	Old growth	Old growth and mixed-old
LL♂	A	A	A	54 (42)*	32 (26)	76 (68)
OC♀	A	A	A	52 (35)*	7 (8)	59 (43)
OC♂	N	A	A	44 (34)	6 (9)	50 (43)
RK♂	A	N	N	36 (13)*	12 (18)	48 (31)
RV♀	A	A	N	10 (5)	35 (27)	45 (32)
SF♀1	A	N	A	53 (31)*	24 (26)	77 (57)
SF♀2	N	N	N	39 (30)	29 (32)	68 (62)
YC♂2	...	N	A	65 (51)	65 (51)

dominance, fractal dimension, proportion of the landscape that was old forest, or the variance in density of old forest. For example, area of old forest used and contagion explained 74% of the variance in area traversed; area of old forest and the variance in density of old forest explained 56% of the variance in area traversed. BIOX was highly correlated with the proportion of the area traversed that was old forest (Table 14). Correlations of the area of old forest used were 0.87 with the amount old forest in the area traversed and 0.78 with the total area traversed.

In the Douglas-fir landscapes, the area of old forest used and the proportion of the area traversed that was old forest accounted for 87% of the variance in area traversed ($F = 19.78$, $df = 2, 6$, $P < .01$). But here the proportion of old forest contributed 42% to the R^2 , and the area of old forest

contributed only 15%, a reversal of relative importance from the among-landscape relationship. The proportion alone explained 72% of the variance in area traversed ($F = 18.04$, $df = 1, 7$, $P < .01$). The proportion of old forest in the area traversed was negatively correlated ($r = -0.85$) with the size of the area traversed. The proportion of old forest was highly correlated ($r = 0.86$) with BIOX, as was area traversed ($r = -0.75$); BIOX was a good ($R^2 = 0.72$) predictor of area traversed. Thus, within forest types (eliminating major differences in prey biomass in old forest), the relative abundance of old forest seemed to be the prime determinant of owl movements.

In the mixed-conifer landscapes, the results were similar: the amount of old forest used and the proportion of the area traversed that was old forest

TABLE 12. Characteristics of five landscapes inhabited by Spotted Owls in southwestern Oregon, 1987–1988. Landscapes were defined by the modified minimum convex polygon (MMCP) encompassing all owl radiotelemetry locations recorded from September 1987 to September 1988.

Area name	Area (ha)	MMCP landscape*				Old‡ forest (%)	MMCP home range†			Mean stand size		
		DOMX	CONX	FDX	VDPX		Old forest (%)	BIOX		Old (ha)	All (ha)	Width (m)
								Pair	Single			
MCC	1793	0.70	10.0	1.2	0.70	47 (44)	53	47	43	94	59	610
MCF1	9190	0.23	6.7	1.3	0.99	33 (31)	35	24	28	83	55	537
MCF2	17316	0.22	7.0	1.3	0.70	44 (45)	52	33	34	88	51	588
DFC	7484	0.48	9.6	1.2	0.68	55 (37)	73	54	58	92	58	569
DFF	9639	0.36	8.0	1.2	0.85	44 (30)	52	31	36	92	66	603

* $DOMX = \ln(n) + \sum P_i \ln(P_i)$, where P_i is the proportion of habitat type i , $i = 1, \dots, 4$; DOMX a potential range of 0–1.39; $CONX = 2n \ln n + \sum \sum P_{ij} \ln P_{ij}$, where P_{ij} is the probability of habitat i being adjacent to habitat j , $j = 1, \dots, 4$; CONX has a potential range of 0–11.09; FDX = twice the slope of the regression of stand area against stand perimeter; VDPX = variance of the density of old forest.

† Landscape indices are compared to biological responses of owls: the percent old forest in the area used (MMCP home range), and the BIOX, i.e., the area of old forest used (within the MMCP home range) divided by the area traversed (MCP home range).

‡ Percent old forest in the MMCP landscape with percent old forest in the UTM-block landscape in parentheses; percent old forest in the MMCP landscape was not significantly different from the percent old forest in the MMCP home ranges ($t = 1.754$, $df = 4$, $.05 < P < .10$).

TABLE 13. Correlations among landscape indices and the proportions of five landscapes that were old forest in southwestern Oregon in 1987–1988. Indices are dominance and contagion of four habitat types and the variance of the density of old forest in 1-km² blocks. Landscapes were defined by Universal Transverse Mercator (UTM) blocks and the modified minimum convex polygon (MMCP) containing Spotted Owl telemetry locations.

	Proportions of old forest in the landscapes		Indices	
	UTM	MMCP	Contagion	Variance
Dominance	0.37	0.58	0.95**	-0.32
Contagion	0.32	0.79	1.00	-0.50
Variance	-0.64	-0.87*	-0.32	1.00

* $P < .05$. ** $P < .01$.

explained 89% of the variance in area traversed ($F = 46.35$, $df = 2, 11$, $P < .01$). The coefficients for the proportion of old forest did not differ between Douglas-fir and mixed-conifer forests (coefficients = 0.002; $P > .05$); the response to fragmentation was identical. However, the proportion of old forest contributed only 31% to the R^2 compared to 73% for the area of old forest used. The proportion of the area traversed that was old forest was negatively correlated ($r = -0.41$) with amount of area traversed but less strikingly so than in the Douglas-fir forests. These results suggest that landscape pattern has a strong influence on owl movements above that generated by the relative abundance of old forest.

