

# HABITAT SELECTION BY NORTHERN SPOTTED OWLS: THE CONSEQUENCES OF PREY SELECTION AND DISTRIBUTION<sup>1</sup>

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**Abstract.** We tested three predictions of a hypothesis that states Northern Spotted Owls (*Strix occidentalis caurina*) select habitat according to the distribution of their primary prey. Our predictions were that Northern Spotted Owls should (1) select larger (> 100 g) species among the assemblage of available prey, (2) select habitats according to the distribution of large prey, and (3) the owl's reproductive success should be influenced by the availability of large prey. We also evaluated the potential energetic value of several prey species. We found that Northern Spotted Owls ( $n = 11$  pairs and 1 single male) in northwestern California differentially selected the dusky-footed woodrat (*Neotoma fuscipes*), a moderately large sigmodontine rodent ( $\bar{x}$  mass = 232 g). When foraging, owls selected late seral forest edge sites where dusky-footed woodrats were more abundant. Although the relationship between site selection, prey abundance, and the owl's breeding success was not statistically significant, the average abundance of dusky-footed woodrats at sites foraged by breeding owls ( $\bar{x} = 11.4$  woodrats 100-trap-nights<sup>-1</sup>) was greater than at sites foraged by nonbreeding owls ( $\bar{x} = 4.7$  woodrats 100-trap-nights<sup>-1</sup>). We estimated that a male Spotted Owl would require 150,015 to 336,232 kJ over a 153-day period while helping to produce one young, and concluded that the selection of woodrats provided a potential energetic benefit over the use of other prey. These findings provide a partial explanation for the owl's affinity for late seral forests.

**Key words:** dusky-footed woodrat, energetic requirements, foraging habitat, late seral forest, Northern Spotted Owl, prey abundance, reproductive success, *Strix occidentalis caurina*.

## INTRODUCTION

During the past decade, considerable concern over the fate of the Northern Spotted Owl (*Strix occidentalis caurina*) has surfaced because of its association with late seral stage forests (Dawson et al. 1987, Thomas et al. 1990). Several hypotheses have been proposed to explain the owl's selection of late seral forests, including (1) greater nest availability, (2) more favorable microclimate, (3) greater abundance of prey, (4) better access to prey, or (5) safer refuge from predators compared to other forest types and seral stages (Carey 1985, Gutiérrez 1985). In greatly fragmented landscapes, competition with larger owl species may restrict Northern Spotted

Owls to patches of late seral forest (Carey et al. 1992). It also is possible that Northern Spotted Owls have co-evolved with a suite of relatively stable conditions found in late seral forests (Carey 1985).

In this study, we tested the hypothesis that Northern Spotted Owls select habitat according to the distribution of primary prey. Under this hypothesis, we assumed that owls were selecting habitat proximately because favored prey were abundant and accessible, and ultimately because these choices improved the owls' fitness (Hildén 1965). Although related, the prey distribution hypothesis differed from 3 and 4 above by considering prey abundance and availability as interacting factors of habitat selection, and by conveying the relevance of fitness in assessing the owl's habitat choices (Van Horne 1983).

Numerous studies of strigids have shown positive correlations between prey abundance and either nest success or number of fledglings produced (reviewed by Verner et al. 1992). Furthermore, food supplementation increases reproductive performance in many avian species in-

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cluding owls (Korpimäki 1989, Boutin 1990). Thus, it is not unreasonable to suspect that the distribution of prey exerts influence on habitat selection and fitness of Spotted Owls.

Prior to our study, limited evidence indicated that Spotted Owls benefited by consuming moderately-large rodents. For example, Barrows (1985, 1987) postulated from dietary analysis that successful reproduction of Northern and California Spotted Owls (*S. o. occidentalis*) was correlated with the availability of large (> 100 g) prey. Thraikill and Bias (1989) noted a similar pattern for California Spotted Owls. However, neither study demonstrated that these owls were selecting large prey relative to its availability (Johnson 1980). After our study was completed, Carey et al. (1992) demonstrated that the large amounts of late seral forest traversed and used by Northern Spotted Owls in southwestern Oregon was related to the character of the prey base, forest type, and extent of forest fragmentation. Northern Spotted Owls that consumed primarily northern flying squirrels ( $\bar{x}$  mass = 122 g; Carey 1991) and hunted among fragmented forests dominated by Douglas-fir (*Pseudotsuga menziesii*) used more land area than Spotted Owls that consumed woodrats ( $\bar{x}$  mass = 227 to 284 g; Carey 1991) and flying squirrels while hunting within relatively intact forests of mixed-conifer. Carey et al. (1992) also postulated that areas used by Spotted Owls should be even smaller if they occurred in mixed-conifer forests and consumed primarily woodrats. Zabel et al. (1995) verified this trend by demonstrating a negative, linear relationship between home range size during the breeding season and the proportion of woodrats in the diet of Northern Spotted Owls. Our study differed from these studies by attempting to determine if specific prey species were being selected by Northern Spotted Owls and whether this selection was related to habitat choice and the owl's reproductive success. In Johnson's (1980) terminology, we examined resource selection by Northern Spotted Owls at third (sites within a home range) and fourth (food resource) order scales.

## METHODS

We evaluated our hypothesis by attempting to refute three competing predictions. We reasoned that Northern Spotted Owls would not select late seral stage forests according to the distribution

of larger prey if these owls (1) did not select among acceptable prey species, (2) did not select late seral forest according to the distribution of large (>100 g) prey, and (3) the availability of selected prey did not influence the owl's reproductive success. In addition, we calculated areas of late seral forest that would be required by these Spotted Owls from energetic costs for the production of one young and estimates of prey density. Comparison of predicted and observed areas of late seral forest under varying assumptions about prey consumption provided additional evaluation of the influence of prey distribution on this owl.

This study was conducted concurrently with a study of Northern Spotted Owl habitat selection (Zabel et al. 1995). We quantified the owl's diet and estimated abundance of common prey species occurring at foraging sites of radio-transmitted owls monitored during that study and at randomly selected sites. We tested our first prediction by comparing diets of Northern Spotted Owls with expectations calculated from estimates of prey density in late seral forest. We tested our second prediction by comparing relative prey abundance sampled at owl foraging sites to relative prey abundance at randomly selected sites. We tested our third prediction by comparing relative prey abundance between the foraging areas of reproductively successful and unsuccessful owls.

