SPOTTED OWLS: RESOURCE AND SPACE USE IN MOSAIC LANDSCAPES

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ABSTRACT.—Home ranges of 14 pairs of spotted owls (*Strix occidentalis*) were studied over four to six seasons in three southwest Oregon landscapes that differed in prey base and degree of forest fragmentation. The general theory of space use and the biology of spotted owls was used to construct a scheme for spatiotemporal analyses that provided insights beyond those possible with polygon home-range methods. Landscape units, precisely defined by habitat type and aspect, were classified as not used, used ≤expected based on area, and used > expected (selected). Selected units were categorized further by consistency of use: frequent, intermittent, and sporadic. Ratios of use categories and costs of use based on distances to units from activity centers revealed that spotted owls adopted different tactics depending on prey base and degree and type of fragmentation. Strategies were in accordance with predictions for central-place foragers exploiting patchy environments. Owls generally concentrated their foraging in old forests, but selectively used particular young forest units, especially when dusky-footed woodrats (*Neotoma fuscipes*) were present. Costs of fragmentation were high, equivalent to the zoogeographic gain of adding the dusky-footed woodrat to the prey base. Selective use of young forests suggests that manipulation of young forests to provide habitat for prey and foraging by the owl would be of value in conservation efforts in this region.

KEY WORDS: *home range; optimal foraging; Oregon; space use; spotted owl;* Strix occidentalis.

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Strix occidentalis: recursos y uso espacial en un mosaico de paisajes

RESUMEN.—Se estudiaron los rangos de hogar de 14 parejas de la especie *Strix occidentalis,* durante cuatro a seis estaciones en tres paisajes del suroeste de Oregon, que diferían en la base de presas y el grado de fragmentación del bosque. La teoría general de uso del espacio y la biología de *S. occidentalis* fueron usadas para construir un esquema para análisis espacio-temporal que entregara claridad hasta donde fuese posible con métodos de polígonos para ámbito de hogar. Unidades de paisaje, definidos precisamente por tipos de hábitat y aspecto, fueron clasificadas como no usadas, usadas < esperadas basadas en área y usadas > esperadas (seleccionadas). Unidades seleccionadas fueron categorizadas además por consistencia de uso: frecuencia, intermitencia y esporadicidad. Razones de categorías de uso y costo de uso basados en la distancia a unidades de centro de actividad revelaron que *S. occidentalis* adoptó diferentes tácticas dependiendo de la base de presas y del grado y tipo de fragmentación. Las estrategias estuvieron en concordancia con las predicciones para consumidores de sitio central, explotando ambientes parchosos. Los búhos generalmente se concentraron en bosques viejos para consumir, pero selectivamente usaron unidades de bosques jovenes, especialmente cuando *Neotoma fuscipes* estaba presente. Los costos de fragmentatión fueron altos. Uso selectivo de bosques jovenes sugiere que la manipulación de ellos para proveer habitat para presa y consumo por el búho, podría ser de valor en esfuerzos de conservación en esta región.

[Traducción de Ivan Lazo]

Spotted owls (*Strix occidentalis*) have been the focus of intensive research and conservation efforts because of the large amounts of old forest they require (Thomas et al. 1990). Because of this intensive examination, spotted owls provide an important case history for raptor conservation efforts.

Sizes of home ranges, amounts of old forest, and habitat types used by spotted owls have been studied with radiotelemetry. Analyses generally have been based on minimum convex polygon (MCP) and modified minimum convex polygon(MMCP) delimited annual some-times seasonal) ranges (Forsman et al. 984, Carey et al. 1990, 1992, Thomas et al. 1990). But polygons have major shortcomings as measures of the

distribution of an animal's activity in space, including use of resources (Waser and Wiley 1979) because they obscure much of the information available from radiotelemetry. Apportionment of 1 activity in space and time often is ignored with potentially misleading results about resources use.

Many methods exist for examining space use by animals (Waser and Wiley 1979, Loehle 1990, Harvey and Portier 1991). None provide or use explicit criteria by which both spatial and temporal limits of home ranges may be determined (Cooper 1978). Polygon and utilization-distribution methods rarely address use of space over time. These methods and the grid-cell summation method do not address well the use of discrete landscape units that are variable in size, but still small relative to home range and varied in type and arrangement (MacDonald et al. 1980, Ford 1983, Carey et al. 1989, Loehle 1990). Currently available methods do not lend themselves readily to examining questions such as: (1) Is a 50% increase in home range size among years stochastic or deterministic? (2) Does the temporal pattern of foraging site selection support hypotheses of avoiding prey depletion (not depleting prey near nest groves and avoiding areas where prey have been depleted)? (3) Does selection of landscape units over space and time differ from habitat-type selection at the home range and landscape level?