DISCUSSION

The most serious threat to conservation of raptors worldwide is forest fragmentation; yet, because of the

difficulty of studying forest raptors, little is known about their ecology or the influence of fragmentation on individuals and local populations (Thiollay 1985). Much of what has been written on the effects of fragmentation deals with maintenance of biodiversity (Robinson and Wilcove 1989, Thiollay 1989). Old forests in the Pacific Northwest have been declining in abundance since 1850; numbers of Spotted Owls have declined concomitantly (Thomas et al. 1990). As naturally large, heterogeneous, and stable old forests are replaced with small, managed stands of simple structure, prey populations are becoming isolated in discrete, local populations. Management of landscapes to maintain viable populations of Spotted Owls also entails management of forest upon which prey species depend. Understanding the processes operating at different ecological scales is essential to effective landscape management. Furthermore, the present distribution of old forest is inadequate to maintain a network of interactive local populations of Spotted Owls throughout their former range (Thomas et al. 1990). Managing young forests, to create suitable environments for Spotted Owls where old forest is lacking, requires understanding factors that influence habitat selection by owls and their prey. Thus, we discuss (1) geographic variation in prey abundance and areas used by owls; (2) the history and character of the landscapes that we studied in Oregon; (3) responses of owls to those landscapes; (4) patterns of prey abundance in Oregon; and (5) habitat selection by Spotted Owls.

Geographic Variation in Owls and Prey

Geographic variation in the areas traversed and amounts of old forest used by Spotted Owls reflected similar variation in the abundance and diversity of the medium-sized mammals that are preferred prey of the owl. Across forest types, the areas traversed by the 23 pairs we studied in Oregon were best characterized by the amounts of

TABLE 14. Correlations among landscape indices, old forest in areas traversed and areas used by Spotted Owls, and a measure (BIOX) of old-forest concentration within the areas used by 23 pairs of Spotted Owls in southwestern Oregon in 1987–1988. Landscape indices are dominance and contagion of four habitat types and the variance of the density of old forest in 1-km² blocks.

Landscape indices	Correlation coefficients				
	Areas traversed		Areas used		Concentration of old forest
	Area of old forest	Percentage of old forest	Area of old forest	Percentage of old forest	
Dominance	-0.03	0.57**	0.01	0.55**	0.62**
Contagion	0.11	0.68**	0.12	0.69**	0.68**
Variance	-0.23	-0.57**	-0.18	-0.60**	-0.43**
Concentration	0.03	0.90**	0.20	0.88**	1.00
Percent old forest in					
Areas traversed	0.09		0.06		
Areas used	0.26		0.31		

** $P < .01$.

old forest they used, and secondarily, by the proportion of old forest in the areas they traversed. The major influence was based on habitat area, determined by forest type. Forest type and the attendant differences in prey biomass were accompanied by a twofold difference in the amount of old forest used by pairs of Spotted Owls. Spotted Owls used 813 ± 133 ha of old forest in the Douglas-fir forest type and 454 ± 84 ha of old forest in the mixed-conifer type, reflecting 34% more prey biomass in the mixed-conifer forest. When the data from Washington and Oregon were combined, an increase in area with decreasing medium-sized prey biomass was apparent (Fig. 8).

Douglas-fir vs. western hemlock forests.—In Douglas-fir forest, a nesting pair of Spotted Owls consumes up to 620 flying squirrels/yr and a non-nesting pair consumes up to 444 flying squirrels/yr (assuming flying squirrels comprise 46% of the biomass of the diet: Forsman 1980). Old forests in southwestern Oregon supported an average density of 2 flying squirrels/ha. Litter size in flying squirrels in southwestern Oregon averaged 2.5-3.0 young (Carey 1991). Thus, a crude estimate of the area of old forest required to produce 444-620 squirrels/yr would be 900-1200 ha; spotted owls foraged over 938 ± 260 ha in the DFF in non-nesting years (Table 9), where flying squirrels composed 45% of the biomass consumed (Forsman et al. 1991). In Washington, flying squirrels composed 61% of the biomass consumed (Forsman et al. 1991) and occurred at low densities (0.5 ± 0.2 squirrels/ha) in old forest. Areas traversed by owl pairs were the largest that have been reported for the Northern Spotted Owl; the amount of old forest used averaged 1700 ha (Dawson et al. 1987, Thomas et al. 1990). In our other study areas, both woodrats and flying squirrels were important components of owl diets and the amounts of old forest used by owls were much lower than in the DFF and Washington. Flying squirrels apparently played a major role in determining the carrying capacity of Douglas-fir and western hemlock landscapes for Spotted Owls; their influence was less in areas where woodrats were abundant.

Douglas-fir vs. mixed-conifer forest.—Southwestern Oregon is a transition zone with the fauna reflecting both northern and southern species. Our mixed-conifer study areas were probably the area of maximum overlap between the dusky-footed woodrat and the bushy-tailed woodrat. Our study areas are at the northern limit of the dusky-footed woodrat in upland, forested areas. In the transition zone, especially in old growth, the two species coexist (although their densities are negatively correlated); further south, it appears the bushy-tailed woodrat is confined to rock outcrops (Carey 1991). Thus, with two species of woodrats and the flying squirrel, the transition zone provides a large and diverse prey base for the owl. The amounts of old forest (454 ha) used annually by pairs in the clumped, mixed-conifer forest are the smallest ever reported for the Northern Spotted Owl.