## STUDY AREA

This study was conducted in an approximate 11-km<sup>2</sup> area near Dinsmore, Humboldt County, California. Most of the study area was administered by the Mad River Ranger District, Six Rivers National Forest with some private land adjacent to and within the National Forest boundaries. Commercial forestry was the dominant land use. Elevations ranged from 850 m to 1,340 m above sea level. Cool, wet winters and hot, dry summers characterized the climate. Vegetation was comprised of two major forest types, a mixed evergreen forest and a northern oak woodland (Küchler 1977). The mixed-evergreen forest comprised approximately 70% of the area and occurred in several seral stages. Old and mature forest stages (> 180 yr) comprised approximately 64% of the area (Zabel et al. 1995) and were generally multilayered, dominated by Douglas-fir in the overstory with other species of conifers and hardwoods in the understory (Bingham and

Sawyer 1991). The understory within some of the mature stands that we studied had been removed as part of a silvicultural treatment prior to our investigation. The northern oak woodland type (Griffin 1977), dominated by Oregon white oak (*Quercus garryana*), comprised approximately 30% of the study area. The vegetation was described further by Ward (1990) and Zabel et al. (1995).

#### PREY SPECIES

Spotted Owls occupying mixed conifer or mixed evergreen forests in northwestern California during spring and summer months commonly consume several species of small mammals. These species include the dusky-footed woodrat (*Neotoma fuscipes*), red tree vole (*Phenacomys longicaudus*), northern flying squirrel (*Glaucomys sabrinus*), terrestrial voles (*Microtus californicus*, *M. oregoni*, and *Clethrionomys californicus*), and white-footed mice (*Peromyscus maniculatus*, *P. boylii*, *P. truei*). Together, these species comprise 88% to 99% of prey biomass in the owl's diet (Barrows 1987, White 1996).

#### SAMPLING DESIGN AND FIELD METHODS

We sampled the diet of Northern Spotted Owls by gathering regurgitated pellets beneath roosts and nests. We assumed that the prey items found within regurgitated pellets adequately represented the diet of each owl family. These procedures were consistent with other studies of the Spotted Owl's diet (Barrows 1980, Forsman et al. 1984). The owls' reproductive status was assessed by feeding adults live mice and following the owls to mates, nests, or young (Forsman 1983). The amount of food given to an owl pair during a breeding season varied between 20 g to 240 g and was not considered enough to influence the owl's reproductive success. Reproduction was considered successful if one or more fledglings were observed at a nest site.

To estimate prey abundance with respect to site selection by owls, we defined a foraging area for each radio-tagged, male Spotted Owl using the minimum convex polygon method (Hayne 1949) around 25 to 30 night-time locations estimated with radiotelemetry. Procedures and materials used to capture, affix radio transmitters, and monitor individual owls have been described by Zabel et al. (1995). The foraging area represented the region in which a male owl hunted for approximately one month prior to

when we sampled prey abundance and was a subset of the entire breeding-season home range estimated by Zabel et al. (1995). Sampling was restricted to the foraging areas of males because males supply most of the food for an owl pair during breeding periods (Forsman et al. 1984). Estimating foraging areas was necessary to determine two sampling frames: first, the area most used for foraging, and second, a subset of the landscape (i.e., outside of the foraging areas) seldom used by these males during the sampling period (discussed further, below). Owl locations were excluded from estimating foraging areas when (1) point estimates of error polygons were  $> 0.8$  ha, which indicated greater chance of signal distortion (Springer 1979) or (2) nonforaging activity was apparent (e.g., owls vocalizing for territorial defense). We assumed that all other night-time locations represented foraging sites.

During the period when young owls were fed by parents (June through August), five foraging sites were randomly selected from all observations used to define the foraging area of each male owl and sampled to estimate relative prey abundance. More intensive sampling was conducted at one of these five sites during the same period to estimate actual densities of prey. Only sites classified as late seral stage mixed evergreen forest with  $> 40\%$  canopy closure were sampled to estimate prey density because prior studies indicated that this habitat type was more frequently selected for foraging by Northern Spotted Owls occurring in northwestern California (Solis and Gutiérrez 1990). Four sites outside of each owl's foraging area, but within a 2.4-km radius from nest or roost core, also were selected for estimating relative prey abundance. These sites represented the random distribution of locations that were potentially available to each male owl for hunting but had a low likelihood of use during the period when prey were sampled. The 2.4-km distance was the radius for an average home range size of Spotted Owls in Oregon and a distance previously used for management of the species (USDA 1988). Site placement was determined by randomly selecting Universal Transverse Mercator (UTM) coordinates within vegetation types similar to that sampled at the owl's foraging sites.

Density of white-footed mice, terrestrial voles, and insectivores was sampled using 144 Sherman live traps ( $7.6 \times 8.9 \times 22.9$  cm) arranged in a 12 by 12 grid during 1987, and 196

traps arranged in a 14 by 14 grid during 1988. Traps were placed 10 m apart. Density of woodrats and Allen's chipmunk (*Tamias senex*) was sampled using 64 ground-placed Tomahawk live traps (12.5 × 12.5 × 40.0 cm) arranged in a 8 by 8 grid (one site) or using 100 ground-placed live traps in a 10 by 10 grid (three sites) during 1987. Traps were spaced 20 m apart. Density of flying squirrels was sampled using 25 tree-mounted Tomahawk live traps arranged in a 5 by 5 grid with 40-m spacing between traps during 1987. Tree-mounted traps were placed 1.0 to 1.5 m above the ground (Carey et al. 1991). During 1988, density of woodrats, chipmunks, and flying squirrels was sampled using 144 ground-placed Tomahawk traps arranged in a 12 by 12 grid with 20 m spacing between traps. Justification for trap spacing was described by Ward (1990). Trap numbers were increased between years in an attempt to improve density estimation. Traps were supplied with bedding, baited, set for six to eight consecutive nights, and checked each subsequent morning. Captured individuals were weighed, aged, sexed, and released at the capture site. Except for insectivores (shrews, *Sorex* spp. and the shrew mole, *Neurotrichus gibbsii*), individuals were marked on both ears using numbered ear tags.