Carey et al. (1992) stated that before they addressed questions about use of resources and space, they would have to redefine their landscape units to reflect natural topographic boundaries as well as habitat type. In this paper, we present a reanalysis of Carey et al.'s (1992) landscapes and telemetry data. We examine space use over time by spotted owls to address questions about increasing range size, costs of forest fragmentation, avoidance of prey depletion, and selection of landscape units as opposed to habitat types. We address these questions under the hypothesis posed by Carey (1985, 1995a) and Carey et al. (1992) that many aspects of the spotted owl's biology are influenced by patterns of abundance, diversity, and total biomass of medium-sized, mammalian prey. A new approach to examining space use, based on natural landscape units and cat-egorization of units by use, is presented herein.

SPOTTED OWLS AND SPACE-USE THEORY

Understanding and interpreting use of home must be conditioned on an understanding of (1) the social behavior of the spotted owl, (2) the dispersion of its prey over space and time, (3) apportionment of

space at the landscape level, (4) insights into use of resources at the home-range level, and (5) foraging theory. Forsman et al. (1984) and Gutierrez (1985) summarized the owl's life history. Carey (1985) formulated six hypotheses about why spotted owls might use large amounts of old forest; two of them dealt with prey—abundance and availability. Forsman et al (1991), Carey et al. (1992), and Carey (1993) described (the prey of the spotted owl in southwestern Oregon. Carey (1989, 1991, 1995a,b), Carey et al. (1992), and Carey and Johnson (1995) described the natural history and the patterns of abundance of the owl's prey in southwestern Oregon. Carey et al. (1990, 1992) also examined the influence of landscape pattern and prey base on spacing and sizes of home ranges of spotted owls, and Carey et al. (1989, 1990, 1992) examined foraging activity and use of home ranges by spotted owls. We summarized information from these authors to make assumptions about the spotted owl and its prey in our study areas that were relevant to theories about space use (Brown and Orians 1970, Orians and Pearson 1979, Waser and Wiley 1979). Then we constructed measures of and pre-dictions about space use at the home-range level, building on those presented by Waser and Wiley (1979; proximate and ultimate controls of spacing) and Ford (1983; optimal foraging in patchy environments). Summaries of these efforts are presented here.

ASSUMPTIONS BASED ON EMPIRICAL DATA

Social Behavior. The pair was the primary social unit of the spotted owls in the study areas. Spotted owl had fidelity to nest sites which were the source of a cohesion or central base for the pair. While breeding and rearing young, females were sedentary and males returned to the nest to bring food to the female and young. Spacing between members of a pair increased after courtship if no young were produced and after fledging when young were produced. Spacing among pairs was achieved primarily by spacing signals (long-distance signals that elicit avoidance), as opposed to agonistic interactions.

Prey. Spotted owls selected medium-sized prey (100-400 g, the largest the owl can handle), as would be expected of central-place foragers exploiting a dispersed resource. Nest sites were the sources of cohesion or central bases (Waser and Wiley 1979) and pairs appeared to act as central-place foragers (Brown and Orians 1970, Orians and Pearson 1979, Ford 1983) on a weekly basis (Carey et al.

1989). Maximizing expected energy delivery rate on a round-trip basis requires prey size to increase with distance from the central place to the foraging patch (Orians and Pearson 1979). Medium-sized prey in the Douglas-fir forests of southwestern Oregon were northern flying squirrels (*Glaucomys sabrinus*) and bushy-tailed woodrats (*Netoma cinerea*). Flying squirrels were consistently present in both Douglas-fir and mixed-conifer closed-canopy forests. Closed-canopy forests were mostly old (with multi-layered canopies and developed understories, large coarse woody debris, a cohort of live trees >200 yr old and > 100 cm diameter at breast height (dbh), and a second cohort 80-200 yr old that could predominate) or young (even-aged, stem-exclusion stage forest with one cohort of trees 40-80 yr old with dominant trees 11-50 cm dbh). Mean density of flying squirrels in old forests was twice the mean (1 squirrel/ha larger) in young forest. Maximum densities in old forests were often three times maxima in young forests. Bushy-tailed woodrats varied markedly in abundance over time in Douglas-fir forests—they were absent as often as they were present; they were absent from young, upland Douglas-fir forests.