Comparisons with other owls.—Northern Spotted Owls are nonmigratory, nocturnal, sit-and-wait

predators of small- to medium-sized mammals in coniferous forests. Because they are nonmigratory, they must maintain home ranges that meet their needs throughout the seasons and over several years. Their sit-and-wait foraging strategy reflects their nocturnality and the denseness of forest vegetation. Because of the low abundance of their prey, Spotted Owls require large areas of foraging habitat. Thus, even individual owls (and pairs) must contend with forest fragmentation. Even the seasonal home ranges of Spotted Owls are very large compared to those of other birds (Schoener 1968, Carey et al. 1990). Moving across fragmented landscapes to find patches of foraging habitat is energetically costly because the owl cannot forage efficiently while moving. These conditions differ dramatically from those of many migratory, diurnal raptors. Other northern forest owls live under similar conditions. But, unlike many northern forest owls, the Spotted Owl does not specialize in cyclic, microtine prey. For example, the Boreal Owl (*Aegolius funereus*), selects particular kinds of environments for foraging and sits and waits for prey (Sonerud et al. 1986) but specializes on cyclic microtines (Lundberg 1979, Korpimaki 1985). Female Boreal Owls are site tenacious during vole peaks, but nomadic during periods of low abundance of voles (Lofgren et al. 1986). The Tawny Owl (*S. aluco*) is a sit-and-wait, forest predator that specializes on cyclic microtines, but which easily switches to other prey when vole populations are low (Southern 1970, Wendland 1984). The Spotted Owl specializes on relatively stable prey (e.g., flying squirrels) avoiding the requirement of nomadism, but exhibiting less flexibility than the Tawny Owl. Owls, in general, use various strategies in dealing with fluctuations in prey abundance, environmental heterogeneity, and ecosystem stability; these strategies range from philopatry to migration (Andersson 1980). The full range of strategies can be found within single species, especially when that species occupies a broad range of environments (Herrera and Hiraldo 1976). The Boreal Owl is a resident, generalist predator in Central Europe, exhibits a partial migration strategy in southern and in western Finland, and is a nomadic, specialist predator in northern Fennoscandia (Korpimaki 1986). The Northern Spotted Owls exhibit much less behavioral flexibility and, thus, must contend more with the effects of forest fragmentation.

Landscape character

Our Oregon study areas were a checkerboard of federal and private industrial forest land with ownership alternating between sections (259-ha blocks). Private lands were generally cut-over and intensively managed for wood products; property lines are readily apparent in Fig. 2. Federal lands were naturally regenerated forest (including old-growth, mixed-age, mature, and young stands) mixed with managed forests (clear-cut, sapling, pole, and young stands). The DFC area differed from the other areas in that there were two groups of adjacent sections (eight and four sections) of federal land that contained large amounts of old forest (USDI 1982). The DFF had nine adjacent sections of federal

land, but much of that land was covered with mixed-age forest. The MCF1 had the least proportion ($\approx 50\%$) of federal land and the MCF2 had four adjacent sections of private land. The three pairs of owls in the MCC were on federal lands and two of the three sections were adjacent. The land ownership pattern dominated the landscape, overriding patterns due to the natural development of plant communities, including the influence of catastrophic fires.

In the past, catastrophic fires spanned large areas (up to 200 000 ha), creating the 200-550 yr-old old growth present now (Juday 1977). However, timber harvests (both large and small scale) and small-scale fires have obscured the pattern induced by the catastrophic fires. Stand size for old forest averaged 83-94 ha (Table 13), but maxima ranged from 412 ha in the MCC to 2690 ha in the DFC. Overall (natural and managed) mean stand sizes were 51-66 ha. Wildfire frequency also varies north to south, with more frequent fires (often of lower intensity) in the south, and with elevation and aspect. However, the DFF had unusually frequent fires of moderate intensity that resulted in a finer environmental "grain" and, consequently, larger amounts of mixed-age stands than the other areas.

Logging on private lands fragmented the virgin forest resulting from wildfire at the scale of sections (259 ha). Logging on federal lands is fragmenting the remaining natural forest, but on a much smaller scale (17-45 ha), though the cumulative effects have the potential for matching the impact of logging on private lands. Thus the human activities (large- and small-scale logging) are overlain on a landscape of natural forest whose character reflected physiography and catastrophic wildfires. Small scale and low intensity wildfires added further complexity by altering both natural and second-growth forests.

Owl responses to landscapes

The landscapes defined by the ranges of the members of the owl populations showed a concentration of old forest above that in the gross landscapes studied. If we had extended the size of our gross landscapes, the difference in concentration would have been more marked. The areas used by Spotted Owls showed a concentration of old forest that was 1.5 times that in the gross landscapes. Only in MCF 1 were the owls unable to find concentrations of old forest. The MCF1 had the least contagion and the greatest variance of the density of old forest. The MCF 1 had low proportions of old forest and federal land (the lowest among the landscapes).