Relative abundance of white-footed mice, terrestrial voles, and insectivores was sampled using 34 Sherman live traps placed systematically along two perpendicular trap lines (one oriented north-south; another east-west) intersected at the midpoints. The estimated location of a foraging owl or randomly drawn UTM coordinate determined the intersection point of the trap lines. One Sherman trap was placed within 1.5 m of each trap station. Trap stations were spaced 13.3 m apart (ground distance) along the trap lines. One additional Sherman trap was placed at each station occurring at the (1) intersection of both lines, (2) 40 m from, and (3) 80 m from the intersection (hereafter referred to as double-trap stations). Because of their arboreal nature, red tree voles were not sampled. In 1987, relative abundance of the dusky-footed woodrat and Allen's chipmunk was sampled using nine Tomahawk live traps placed on the ground at double-trap stations at each site. Northern flying squirrels were sampled using nine Tomahawk live traps mounted on trees at the double-trap stations. In 1988, tree-mounted traps were abandoned because of low capture success, and

woodrats, chipmunks, and flying squirrels were sampled using nine live traps placed on the ground, following the procedure used in 1987. Traps were baited, supplied with bedding, and set for three consecutive nights and checked each morning. Although chipmunks are rarely taken by Northern Spotted Owls, we used their abundance as a reference when comparing prey distributions. For example, we would be skeptical of inferences about site selection by foraging owls drawn from tests where distribution patterns of prey were similar to nonprey.

#### DATA ANALYSIS

Owl diets were quantified using frequency of prey items and prey biomass (%) in regurgitated pellets following the methods of Forsman et al. (1984) and Marti (1987). Prey biomass was calculated as a product of a prey's frequency and its average mass. The latter was estimated from measurements of captured individuals or from museum specimens and published estimates when species were not captured.

Prey density was estimated using closed population estimators (Program CAPTURE, Otis et al. 1978, Rexstad and Burnham 1992). Relative prey abundance was calculated as catch per unit effort (CPUE) for each site by summing the number of individuals captured once and then dividing by the total number of traps available during three nights of trapping (Caughley 1977). Total number of traps available was calculated by subtracting the number of traps tripped but empty and one half of the traps occupied by all animals from the total number of traps set (Nelson and Clark 1973). Relative abundance was expressed per 100 trap-nights by multiplying CPUE by 100. For parametric analyses, CPUE was treated as a proportion and transformed using an arcsine function (Zar 1984).

We used two analyses of the owl's diet to examine the differential use of prey. First, we used a chi-square contingency table to compare frequencies of prey species in the diets of owls that produced young and of owls that did not produce young to test for differential use between breeding and nonbreeding owls. Second, we conducted two log-likelihood tests of independence and quantified selection ratios from the frequencies of prey consumed by owls and the preys' abundance in late seral stage forest to test for prey selection. Following Manly et al. (1993), we estimated the likelihood that owls

differed in their use of each prey ( $X_{L1}^2$ ) and that this use was independent of the prey's abundance ( $X_{L2}^2$ ). The difference between these log likelihood tests was compared to a chi-square distribution with  $(L2-L1)$  degrees of freedom to determine if prey selection occurred while accounting for variability in prey use among owls. Selection ratios ( $w_i$ ), the ratio of prey use to that expected given the prey's abundance, were estimated to determine which prey were being selected when the log likelihood tests proved significant, where:

$$\hat{w}_i = u_{i+} / (\hat{\pi}_i u_{++})$$

and  $u_{i+}$  is the number of prey in category  $i$  used by all sampled owls,  $\hat{\pi}_i$  is the estimate of the proportion of prey  $i$  available to the owl population, and  $u_{++}$  is the total number of used prey summed across all examined categories (Manly et al. 1993). Prey use ( $u_{i+}$ ,  $u_{++}$ ) was determined from dietary frequencies. The proportion of each prey available to owls ( $\hat{\pi}_i$ ) was estimated as the average proportion of the total density of all examined species. Bonferroni confidence limits, adjusted for multiple, simultaneous comparisons, were estimated to determine which  $w_i$  were significant.

We tested statistical hypotheses associated with our second prediction, prey are more abundant at sites foraged by male Spotted Owls, using a two-factor analysis of variance (ANOVA) and Tukey's multiple comparisons of CPUE data (Zar 1984). The first factor represented Spotted Owl activity; a foraging or randomly selected site. The second factor represented habitat type with three categories, "conifer-hardwood edge," "conifer over hardwood," and "conifer." The conifer-hardwood edge category represented the ecotone between late and early seral mixed evergreen forest. Conifer over hardwoods distinguished sites of late seral mixed evergreen forest that included a developed understory. The strict conifer category did not include a developed understory. CPUE was stratified by these habitat types to account for the variability in prey abundance arising from habitat differences independent of the owl's site choice. Habitat classification of sites was based upon direct observation and followed definitions used by the United States Forest Service (Six Rivers National Forest, Eureka, California; Ward 1990).

We tested statistical hypotheses associated

with our third prediction, prey are more abundant in foraging areas of reproductively successful owls, using a nested, single-factor ANOVA (Type I) and multiple comparisons of the variance in CPUE (Zar 1984). By nesting data, we segregated the variability of relative prey abundance in each owl's foraging range. Statistical hypotheses were rejected if the probability of committing a Type I error was  $\leq 0.05$ . Retrospective power of our ability to detect a difference in prey abundance that corresponded to the amount of energy required to produce one owl young was estimated following procedures in Thomas (1997).

#### ENERGETIC CONTRIBUTION OF PREY

A rigorous assessment of the influence of prey abundance and distribution on raptor fitness also requires knowledge of the energetic contribution of prey and the raptor's energy needs (Stalmaster 1987). Although we did not directly measure the energetic costs of reproduction to Northern Spotted Owls, we could approximate the potential contribution of the owl's common prey based upon an energetic model and inputs taken from other published sources. In our model, total energy (kJ) required to produce one fledgling is the summation of (1) a male parent's maintenance metabolic cost from late courtship (1 March) until food provisioning to young and mate ceases (about 1 August), (2) a female parent's maintenance metabolic cost from 1 March to 15 days after the young leaves the nest (15 June), (3) the cost of egg production, and (4) the cost of growth and maintenance of one fledgling from hatching to 1 August. The model did not include costs for flight or prey delivery and were therefore treated as minimum total costs. Once calculated, the computed total cost was used to estimate the number of each common prey species and the area of late seral forest that a male Northern Spotted Owl would need to successfully produce one fledgling. We predicted the size of this area by partitioning the owl's energetic cost among prey categories according to the average proportions of prey biomass found in their diet and then dividing these calculations by average prey densities. Predicted areas were compared to the 95% CI of late seral forest area used by these owls to determine if energetic demand was a reasonable explanation for the owl's choice of prey and habitat area. The amount of

TABLE 1. Density of small mammals in late seral mixed evergreen forests in northwestern California, June through August, 1987 and 1988 ( $n = 8$  sites).