Flying squirrels, bushy-tailed woodrats, and dusky-footed woodrats (*Neotoma fuscipes*) were primary prey in mixed-conifer forests. Flying squirrels were more abundant in old mixed-conifer forests than in young, mixed-conifer forests. Occupancy of mixed-conifer old forests by bushy-tailed woodrats was less variable over time than in Douglas-fir old forests and, overall, bushy-tailed woodrats were five times more abundant in mixed-conifer old forests than in Douglas-fir forests. A major difference between the forest types, however, was the presence of the dusky-footed woodrat in the mixed-conifer forests. Dusky-footed woodrats were consistently abundant in mixed-conifer old forests, but they were often absent from patches of young forest. Nevertheless, dusky-footed woodrats were typically two to three times more abundant in young, stem-exclusion stage, mixed-conifer forests and streamside forests than in upland old forests.

In summary, prey abundance was more consistent and greater in old forests than in young forests. Biomass of medium-sized prey in mixed-conifer old forests was 1.6 times the biomass in Douglas-fir old forests. Numbers of northern flying squirrels could have been reduced by predation and local populations of bushy-tailed woodrats could have been extirpated by predation. We assumed that abundance of prey was equivalent to availability of prey (Carey 1985, 1995a).

Use of Landscapes. Pairs selected home ranges in areas where old forests were concentrated. Thus, at the landscape scale, home ranges were aggregated as predicted by the general theory of space use (Horn 1968, Waser and Wiley 1979). Old forest, with its consistently abundant prey, was the only preferred habitat type. Within aggregations, pairs maintained discrete, evenly dispersed home ranges as would be expected under the first principle of the general theory of space use when the availability of resources does not vary appreciably in space or time within the foraging range of a pair of owls. But, in one landscape where old forest was fragmented and well-dispersed (relative to the foraging ranges of spotted owls), significant overlap occurred among neighboring pairs of owls.

Home Ranges. Patterns of prey abundance affected spacing below the landscape level. Spacing between members of pairs varied seasonally (increased after breeding activity). In the unfragmented, mixed-conifer landscape with multiple species of prey and high prey biomass, overlap of annual MCP ranges of pair members was high (75%)—activity was aggregated. In the unfragmented, Douglas-fir landscape with moderate prey biomass, overlap between pair members was moderate (47-54%). In the fragmented, Douglas-fir landscape with the lowest prey biomass, overlap between pair members was low (28%). Pairs increasingly divided their home ranges with decreasing density of prey, just as local populations divided the areas of concentrated old growth in the landscape. But, at the landscape level, dispersion of pairs became more even as resources were more abundant and evenly distributed.

A habitat with sparse, evenly distributed food specifically favors overdispersed bases of operations, because regular spacing minimizes travel time from the base to locations with food. This spacing behavior operated at both the social unit and individual level. In areas of concentrated resources, pairs remained evenly dispersed, but members of the pair aggregated their activity. Foraging in patches can result in either exploitation depression (reduced abundance of flying squirrels in areas of moderate prey abundance) or behavioral depression (changed behavior of the prey that makes capturing them more difficult). In areas of low prey density (where prey depletion was most likely), pair members maintained dispersed fields of activity. When home ranges became too large, spacing among social units based on long-distance contact calls broke down.

Spacing behavior takes time and energy and involves some risk of injury or exposure to predation

(Waser and Wiley 1979). Home range or activity space is an important, predictable aspect of an animal's feeding strategy related to food density, metabolic needs, and efficiency of movement (Schoener 1981). The question is: how do we best characterize the home range-activity field? Optimal foraging theory provides some useful criteria.

Foraging Behavior. Ford (1983) found that most models of resource use made simplifying assumptions about the shape of home ranges, the shape of decay functions for intensity of use, and distribution of resources. Particularly important is the assumption of homogeneously distributed resources because use of space depends so strongly on resource distribution (see Covich 1976, for examples). More realistic models incorporate more realistic assumptions: (1) higher vertebrates are capable of remembering the locations of resource-rich patches, (2) the rate at which an animal can assimilate food while feeding in a patch is proportional to the density of food in the patch, (3) different patches have different histories of use so that food density (patch quality) varies at any point in time, and (4) if use depletes resources, renewal rates for the resource play an important role in shaping foraging behavior (Ford 1983). These assumptions probably are reasonable for spotted owls, and we adopted them.