Spotted Owls appeared to search out concentrations of old forest in the landscape. They usually responded to fragmentation of the old forest by traversing larger areas. Where fragmentation was on a large scale (exceeding the level of sections, i.e., MCF2), the difference in the amounts of old forest between areas traversed and areas used were extreme. Where fragmentation was small scale (DFF, MCF 1), the differences in percentage of old forest between areas traversed and used were most marked. Where fragmentation was minimal (MCC), there was little difference in the amounts of old forest between the areas

traversed and used. The mean amount of old forest in the areas used did not differ significantly among landscapes within forest types; however, the mean amount of old forest in the areas traversed did differ significantly among landscapes in mixed-conifer forest. These differences appeared to be due to the marked expansion of home ranges in response to fragmentation, and to differences in the scale of fragmentation between the landscapes.

Increased home range size was accompanied by decreased overlap of areas traversed by members of pairs and increased overlap among neighboring pairs. Large home ranges thus resulted in decreased sharing of resources by members of pairs, but in increased sharing among pairs. In the area with the largest ranges and most fragmented old forest (DFF), members of pairs were most separated, overlap among areas traversed and used by pairs was highest, and there was evidence of abnormal social structure: mate changes were frequent, proportion of pairs with subadult members was high, and nomadism by females was observed.

Across forest types, the areas traversed by our 23 pairs were best characterized by the amounts of old forest they used, and secondarily, by the proportion of old forest in the areas they traversed. The major influence was based on habitat area, determined by forest type, with a lesser, but statistically significant, influence of fragmentation. Landscape indices were of low predictive value. The owls searched out concentrations of old forest and did not limit their home ranges to particular geometric shapes or to a particular orientation with respect to their nest grove. Such active selection of ranges differs markedly from random or systematic sampling, the frameworks for calculating indices.

Information theory indices (dominance and contagion) and even the variance of the density of old forest did not predict home range size well compared to an empirical index of biological response (BIOX). The BIOX is a direct measure of landscape quality for Spotted Owls; it reflects the ability of owls to incorporate concentrations of preferred habitat in their ranges. For example, BIOX was lowest in MCF1 (28 for individuals) where owls could not concentrate in old forest, and highest in the DFC (58) where the maximum stand size for old forest was found and where the areas used contained 40% more old forest (73% of the range) than in the other landscapes (BIOX, 28-43; old forest, 35-53%). But forest type is too high a level at which to examine effects of fragmentation; the absolute need for old forest (as determined by the prey base) appears to be the overriding factor.

Douglas-fir forest.—Fragmentation (as measured by the proportion of the area traversed that was old forest) explained 4 times more variance in area traversed than did the amount of old forest used. As we reported previously (Carey et al. 1990), amount of old forest in the areas traversed was relatively invariant compared to home range size. Removing the effect of forest type (prey base) resulted in fragmentation being the dominant influence on home range size. Because of the contiguity of federal lands, fragmentation of old forest

was small scale, at the level of weekly movements of owls. Owls traversed from ≈ 1600 ha where old forest was clumped to 2900 ha where old forest was dispersed. We found no significant differences in the amount of old forest in the home ranges between the two landscapes. And the amounts of old forest in the areas traversed (971 ± 115 ha) did not differ significantly from the amount of old forest in the areas used (813 ± 130 ha).

Mixed-conifer forest.—In contrast to fragmentation in the Douglas-fir type, amount of old forest used was the most informative predictor of area traversed in the mixed-conifer forest. Proportion of old forest in the area traversed was of secondary importance. However, BIOX alone could explain 61% of the variance in area traversed and contagion could explain 48%. Proportion of old forest alone could explain only 43%. It appears that in fragmented mixed-conifer landscapes, the pattern of abundance of old forest was one of relatively low contagion with intervening early seral types being generally avoided by owls. Owls probably added old forest to their ranges in discrete patches, rather than by gradual home range expansion, resulting in high variances for the mean amount of old forest within areas traversed. Variance was greatest in MCF2 ($cv = 62\%$), probably due to the pattern of land ownership. Variance was high in MCF1 ($cv = 46\%$) where contagion, proportion of the landscape that was old forest, and proportion of the area used that was old forest was lowest, and where variance in density of old forest was highest. Coefficients of variation were 13% for the MCC, 30% for the DFF, and 41% for the DFC. In Douglas-fir forest, intervening types tended to be neutral with respect to use, but in mixed-conifer forest, intervening types tended to be those that were generally avoided.

Fragmentation in the mixed-conifer landscapes was of two types: highly dispersed old forest separated by a variety of stand types and a checkerboard of cutover sections and sections of fragmented old forest. Home range sizes in the two fragmented landscapes were > 3 times as large as in the clumped landscape. Owls were unable to find concentrations of old forest in the dispersed old-forest landscape, but were able to select areas of concentrated old forest in the checkerboard landscape. The clumped old-forest home ranges were small, and members of pairs used much the same area (75% overlap). The areas traversed and the areas used were the same. In fragmented areas, separation of pairs increased (overlap in individual ranges was 47%) and pairs traversed 45-49% more area than they used for foraging. Greater amounts of old forest were traversed in the large ranges, but amounts of old forest used did not differ between fragmented and clumped landscapes.