Species	Number ha <sup>-1</sup>	
	$\bar{x} \pm SE$	CV
<i>Peromyscus</i> spp. <sup>a</sup>	7.7 $\pm$ 1.8	64.9%
<i>Microtus</i> spp. <sup>b</sup> , <i>Clethrionomys californicus</i>	2.4 $\pm$ 1.1	126.2%
<i>Sorex</i> spp. <sup>c</sup> , <i>Neurotricus gibbsii</i>	8.7 $\pm$ 2.3	75.3%
<i>Neotoma fuscipes</i>	0.9 $\pm$ 0.3	92.0%
<i>Glaucomys sabrinus</i>	0.4 $\pm$ 0.2	155.6%
<i>Tamias senex</i>	1.5 $\pm$ 0.4	69.2%

<sup>a</sup> *Peromyscus maniculatus*, *P. boylii*, *P. truei*.

<sup>b</sup> *Microtus californicus*, *M. oregoni*.

<sup>c</sup> *Sorex trowbridgii*, *S. pacificus*.

late seral forest used by these owls was estimated from data in Zabel et al. (1995: Table 1).

## RESULTS

We collected 339 regurgitated pellets from eight Northern Spotted Owl pairs and one single owl from March to September 1987 and 1988. A total of 495 prey items (range 20 to 96 items per owl pair) were identified from the dissection of these pellets. Two of the sampled owl pairs produced two young each in 1987 and three pairs produced one young each in 1988. Between 11 June and 16 September 1987, abundance of primary prey was sampled within the foraging areas of four male owls. Between 1 June and 19 August 1988, the foraging areas of eight male owls were sampled.

A total of 16,520 trap-nights were allocated to estimating prey density at eight sites in late seral, mixed evergreen forest during both summers. Density estimates ranged from 0.4 individual flying squirrels ha<sup>-1</sup> to 8.7 insectivores ha<sup>-1</sup> (Table 1). Coefficients of variation among the eight sites (Table 1) showed that density of northern flying squirrels was quite variable in late-seral stage forest (156%), whereas density of white-footed mice was more consistent (65%). The variability of dusky-footed woodrat density was moderately high (CV = 92%).

Approximately 14,460 trap-nights were allocated to estimating relative prey abundance at 59 owl foraging sites and 44 random sites during both summers. Relative abundance of dusky-footed woodrats, northern flying squirrels, and Allen's chipmunks sampled at two owl foraging sites and three random sites were excluded from analyses because 30% or more of live traps were

disturbed by striped skunks (*Mephitis mephitis*) or black bears (*Ursus americanus*). Frequency distributions of CPUE (Fig. 1) indicated that relative abundance of terrestrial voles, northern flying squirrels, and insectivores was too low for meaningful comparisons. Thus, only CPUE of white-footed mice, the dusky-footed woodrat, and Allen's chipmunk was used for testing predictions concerning prey distribution. Data from these species provided three useful scenarios for testing our second and third predictions: (1) a predominately used large prey (dusky-footed woodrat), (2) a moderately used small prey (white-footed mice), and (3) a non-used species (Allen's chipmunk).

## PREY SELECTION

During both summers, owls consistently consumed a large percentage of dusky-footed woodrats, whereas fewer terrestrial voles, northern flying squirrels, and white-footed mice were consumed with less consistency (Table 2). Remains of Allen's chipmunk constituted 1 of the 495 prey items, confirming our original assumption that this species was rarely consumed, and therefore provided an "out group" for evaluating patterns observed for common prey (Table 2). We did not have abundance estimates for brush rabbits (*Sylvilagus bachmani*), pocket gophers (*Thomomys bottae*), birds, or insects, and therefore could not test predictions about selection of these prey. However, diet frequencies indicated that brush rabbits, pocket gophers, and birds were taken infrequently and, with the exception of brush rabbits, contributed little biomass to the owls. The estimated 7% of biomass contributed by brush rabbits was the function of a mass value of 300 g and was likely overestimated. The true size of brush rabbits captured by Spotted Owls could range from 50 g to 300 g. Because of this uncertainty, we refrained from considering brush rabbits as common prey. Insects were relatively frequent in the owl's diet but contributed little to dietary biomass. Although insectivores were not commonly consumed by these owls (Table 2), we did have abundance estimates for these species and included them in subsequent analyses for comparative purposes.

The proportion of prey larger than 100 g taken by owls that produced young was not significantly different from proportions taken by owls that did not produce young ( $\chi^2_1 = 0.6$ ,  $P =$

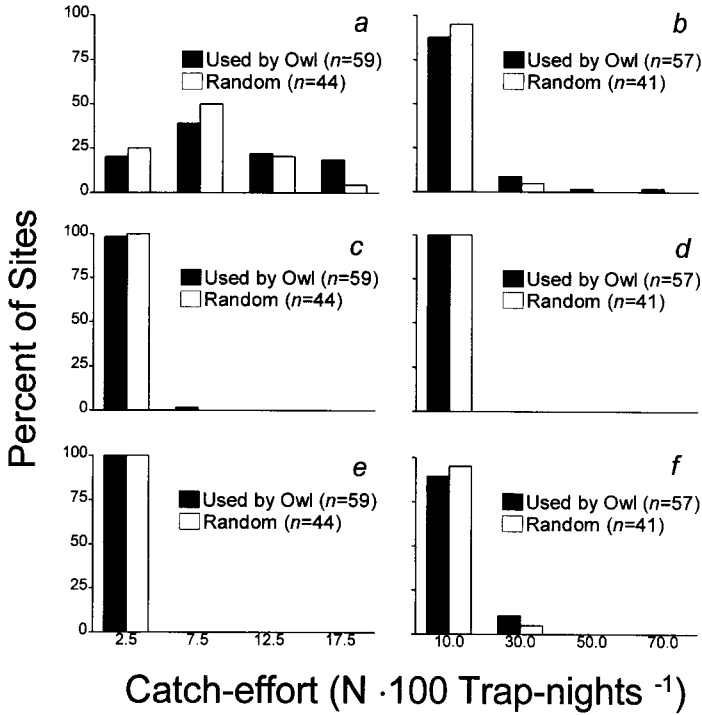


FIGURE 1. Frequency distribution of catch per unit effort of (a) *Peromyscus maniculatus*, *P. boylii*, and *P. truei*, (b) *Neotoma fuscipes*, (c) *Microtus californicus*, *M. oregoni*, and *Clethrionomys californicus*, (d) *Glaucomys sabrinus*, (e) *Sorex trowbridgii*, *S. pacificus*, and *Neurotrichus gibbsii*, and (f) *Tamias senex* occurring at sites used by male Northern Spotted Owls and at random sites. Labels on the x-axis are mid-points of abundance classes.