Adult owls moved 1.0-1.5 km to foraging sites and usually foraged apart from one another. Maximum distances across pair annual MCP ranges averaged 35 km. All parts of a home range were visited frequently enough that a pair should have been able to monitor changing resource abundance across its range. Spotted owls are sit-and-wait predators and moved 0-500 m/hr (averaging <300 m/hr) while foraging. Movement in one night averaged 500 m and an owl tended to forage in the same 20-ha patch for one to three nights. Owls roosted in foraging patches, nest stands, and other stands. We know relatively little about depletion and renewal rates for depleted prey populations. But, it appeared that after intensive predation pressure, one to three seasons were required for flying squirrel populations to recover; bushy-tailed woodrats showed similar periodicities in Douglas-fir old growth.

PREDICTIONS BASED ON SPACE-USE THEORY

Using theories about central-place foragers in patchy environments (endowed with perfect knowledge of the location and status of each patch)

and the assumptions we based on empirical data on the spotted owl and its prey, we made specific predictions on a seasonal (breeding versus nonbreeding) basis: (1) Both the size of the home range and a core activity area (Ford 1983) should decrease with increasing abundance of medium-sized prey; (a) range size in mixed-conifer forests be less than range size in Douglas-fir; and (b) range size in mixed-conifer old forest fragmented by young forests should be less than range size in forests fragmented by clearcuts. (2) Where there is a variety of medium-sized prey (and larger total biomass), less depletion (and faster recovery) for any one species is expected. Thus, ranges in Douglas-fir forests (with two primary prey species and greater potential for depletion) should show more evidence of intermittent use of foraging patches (landscape units), on a seasonal basis, than ranges in mixed-conifer forests. (3) Fragmentation of mixed-conifer old forest by clearcuts (which are avoided by spotted owls) should result in (a) lower prey density across the range, (b) larger home-range sizes, (c) greater predation pressure on foraging patches, and, consequently, (d) a greater intermittent use of foraging patches than in old forest fragmented by young forest that may support moderate densities of flying squirrels and high densities of dusky-footed woodrats. (4) Depletion of prey in patches requires finding new patches in which to forage. The proportion of the home range used in any one season, then, should be a function of the renewal rate for depleted prey populations (i.e., zero to two seasons). Taking one season as an intermediate value, about 0.50 would be expected for simple prey bases of one to two species. In this case, more than two seasons would be necessary to identify the majority of the home range. Because we have no information on depletion rates for dusky-footed woodrats or for northern flying squirrels and bushy-tailed woodrats in areas of complex prey bases, our only prediction was that the proportion of the home range used in any one season should be higher (but < 1.0) than for simple prey bases. (5) Activity should be concentrated in sub-regions of old forest and nearby young forest (a habitat type with lower, or less predictable, maximum prey densities) where prey densities are easily monitored. Although habitat-type selection reflects long-term predictability of prey abundance (overall means and maxima), landscape-unit selection should differ by reflecting knowledge of short-term abundance and spatial relationship to the preferred old forest: (a) where dusky-footed woodrats are

abundant, owls should preferentially use units of young forest near their core area (the region of greatest familiarity); (b) where flying squirrels are the primary prey, owls should use young forests from time to time (reflecting maxima in young forests > means in old forests), especially when old forests are limited in area and populations may be depleted. (6) Home-range shape should conform to the pattern of old forest as determined by forest fragmentation and to unusually high (much greater than average) concentrations of prey in young forests.

MCP and MMCP home ranges are not adequate for testing such predictions because (1) they contain unused areas and the amount of unused area within the home range seems primarily to be a consequence of forest fragmentation and not of the carrying capacity for prey of the preferred habitat type, (2) they do not consider spatial or temporal intensity of use, and (3) no core area is considered or defined. Thus, we attempted to develop methods and metrics that could be used to test our predictions.

STUDY AREA

We used three of the five landscapes described by Carey et al. (1992): (1) Douglas-fir, clumped old-growth forest north of Roseburg, Oregon (DFLUMP), (2) mixed-conifer, clumped old-growth forest (MCLUMP) south of Roseburg, and (3) mixed-coni-fer, fragmented old-growth forest (MCFRAG) south of Roseburg. We did not analyze the Douglas-fir, fragmented old-growth or the mixed-conifer fragmented old-growth forests north of Roseburg studied by Carey et al. (1992) because those areas were inhabited by fewer than three stable pairs of adult owls (Carey et al. 1992).