Addition of large chunks of old forest resulted in marked expansion of the area traversed and incorporation of little-used stand types and nearby, but unused, old forest. Thus, in the mixed-conifer study areas, scale of landscape pattern appeared to be a major influence on both area traversed and amount of old forest used. Amount of old forest traversed differed between the fragmented and clumped mixed-conifer

landscapes and averaged 596 ± 104 ha. But the area of old forest used did not differ among landscapes and averaged 454 ± 84 ha. The mean amount of old forest used averaged 84% of that traversed in Douglas-fir landscapes but only 76% of that traversed in mixed-conifer landscapes. Estimates of amount of old forest needed based on areas traversed in fragmented landscapes are positively biased compared to estimates based on areas used. Subdivision of landscapes into finer units than we used and summing the area of old forest units used might result in a lower estimate of the area of old forest used; however, such fine subdivisions could lead to underestimates when an optimal sampling procedure (like ours) is used.

Area requirements

We feel that our estimates of old forest used are reasonable approximations of the amount of old forest needed for survival in 1 yr. The amounts of old forest used over 2 yr were 40-43% greater. We did not observe a corresponding increase after 3 yr, but our sample sizes were too small to conclude that an asymptote had been reached. It is likely that the amount of old forest required to sustain a pair of owls exceeds that used in 1 yr. Whether or not 40% more old forest is required is unknown because some of the 40% increase could be due to random range shifts, timber harvesting, or other disturbances within the home range, as well as to prey depletion as a result of predation or other changes in prey abundance.

The areas traversed by our Spotted Owls were large compared to traversed by other owls. Barred Owls in Minnesota traversed 84-498 ha; Great Horned Owls traversed 71-560 ha (Fuller 1979). The Barred Owl is slightly larger, and the Great Horned Owl is considerably larger, than the Spotted Owl. The Tawny Owl (*Strix aluco*) is slightly smaller than the Spotted Owl and maintains territories of 12-20 ha in England and 27-182 ha in other parts of Europe (Southern 1970). Territory sizes maintained by Tawny Owls were related to ground cover; mean territory size was adapted to mean prey level; and, when territories were too small, the owls abandoned them or died. Korpimäki (1988) found that Boreal Owls benefitted from maintaining territories that were mixtures of forest and fields because the owls could forage in the forest when their preferred prey were rare in the fields. Advances in radiotelemetry have stimulated numerous studies of raptor foraging and habitat use (see Nero et al. 1987 for examples), but few studies have reported the effects of forest fragmentation on raptors. Kenward (1982) studied four goshawks for up to 29 d each and concluded that range size was related to the proportion of the range that was woodland edge and to prey availability. Only with recent advances in geographic information systems and in methodologies for characterizing landscapes (O'Neill et al. 1988a) has it been practical to attempt to measure raptor responses to landscape character. We know of no previous study that looks at annual home ranges and habitat use of raptors in relation to landscape pattern and patterns of abundance of prey.

Effects of fragmentation on social behavior

Spotted Owls reuse nest sites and occupy the same general areas year after year; they defend their nests and young, but do not aggressively defend their home range (Forsman et al. 1984). Our data show that resident Spotted Owls have regular contacts with their neighbors. Familiarity between resident adults could facilitate formation of new pairs by residents that lose mates. This contact also may function to maintain spacing between pairs of owls, even without agonistic behavior. In all our study areas, overlap among areas used was low, although overlap in areas traversed was variable, and in the fragmented Douglas-fir forest, high. High overlap and high frequency of contact among pairs may indicate poor or declining habitat quality and promote adult dispersal or nomadism, such as we observed in the fragmented Douglas-fir forest.

More viability was seen in the overlap in areas used by members of pairs; where old forest was heavily fragmented, greater spacing occurred. Spacing varied seasonally. Spacing between members of pairs increased after the breeding season, beginning in September and peaking from November through January. Spacing among pairs also increased during November-January, which is immediately before the breeding season. Increasing spacing in the non-breeding season may be a strategy for minimizing competition for prey, and, perhaps, relaxing predation pressure in the vicinity of the nest grove. Spacing within pairs decreases during the breeding season, when the male may have to forage not only feed to himself, but also to forage and return frequently to the nest grove to feed his mate, and in years of successful reproduction, his young. Separation of individual ranges during the breeding season due to fragmentation could thus interfere with reproduction.

Spotted Owls tolerated subadult (<3 yr) owls, even during the breeding season. Spotted Owls may breed at 2 yr (Barrows 1985, Miller et al. 1985), but breeding by subadults is not common (Gutierrez 1985, Dawson et al. 1987). From the standpoint of self-sustaining populations, room for subadults may be an important aspect of habitat quality that could be adversely affected by heavy fragmentation.