TABLE 2. Mass and relative amounts of prey consumed by eight pairs and one single Northern Spotted Owl during the breeding season in 1987 and 1988. Calculations are based on 495 prey items from 339 regurgitated pellets. SD and CV indicate variation among owls.

Prey species	Mean mass (g) <sup>a</sup>	Frequency of items (%)		Percentage of biomass	
		$\bar{x} \pm SD$	CV	$\bar{x} \pm SD$	CV
<i>Sorex</i> spp.	4.8	0.9 ± 1.6	179.1	<0.1 ± 0.1	184.1
<i>Neurotrichus gibbsii</i>	9.4	0.1 ± 0.3	282.8	<0.1 ± <0.1	282.8
<i>Scapanus</i> spp.	45.9	1.8 ± 2.3	129.0	0.7 ± 0.9	126.9
<i>Sylvilagus bachmani</i>	300.0	2.8 ± 2.5	89.9	7.0 ± 6.4	91.8
<i>Tamias</i> spp.	77.9	0.2 ± 0.6	282.8	0.2 ± 0.4	282.8
<i>Sciurus griseus</i>	265.0	0.3 ± 0.6	195.6	0.6 ± 1.3	201.8
<i>Tamiasciurus douglasii</i>	208.0	0.5 ± 0.7	147.3	0.8 ± 1.2	144.4
<i>Glaucomys sabrinus</i>	108.6	10.1 ± 7.7	75.9	9.3 ± 7.4	79.0
<i>Thomomys bottae</i>	55.4	4.6 ± 4.4	96.7	2.2 ± 2.1	99.0
<i>Peromyscus</i> spp.	19.9	6.8 ± 5.0	73.1	1.3 ± 1.1	87.8
<i>Neotoma fuscipes</i>	231.9	38.5 ± 14.5	37.7	70.9 ± 13.4	18.9
<i>Clethrionomys californicus</i>	20.7	2.1 ± 2.5	117.6	0.4 ± 0.6	130.4
<i>Phenacomys longicaudus</i>	23.3	8.8 ± 6.0	73.0	1.7 ± 1.4	83.3
<i>Microtus californicus</i>	38.9	2.6 ± 2.7	104.6	0.9 ± 1.0	109.8
<i>Microtus oregoni</i>	18.3	2.3 ± 3.2	140.2	0.4 ± 0.7	162.3
<i>Microtus</i> spp.	32.4	5.8 ± 10.4	178.9	1.6 ± 3.0	189.7
Small bird	30.0	3.3 ± 3.0	90.5	1.0 ± 1.1	114.0
Medium bird	70.0	1.3 ± 2.0	147.9	1.0 ± 1.5	158.8
Insect	1.0	7.6 ± 4.0	52.8	0.1 ± <0.1	63.7

<sup>a</sup> Sources for average mass: Forsman et al. (1984), Laymon (1988), USDA Forest Service, Redwood Sciences Laboratory, unpubl. data; this study.

TABLE 3. Selection ratios ( $w_i$ ) of prey frequencies in Northern Spotted Owl diets to prey availability in late seral stage forests of northwestern California during breeding seasons of 1987 and 1988. Diet frequencies pertain to owls occurring in nine territories. Prey availability was based on density proportions averaged among eight sites. Bonferroni 95% confidence intervals with a lower limit  $>1$  (\*) indicate significant selection of prey by these owls at  $P < 0.05$ .

Prey	$w_i \pm SE$	Bonferroni CI
<i>Peromyscus</i> spp.	0.33 $\pm$ 0.05	0.19–0.46
<i>Microtus</i> spp., <i>Clethrionomys californicus</i>	1.73 $\pm$ 0.30	0.98–2.49
<i>Sorex</i> spp., <i>Neurotrichus gibbsii</i>	0.24 $\pm$ 0.06	0.07–0.41
<i>Neotoma fuscipes</i>	4.11 $\pm$ 0.41	3.04–5.18*
<i>Glaucomys sabrinus</i>	2.61 $\pm$ 0.58	1.07–4.15*
<i>Tamias senex</i>	0.01 $\pm$ 0.01	-0.02–0.04

0.45). Likewise, the proportion of woodrats consumed relative to all other prey was independent of the owl's reproductive success ( $\chi^2_1 = 0.0$ ,  $P = 1.00$ ). The difference between the two log-likelihood tests of independence was highly significant ( $X_{L,2}^2 - X_{L,1}^2 = 110.9$ ,  $df = 5$ ,  $P < 0.001$ ), indicating that selection of some prey was occurring among all owls. Selection ratios (Table 3) were greatest for dusky-footed woodrats ( $w_i = 4.1$ ) and northern flying squirrels ( $w_i = 2.6$ ). These values were significant as shown by Bonferroni confidence limits (Table 3).

#### OWL FORAGING AND PREY DISTRIBUTION

The relative abundance of dusky-footed woodrats ( $F_{1,96} = 2.4$ ,  $P = 0.13$ ) and Allen's chipmunks ( $F_{1,96} = 0.2$ ,  $P = 0.66$ ) were not different between years, and were pooled across years. Relative abundance of white-footed mice varied between years ( $F_{1,96} = 24.9$ ,  $P < 0.001$ ), and was therefore analyzed separately by year. When comparing CPUE from owl foraging sites and random sites, we found that dusky-footed woodrat abundance was greater at sites used by owls ( $F_{1,91} = 3.9$ ,  $P = 0.05$ ; Fig. 2a). Woodrat abundance was significantly different among the three habitats ( $F_{2,91} = 13.4$ ,  $P < 0.001$ ), exhibiting greater abundance at the conifer-hardwood edge (Fig. 2a). Woodrat abundance showed no interaction between owl activity and habitat ( $F_{2,91} = 1.5$ ,  $P = 0.24$ ). White-footed mouse abundance in 1987 did not differ between site-use categories or habitat types ( $F_{3,29} = 1.0$ ,  $P = 0.44$ , Fig. 2b). In 1988, white-footed mouse abundance was significantly greater at owl foraging sites ( $F_{1,56} = 5.7$ ,  $P = 0.02$ ) and nearly significant among habitats ( $F_{2,56} = 4.0$ ,  $P = 0.06$ , Fig. 2c) with the greatest abundance occurring at the conifer-hardwood edge. There was no sig-

nificant interaction between owl activity and habitat ( $F_{2,56} = 0.3$ ,  $P = 0.76$ ). Allen's chipmunk abundance was not significantly different between site-use categories ( $F_{1,91} = 2.8$ ,  $P = 0.10$ ) nor among habitat types ( $F_{2,91} = 1.6$ ,  $P = 0.20$ ). However, there was a significant interaction effect ( $F_{2,91} = 3.7$ ,  $P = 0.03$ ). Multiple comparison tests indicated that the interaction occurred because chipmunks were more abundant within conifer-hardwood edge and pure conifer habitats and less abundant in conifer over hardwood habitats where owls foraged, whereas chipmunk abundance at randomly selected sites showed an opposite pattern (Fig. 2d).

#### OWL REPRODUCTION AND PREY ABUNDANCE

No prey species were significantly more abundant in foraging areas where young owls were produced ( $F_G$ ; Table 4). However, the power of this test to detect a biologically relevant difference was low, primarily because relative prey abundance varied greatly among owl foraging areas (Table 4). Of the three prey groups examined, dusky-footed woodrat abundance differed the most between owl reproductive groups. Although woodrats were nearly three times as abundant in foraging areas of owls that raised young, their abundance was quite variable (Table 4).

Relative abundance of all three species was significantly different among foraging areas of owls within the same reproductive class ( $F_S$ ; Table 4). This test indicated that the abundance of each small mammal species was significantly different among the owls' foraging areas. Multiple comparisons of the variation of prey abundance within foraging areas of owls with the same reproductive success indicated that the



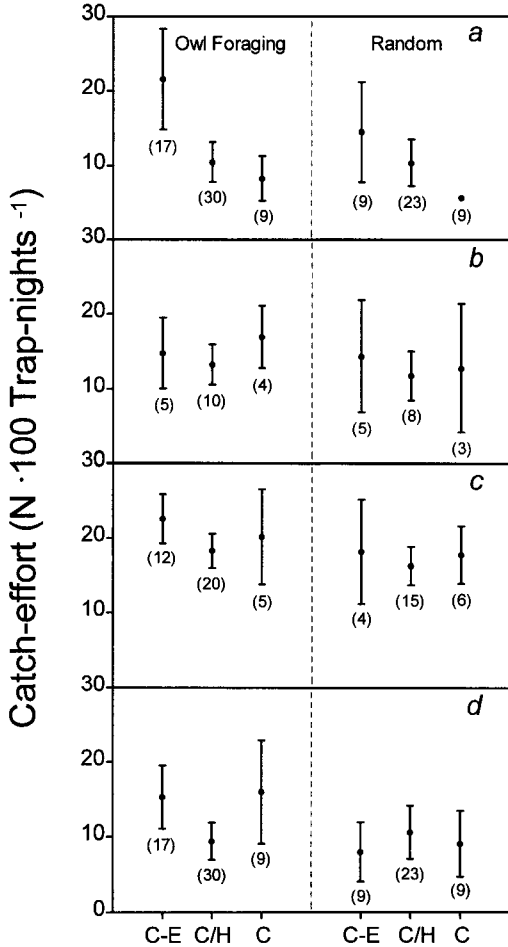


FIGURE 2. Relative abundance (transformed catch-effort  $\bar{x} \pm 95\%$  CI) of (a) *Neotoma fuscipes* (1987 and 1988), (b) *Peromyscus maniculatus*, *P. boylii*, and *P. truei* (1987), (c) *Peromyscus* spp. (1988), and (d) *Tamias senex* (1987 and 1988), stratified among foraging sites of male Northern Spotted Owls, randomly selected sites, and three habitat types (C-E = conifer-hardwood edge; C/H = conifer over hardwood understorey; C = conifer only). Numbers in parenthesis are number of sites examined.

variability of white-footed mouse abundance was more similar among foraging areas where young owls were not produced compared to the foraging areas of owls with young. In contrast, the variability of dusky-footed woodrat abundance was more similar among foraging areas where young were produced compared to foraging areas of owls without young. Variability in the abundance of Allen's chipmunks was equal. Although limited, this evidence suggests

that spatial variability of primary prey also may influence the owl's reproduction.

ENERGETIC CONTRIBUTION OF PREY

The estimated energetic cost to a male Spotted Owl providing food for itself, nesting mate, and one young during a 153-day period was 150,015 kJ (Table 5). This value was calculated using (1) an average mass of 580 g and 665 g for adult male and female Northern Spotted Owls, respectively (Blakesley et al. 1990), (2) an experimentally determined basal metabolic rate (BMR) for Mexican Spotted Owls (*S. o. lucida*) of 0.84 ccO<sub>2</sub> g<sup>-1</sup> hr<sup>-1</sup> (Ganey et al. 1994), (3) a conversion of 1.7BMR for daily maintenance costs (King 1973), (4) 252 kJ for egg production calculated using methods in Walsberg (1983), and (5) an allometric equation for calculating total metabolic cost of producing one fledgling (TME) from its mass (600 g) and growth time ( $t_n = 90$  days;  $TME = 6.65M^{0.852} t_n^{0.710}$ ; Weathers 1991). Given an average energy equivalent of 18.4 kJ g<sup>-1</sup> of prey (Graber 1962) and a 75% metabolic efficiency by the owl (Wijnandts 1984), production of one young would require the male to procure approximately 10,870 g of prey. Dividing this latter value by prey mass (Table 2) converts the owl's reproductive cost to 47 dusky-footed woodrats, 100 flying squirrels,

TABLE 4. Differences and variability in relative abundance (CPUE; N:100 trap-nights<sup>-1</sup>) of small mammals within and between foraging areas of reproductively successful and unsuccessful Northern Spotted Owls in northwestern California, 1987 and 1988.