Movements of animals away from their home areas are important components of population dynamics and social behavior (Greenwood and Harvey 1982). Strategies for such movements often reflect adaptations to changes in prey abundance, environmental heterogeneity, and ecosystem stability (Andersson 1980). Galushin (1974) hypothesizes that as man changes the landscape, nomadic movements may become even more vital to the species that can exhibit them. Studies of the natal dispersal of Spotted Owls have documented long (>70 km) dispersal distances but high mortality rates; no 1st-yr birds have been followed until they bred, either the birds or the radio transmitters died (Forsman et al. 1984, Allen and Brewer 1985, Gutierrez et al. 1985, Miller and Meslow 1985). These studies did show that after rapid, unidirectional dispersal in the fall, juveniles attempted to settle, but dispersal renewed during the spring. Our data show that subadults (1-2 yr birds) exhibit a pattern

of settling near adults for variable periods (:56 mo) and, if pairing does not occur, may make additional long distance movements (covering up to 204 km² in a year) before settling again. How long owls persist in these movements is not clear; but we did record one instance of a previously unencountered adult attempting to settle and pair with a subadult male in the center of three established home ranges. Subadults, as well as juveniles, seemed to have high mortality rates. Fragmentation of old forests may lead to lower density of adult owls and to more discrete patches of high prey abundance. Thus, fragmentation may increase not only dispersal requirements but also may create a less hospitable environment for recruitment. Subadults were able to survive in highly fragmented environments during the summer, but seemed to suffer high mortality in the fall and winter.

Nomadism (including breeding dispersal) has not been previously reported in the Spotted Owl. We recorded two adult movements we consider to be nomadic (HS-LM-SF and MV) and three instances of changes in mates accompanied by shifts in home range. It appeared that the heavy fragmentation in the fragmented Douglas-fir and mixed-conifer landscapes might have lowered habitat quality, increased changes in mates, and instigated nomadic movements. It also appeared that timber harvesting led to the dissolution and dispersal of the CK pair in the DFC.

Prey abundance

Flying squirrels.—Flying squirrels were twice as abundant in old forest as in young forest in our study areas. They also seemed to maintain more constant abundance in old forest than they did in young forest, except in areas where the owls foraged intensively (Fig. 5). Because flying squirrels seemed to persist at very low densities in old forests on the Olympic Peninsula and occurred in similar densities in young forests in southwestern Oregon, we cannot conclude that fragmentation due to past timber harvesting in Oregon isolated populations of flying squirrels. On the Olympic Peninsula, we found some young stands devoid of flying squirrels; but, we also found squirrels in very low densities in other young stands, even in areas of extensive second growth. These second-growth stands often had trees damaged by wind or freezing and large snags retained from old growth formerly on the site. The damaged trees and large snags contained cavities used by flying squirrels. Fragmentation of old forest does reduce overall numbers of flying squirrels. Stands intensively managed for timber, recent clear-cuttings, and conversion of forest to nonforest did isolate flying squirrel populations. Clear-cutting was extensive in both our southwestern Oregon and Olympic Peninsula study areas.

Factors limiting to populations of flying squirrels seem to be food (especially the availability of sporocarps of hypogeous ectomycorrhizal fungi) and den cavities in trees (Carey 1991); predation also may regulate populations in some instances (Fig. 5). There are major differences in the diversity of hypogeous fungi among the forest types in the

Pacific Northwest; the western hemlock forests of the western Olympic Peninsula seem especially depauperate (D. Luoma, *personal communication*). Production of sporocarps varies considerably (six-fold differences in biomass) by species, seasons, and years (Luoma 1991). Large moderately decayed snags used by cavity-nesting birds (and later, by flying squirrels) are 10 times more abundant in old forest than in young stands (Carey et al. 1991b).

Experiments have shown that cavity-using sciurids in managed forests outside the Pacific Northwest are often limited by den availability (Carey and Sanderson 1981, Carey and Gill 1983). Thus, we feel the best explanation of the difference in densities among forest types is differences in the diversity of fungal sporocarps. Differences among habitat types within forest types probably are best explained by availability of cavities. Differences within habitat types may reflect different intensities of predation (in space and time) and annual production of sporocarps.

Spotted owls avoided early and midseral forests, possibly because of low prey abundance and, perhaps, because they provide an environment that is structurally poor for a sit-and-wait predator. Young forests had a low vertical diversity of vegetation and high canopy closure with few low structures beneath the canopy that would be suitable as hunting perches. Old forests had a high vertical diversity of vegetation and moderate canopy closure (Carey et al. 1991b) that provide hunting perches continuously from the forest floor to the upper canopy; similarly, the irregular canopy produces heterogeneous understory cover resulting in a mixture of open and dense patches of vegetation, an environment that could make the flying squirrel more vulnerable to predation.

Woodrats.—We caught no woodrats on the Olympic Peninsula, but there were no rock outcrops or talus accumulations in our study areas. Bushy-tailed woodrats are abundant along rocky streams in canyons on the eastern Olympic Peninsula (C. Maguire, *personal communication*) and occur in all mountainous areas of Washington where there is an accumulation of talus (Dalquest 1948). Thus, we assume the bushy-tailed woodrats on the Olympic Peninsula are confined to areas with rock outcrops.