Estimate <sup>a</sup> or Ratio	Species		
	<i>Peromyscus</i> spp.	<i>Neotoma fuscipes</i>	<i>Tamias senex</i>
$\bar{x}$ CPUE			
with young (n = 5)	9.4	11.6	6.3
no young (n = 7)	10.4	4.7	6.8
$F_G$ (df = 1, 10)	0.1	2.0	0.2
Power <sup>b</sup>	0.08	0.52	0.55
$F_S$ (df = 10, 45)	3.7 <sup>c</sup>	4.2 <sup>c</sup>	2.7 <sup>c</sup>
VC <sub>G</sub> (%)	0	8.6	0
VC <sub>S</sub> (%)	35.7	36.7	28.2
VC <sub>E</sub> (%)	64.3	54.7	71.8

<sup>a</sup> Where  $F$  =  $F$ -ratio, VC = variance component, df = degrees of freedom and subscripts G, S, and E signify between owl reproductive groups, between owl foraging areas within reproductive groups, and within owl foraging areas, respectively. Variance measures were generated using a Type I, nested ANOVA on transformed data; presented means are not transformed.

<sup>b</sup> Power to detect a difference in prey abundance corresponding to production of one owl young with transformed effect sizes being 1.8 mice, 1.6 woodrats, and 4.7 chipmunks 100-trap-nights<sup>-1</sup>.

<sup>c</sup> Significant at  $P \leq 0.05$  (one-tailed test).

TABLE 5. Predicted amounts of energy and late seral forest area required for production of one Northern Spotted Owl fledgling. Forest areas were predicted from energetic costs and prey density by assuming (1) that these owls only consumed dusky-footed woodrats with a capture probability ( $p_{cw}$ ) = 1.0, (2) the owl consumed multiple prey according to observed dietary proportions with  $p_{cw}$  = 1.0, and (3) the owl consumed multiple prey according to observed dietary proportions while the probability of capturing woodrats varied ( $p_{cw}$  = 0.1 to 0.9).

Measure <sup>a</sup>	Energetic cost (kJ) <sup>b</sup>					Late Seral Forest Area (ha) <sup>c</sup>				
	$M_{em}\delta$	$M_{em}\eta$	Egg	Fledgling	Total	Asmp. 1 (1.0)	Asmp. 2 (1.0)	Asmp. 3 (0.9) (0.5) (0.1)		
Mean	59,985	51,695	252	38,083	150,015	52	79	84	123	471
Upper 95%	59,985	51,695	252	224,300	336,232	117	178*	189*	275	1,055

<sup>a</sup> Estimated using model explained in text with mean coefficients for calculating TME of Weathers (1991) or the upper 95% confidence limit for coefficients of TME.

<sup>b</sup>  $M_{em}$  refers to maintenance metabolism.

<sup>c</sup> Calculated from total energetic cost using a metabolic efficiency of 13.8 kJ g<sup>-1</sup> of prey, average prey mass (g), and average prey density. Values in parenthesis are probabilities of woodrat capture by owls. Asterisks indicate values that fall within 95% confidence intervals of late seral forest areas used by owls in this study (133–264 ha) estimated from data in Zabel et al. (1995).

410 voles, 547 white-footed mice, or 2,021 insectivores. These values do not include foraging or other activity costs to the male beyond daily maintenance and hence are minimum approximations. Regardless, the calculations clearly show the advantage of larger prey, such as woodrats, to Northern Spotted Owls.

The amount of late seral forest predicted from the point estimate of energetic costs (150,015 kJ) was 79 ha. This predicted value was substantially lower than the average amount (198 ha) of late seral forest used by these owls. Recalculating total energetic costs by using the upper 95% confidence limit of TME (Weathers 1991) increased the value to 336,232 kJ, which converted to an area of 178 ha. The latter value fell within the 95% CI of amounts (133–264 ha) of late seral forests used by these owls (Table 5).

The predicted areas were based upon the unrealistic assumption that owls could capture every individual in a prey population (i.e., the probability that an owl captures a given prey [ $p_{ci}$ ] = 1.0). We explored the influence of the probability that owls capture woodrats ( $p_{cw}$ ) being < 1.0 by reducing dusky-footed woodrat density from 90% to 10% of its estimated average and recalculating the amount of late seral forest required using the point and upper estimates of the owl's energetic cost. Reducing  $p_{cw}$  increased the size of predicted areas (Table 5). Predicted values fell within the 95% CI of observed values when  $p_{cw}$  ranged from 0.20 to 0.45 and the point estimate of energetic cost was used. Predicted values also matched observed values when  $p_{cw}$  ranged from 0.53 to 1.00 and the upper estimate of energetic cost was used.

Given these assumptions about prey availability, energetic demand provided a feasible explanation for the amount of late seral forest used by these owls.

#### DISCUSSION

Our results support the hypothesis that Northern Spotted Owls select habitat according to the distribution of large prey. First, we showed that Northern Spotted Owls occurring in mixed-evergreen forests of northwestern California selected the dusky-footed woodrat over other prey species. Second, we found that these owls selected certain foraging sites where dusky-footed woodrats were more abundant. In general, these sites were found near the ecotone between late and early seral mixed-conifer forests. Third, these patterns of prey and site selection appeared to provide an energetic benefit to the owls. Collectively, these findings provided only a partial explanation for the owl's affinity for late seral forests.

Selection of large (> 100 g) prey by Spotted Owls occurring in California has long been suspected given the composition of their diet (Barrows 1987, Thraikill and Bias 1989, White 1996). However, our study provided the first formal quantification of prey selection by this owl species. We were not certain why Spotted Owls selected dusky-footed woodrats, but we suspected that energetic reward was an important factor. Assuming that mass specific energetic values were similar among these prey (Graber 1962), then larger prey would have provided greater energetic reward. We noted that the order of selection among the five prey categories corresponded to prey mass. This pattern may have reflected

optimal foraging whereby owls selected prey to maximize their energetic return (Stephens and Krebs 1986, Carey and Peeler 1995). However, we could not test predictions of optimal foraging theory for lack of additional information (e.g., prey encounter rates, handling times). Other owl species have been shown to select prey according to their size (Marti 1974, Kolter et al. 1988), behavioral characteristics (Longland and Jenkins 1987), sex, and coloration (see review by Mikola 1983).

Our tests for prey selection required accurate estimates of resource availability (Manly et al. 1993). We used prey abundance as a measure of prey availability. The consequences of this assumption on our tests of prey selection depended upon the accessibility of prey to owls and accuracy of our abundance estimates. In our tests for selection, it was assumed that all individuals of a prey population were accessible to capture by Northern Spotted Owls. This assumption would have produced a conservative test of prey selection (i.e., an underestimate of  $w_i$ ) if estimates of prey abundance were unbiased, because a reduction in prey accessibility would translate as a reduction in the availability proportion ( $\hat{\pi}_i$ ) and an inflated selection ratio. Underestimates of prey abundance would have produced overestimates of selection. Our estimates of dusky-footed woodrat density were nearly twice that reported for this forest type by Sakai and Noon (1993) and would have needed to increase 422% to produce insignificant results. However, our estimates of northern flying squirrel abundance were likely biased low because our sampling methods were less suitable for summer periods (Carey et al. 1991). Thus, we were confident in our inferences about woodrats but could not claim that flying squirrels were selected by these owls.

In northwestern California, Spotted Owls typically have selected late seral, mixed evergreen forests when foraging (Solis and Gutiérrez 1990). Our results showed that within this forest type, owls select foraging sites where prey were more abundant. Site selection by owls was most pronounced at the ecotone between late and early seral stages where dusky-footed woodrats were most abundant. Site selection associated with prey distribution was less consistent when examining abundance of white-footed mice (significance occurred in 1 of 2 years), and nonap-

parent when examining abundance of Allen's chipmunks. These results indicated that habitat selection by Spotted Owls at this scale was influenced significantly by prey choice.

Selection of conifer-hardwood edge sites by these owls may have reflected a compromise between finding an abundant versus an accessible supply of dusky-footed woodrats. Early (15 to 40 yr) seral stages of mixed evergreen forest were comprised of brush and sapling hardwoods that created a dense understory around sapling to pole-sized conifers or mature hardwoods where dusky-footed woodrats often attained densities up to 80 ha<sup>-1</sup> (Sakai and Noon 1993). Although dense understory cover in these young forests minimized the owl's ability to capture woodrats, individual woodrats that moved either vertically in young forests or laterally into late seral forests (Sakai and Noon 1997) would become more accessible.

We examined two potential benefits of prey and site selection to Northern Spotted Owls and found conflicting results. The owl's reproductive success did not differ according to diet or patterns of site use despite the clear energetic benefit of preferentially selecting woodrats from within late seral forests. There were several possible reasons for these findings. First, our analysis of dietary frequencies was limited to proportions. Owls raising young could have taken more prey than owls without young while proportions in the diet were equal. Second, meaningful differences in prey abundance between foraging sites of owls with young and owls without young may not have been detected because CPUE was not adequate for measuring large changes in prey density, or because of high variation in prey abundance among foraging ranges. CPUE was weakly to moderately correlated with estimates of prey density (Ward 1990) and large variances limited our ability (statistical power) to detect a meaningful difference if it existed. However, of the three rodent species examined, differences in the abundance of dusky-footed woodrats explained more variation in owl reproductive success. The moderate to large variation in woodrat abundance could be caused by microhabitat heterogeneity, which has been documented for several rodents occurring in late seral forests (Doyle 1990, Carey et al. 1992) or by predatory depletion (Carey et al. 1992, Carey and Peeler 1995). Third, the magnitude of the observed differences in prey abundance between

sites used by breeding and nonbreeding owls also could have been reduced by depletion. The difference in prey abundance would have been reduced if owls with young took more woodrats from the examined sites than owls without young prior to our sampling. Depletion of northern flying squirrels by Northern Spotted Owls has been reported for a few areas in southwestern Oregon (Carey et al. 1992), but was not considered as likely when these owls occurred in mixed-conifer forests that provided a more diverse prey base (Carey and Peeler 1995). We did not consider prey depletion as a primary influence on our results because the owls' foraging activity appeared dispersed rather than concentrated prior to and during our sampling of prey populations. It is more likely that use of relative measures limited our ability to detect meaningful differences in prey abundance.

Our energetic calculations showed that the selection of dusky-footed woodrats provided an indirect benefit to Spotted Owl fitness by reducing the amount of late seral forest required to reproduce successfully. Owls could have reduced their area requirements further by selecting conifer-hardwood edge sites where dusky-footed woodrats were more abundant. Zabel et al. (1995) found that the breeding season home ranges of these owls were smaller when dusky-footed woodrats were more abundant, and that these areas were not correlated with amounts of late seral forest as reported elsewhere (Forsman et al. 1984, Carey et al. 1990). For example, Spotted Owls that occurred in Oregon and consumed primarily northern flying squirrels traversed more area to maintain a relatively fixed amount of late seral forest as fragmentation increased (Carey et al. 1992). Because they consumed primarily dusky-footed woodrats, Spotted Owls in the mixed evergreen forests of northwestern California had two options for meeting their energetic requirements: (1) use greater amounts of late seral forest or (2) locate and use prey-rich, edge sites. Behavioral shifts to using edge sites may well explain the lack of correlation between home range size and late seral forest area for owls occurring in this study area.

Selection of late seral edge sites implies that some degree of fragmentation may provide an energetic benefit to Northern Spotted Owls occurring in areas where young forests produce an abundance of primary prey. However, loss of late seral forest around nest and roost sites is

correlated with lower reproduction and survival (Bart 1995, Raphael et al. 1996). Although the mechanisms responsible for these correlations have not been demonstrated experimentally, we suspect it is because Northern Spotted Owls require habitat structures associated with late seral forest for other biological activities like roosting and nesting (Gutiérrez 1985, Blakesley et al. 1992, Buchanan et al. 1995). We therefore urge a cautious approach to conservation strategies that deliberately reduce late seral forest in favor of creating young-late seral forest edges because (1) the Northern Spotted Owl population in this region has shown a slow rate of decline (Franklin et al. 1996), (2) we have not shown a direct improvement of fitness to Spotted Owls that select edge sites, (3) the optimal ratio between young forest edge and remaining late seral forest has not been determined, and (4) other factors like weather or the distribution of prey during late winter-early spring periods that may play a greater role in the owl's persistence have not been examined. We encourage additional research of these topics to determine the amounts and spatial distribution of forest types and stages that will provide optimal conditions for the Spotted Owl in a managed landscape.

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