In Oregon, we found bushy-tailed woodrats in areas without rocks. They used snags and fallen trees as shelters, as well as making stick nests independent of other shelter as Maser (1965, 1966) and Maser et al. (1981) report. Woodrats were not abundant in the upland Douglas-fir forest but were common along streams. Bushy-tailed woodrats were moderately abundant in some old-growth stands in some years; they were generally absent from young forest (Tables 4 and 5). In mixed-conifer forest in the transition zone, the two species of woodrats coexisted. Both the bushy-tailed woodrat and the dusky-footed woodrat were moderately abundant in old growth and abundant in rocky areas, pole stands, and along streams, but their densities were negatively correlated. Old growth has a greater abundance of tree cavities than other stages of forest development and the broken nature of the old-growth canopy results in greater understory development than is found in younger forests (Carey et al. 1991b). Pole stands

provide a vegetatively dense environment with large amount of dead branches on the dominant trees; these provide dusky-footed woodrats with house material and structures upon which to build arboreal nests (A. B. Carey, *personal observation*). Occupancy of early seral stages, however, was variable (note the large standard error in Table 4), probably reflecting the fragmentation of old forest and the relatively short time the early stages are suitable to woodrats. Full occupancy of discrete patches in a mosaic landscape would require aggressive dispersal. The dusky-footed woodrat is thought to disperse by gradual growth of colonies (Linsdale and Tevis 1951), a strategy that is suited for contiguous old forest and streamsides, but not well-suited to small, isolated patches of suitable habitat. Further south, the dusky-footed woodrat is more abundant overall and most abundant in sapling and old-growth stages (Raphael 1987, 1988); early seral stages in northern California tend to be more brushy (and perhaps more generally suitable) than those in southwestern Oregon. The bushy-tailed woodrat appears to be confined to rock outcrops, once again, in California (Carey 1991).

Escherich (1981) reports that, in the Sierra Nevada, bushy-tailed woodrat colonies regularly disappear (undergo regular local extinctions). He attributes these to the woodrat's harem social structure, which results in a clumping of the population and attraction of predators. Bushy-tailed woodrats in our study areas showed the same male-harem social structure (averaging 1 male/2.3 females). Spotted Owls in our study areas, especially the DFC, fed in large part on bushy-tailed woodrats (Forsman et al. 1991). The trapping data from old growth stands (Table 5) suggest regular local extinctions. Bushy-tailed woodrats were not abundant in upland sites in the Douglas-fir forest; they were most abundant along streams and in particular stands of old growth. Fragmentation of old Douglas-fir forest seems to isolate bushy-tailed woodrat populations even more than their social behavior does. The large areas of early to midseral stages in our Douglas-fir study areas had few bushy-tailed woodrats and certainly contributed to the isolation of woodrat populations in old growth and along streams. Streams, then, seem to be the principal avenue for recolonization of old forest.

Spotted Owls are attracted to woodrat concentrations. Spotted Owls generally avoid pole stands, but we observed owls foraging in two pole stands that had colonies of dusky-footed woodrats. The highest density of woodrats we found was along Bottle Creek. Bottle Creek was used as the primary foraging site by three subadult Spotted Owls and one adult female owl during the summer. The greater amount of herbaceous vegetation and deciduous shrubs along streams (Carey 1988) may provide an attractive food source, as well as protective cover from predation. Small streams were numerous in our study areas but the accuracy of telemetric locations of Spotted Owls and the steepness of stream cuts precludes us from determining if Spotted Owls selectively foraged along streamsides. The owls did frequently roost along streamsides in the summer. The value of streamsides for woodrats and Spotted Owls has

not been previously addressed; it appears streamside areas of great value to both woodrats and Spotted Owls.

Home range use by Spotted Owls

Owls selected old forest for foraging and roosting. Only one owl selected young forest. This young forest was along Bottle Creek, which had an exceptionally high biomass of woodrats (*N. fuscipes* and *N. cinerea*). Doyle (1990) also found high rodent populations in streamside vs. upland forest. Streamside young forest has a greater vertical diversity of vegetation than upland young forest (Carey 1988). Upland young forest provides few hunting perches for Spotted Owls. In addition, upland young forests supported few woodrats; northern flying squirrel populations in young forest are only 50% of those in old forest in southwestern Oregon. Late sapling-closed pole stages of forest development supported colonies of dusky-footed woodrats. We occasionally found owls foraging in such early seral stands. Additionally, these colonies of woodrats were small compared to the maximum size of early seral stands; thus, further selection of these stands may be shown after a redefinition of stand boundaries. Nevertheless, as a type, these stands were generally avoided by owls, seemingly because occupancy by woodrats is quite variable. Closed-pole stands provide a high vertical diversity of perches for the Spotted Owl because low limbs are still attached to the trees. We recorded a little use of clear-cut stands by spotted owls; these stands had remnant trees or groups of trees.

We found that Spotted Owls tended to roost in sites that were thermally neutral, as Barrows (1981), Barrows and Barrows (1978), and Forsman et al. (1984) also report. We found a disproportionately high number of roosts on the cool, low portions of north-facing slopes in summer and on warm, upper slopes in other seasons. A weak inverse relationship was observed between perch height and temperature, and a weak tendency was found for the owls to seek protection in the canopy from precipitation and wind. But the owls did not seem to respond sharply to weather in their selection of roost sites. Little more than 10% of the variance in perch height and only 2% of the variance in protective cover around perches could be explained by regression with weather variables. The owls appeared to select thermally advantageous topography for roosting, but many roosts were not in these sites. Forsman et al. (1984) found the majority of roosts on south aspects in the spring and summer regardless of weather.

The great majority of roosts were in old forests. Roosts in younger stands were in patches that resembled old forests in vertical diversity of vegetation. Owls selected roosts of relatively high vertical diversity, even for old growth; BPI for roosts averaged 2.3 compared to a median BPI for old growth of 1.7 (Carey et al. 1991 *b*). Old-growth forests have a more moderate microclimate than younger forests (Franklin et al. 1981), and the selection of roosts with old-growth structure probably reflects the moderate microclimate. Owls did not seem any more selective of roost sites than

they were for foraging sites. Rather the owls seem to roost nearby the foraging area of the previous night (Carey et al. 1989). The variability in roosts and low predictability of weather variables suggests that roosts and thermoregulation are not the driving forces in the use of old forest by the Spotted Owl, as suggested by the thermoregulation hypothesis.

In all individual home ranges but one, old forest was the only type selected for foraging and roosting. Old-growth forest was preferred over mixed-old forest. Mixed-old forest was more abundant (and use for foraging was greater) in mixed-conifer forest than in Douglas-fir forest. The strong selection of old forest at three scales of selection (population, pair home range, and individual) argues that, in southwestern Oregon, use of old forest reflects a need, not simply a preference. This need for old forest as a foraging environment is reflected by the individual's habitat selection; cumulatively this need is reflected in the selection of pair annual ranges. The marked difference in use of amounts of habitat between forest types reflects the influence of prey base diversity and abundance. In fragmented areas, spotted owls bypassed substantial amounts of young and mature forest to gain access to old forest and tolerated home range overlaps as well.

Implications for Spotted Owl management

The amounts of old forest used by pairs of Spotted Owls in the Douglas-fir forest did not differ significantly from the 800-1000 ha previously reported for western Oregon (Forsman and Meslow 1985, Carey et al. 1990). Managers must decide on how much old forest to reserve for Spotted Owls within Spotted Owl management areas. Our data on pairs provide the best guidance to date. Our annual mean (813 ha) would be inadequate in 33% of the cases (based on the areas used by our nine pairs). If the data were normally distributed, the mean plus 2 standard deviations would ensure a high probability of providing adequate resources for a pair. But the data are not normally distributed and are not a random sample. Another approach would be to use the annual third quartile. The third quartile is 961 ha. The two pairs that used more than this amount were in the heavily fragmented DFF area where the environment seemed marginal for owls. Similarly, 961 ha would have provided for 3 of the 4 pairs we previously studied and 5 of the 6 pairs studied by Forsman and Meslow (1985). However, the biannual third quartile was 1167 ha; annual, and even biannual, figures may underestimate the amount of old forest required to sustain a pair of owls in the short term.

The old forest set aside must be within some area the owl can reasonably traverse. Our range lengths (Table 1) suggest that 5 km is a reasonable distance for owls to traverse on an annual basis. A circle of 2.5 km radius is ≈ 2000 ha. Such a circle could be used as a template. If > 950 ha of old forest were present within the 2000 ha circle, there is a reasonably high expectation that the area could support a pair of owls for 1 yr. If a pair's nest grove was known, but

its foraging range was not known, then moving the circle over a cover-type map, while keeping the nest grove within the circle, would locate concentrations of old forest with high probabilities of supporting a pair. Because we found little overlap among areas used, except in the most heavily fragmented area, multi-pair management areas could simply be based on the sum of the pair requirements.

Applying similar logic to mixed-conifer forests suggests that 500 ha of old forest within a 2.5 km radius would have a reasonably high probability of providing adequate resources for a pair of Spotted Owls for 1 yr; 668 ha would be advisable for 2 yr. However, managing for single pairs would not provide for viable populations in either region because of the need to maintain subadults as replacements for breeding adults that die or leave and to maintain communication between adult members of established pairs to aid in forming new pairs after a loss of mate. In both forest types, areas big enough to sustain several pairs would have a higher expectation of providing an adequate environment for a viable population.

Owl home ranges differed between western Oregon and the Olympic Peninsula of Washington. We found bushy-tailed woodrats to be rare and northern flying squirrel populations to be low, about one-fourth those in southwestern Oregon. Red tree voles and dusky-footed woodrats do not occur in Washington. We would expect that owl response to the environment would change markedly in the southern direction also. Management must be tailored to each biotic region. Changes in response and requirements could be abrupt with changes in biotic region.

EPILOGUE

We, and other researchers currently studying the Spotted Owl, provided our unpublished data and manuscripts to The Interagency Scientific Committee To Address the Conservation of the Northern Spotted Owl (Thomas et al. 1990). This committee has recommended that a network of habitat conservation areas, each capable of sustaining a minimum of 20 pairs of owls, be established throughout the Pacific Northwest in numbers sufficient to maintain a minimum total population size of ≈ 1500 pairs. Both goals (20 and 1500 pairs) were based on analyses of owl demographics and the existing distribution of suitable habitat. Gaps in the distribution of suitable habitat were identified and the committee recommended setting aside young forest to provide habitat in these areas in the future. Minimum sizes of the habitat conservation areas would vary geographically, based on known distributions of pairs and, when the population had not been described, 75% of the median annual MCP home range (area traversed) of owls in that area, to allow for a 25% overlap among pairs. When we calculated the areas recommended by Thomas et

al. (1990) for the DFBR and the MCBR, we found they were within 5% of our annual third quartile figures. Information on cumulative home range sizes and composition were not available to the committee.

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