The DFLUMP was 37% old forest, 33% young forest, and 26% nonforest (clearcuts and farmland). The MCLUMP was 44% old, 43% young (with residual large live, standing dead, and fallen trees), and 12% nonforest; MCFRAG was 45% old, 21% young, and 32% nonforest. Although the old forest in all three landscapes was fragmented, the nature of fragmentation differed. In DFLUMP and MCLUMP the remaining old forest was clumped in distribution and spotted owls were able to establish ranges in areas with high percentages of old forest. Old forest comprised 73% of DFLUMP MMCP home ranges and 53% of MCLUMP MMCP home ranges. The MCFRAG was characterized by a checkerboard pattern of old and clearcut forests (reflecting federal and private owner-ships) with blocks of 259 ha creating a coarse-grained fragmentation. MMCP ranges (areas used) still

were 52% old forests, but owls had to traverse areas (MCP ranges) about three times greater than in the MCLUMP to use the old forest (Carey et al. 1992).

METHODS

Data Collection. The selection and description of sites, development and implementation of telemetry methodology, rationale for sampling schemes, and data sites, development and implementation of telemetry methodology, rationale for sampling schemes, and data collected were reported by Carey et al. (1989, 1990, 1992) and Guetterman et al. (1991). An optimal sampling scheme was used to obtain systematically the maximum number of independent telemetry locations, with five nighttime locations and one daytime location per owl for each 2-wk period. We attempted (and were largely successful) in obtaining two foraging locations, separated by one night, 1 wk and three foraging locations, separated by one night the next week. The number of relocations per pair per season was nearly equal. Accuracy of telemetry locations averaged 68 m (SE = 4); Carey et al. 1992). Because our data were independent, and our interest lay in the use of the home range by the social unit (pair), we did not extend our analysis to the finer scale of movement sequence and rate.

We studied mated pairs that were >3 yr old and that had successfully produced more than one young prior to our study. In this paper, we report on pairs that were radiotracked for at least four seasons (two seasons per year, breeding and nonbreeding). During our study some individual members of pairs died and were replaced by other individuals that form-ed pair bonds with the surviving mates. Reproduction in spotted owls is sporadic and during our study few owls fledged young; none fledged young in each year of study. It is possible that various stresses associated with being located, caught, and handled and carrying a radio hindered reproduction (Foster et al. 1992).

Redefinition of Landscape Units. Initial (Carey et al. 1992) delineation of landscape units was based on interpretation of 1:12000 aerial photographs and 1:15 840 orthophotographs. Units which varied in size and shape were assigned to one of eight stand con-ditions (clearcut, sapling, pole, young, mature, mixed-age, and old-growth coniferous forest and deciduous forest) based on interpretation of aerial photographs, U.S. Bureau of Land Management records, recon-naissance in the field, and measured vegetation plots (Carey et al. 1992). Where little timber harvest had occurred, large, contiguous areas of fire regenerated

Table 1. Distribution of landscape units by size class and mean unit size for the Douglas-fir, clumped (DFLUMP), mixed-conifer, clumped (MCLUMP), and mixed-conifer, fragmented (MCFRAG) old-growth landscapes near Roseburg, Oregon, 1988, before (B) and after (A) sub-division by aspect.

| Size Class (ha) | Landscape[a] | | | | | |
| | DFLUMP | | MCLUMP | | MCFRAG | |
	B	A	B	A	B	A
<10	110	548	23	135	178	946
10–20	90	350	28	97	183	614
20–40	84	257	18	66	113	298
40–100	71	103	19	33	98	142
>100	53	12	20	1	86	13
Total	408	1270	108	342	657	2013
Mean size	58	19	59	19	51	16

[a] Total area, ha: DFLUMP = 23 518; MCLUMP = 6413; MCFRAG = 33 198.

forest were delineated as single landscape units. Where timber harvest had occurred on a large scale in a short time, large, contiguous areas of second-growth forest were delineated as single landscape units. The three landscapes contained 108-657 units each (Table 1).

Examination of space use can be based on the frequency of use of landscape units or quadrats placed over a map of the landscape. Unit size, however, should be selected for biological reasons; for example, the approximate area that might be scanned for resources by the organism of interest. Alternatively, the unit could match the size of resources patches (Waser and Wiley 1979). To achieve a discrete set of more natural landscape units that would allow us to examine owl use of individual units, we developed new geographic information system (GIS) coverages with 4-ha resolution using six aspect classes differing 60° from one another. The six classes were chosen by a computerized GIS algorithm applied to the landscape data. Thus, our new coverage incorporated both stand condition (as assigned by Carey et al. 1992) and natural discon-tinuities in topography. We examined the resulting distribution of units by size class and found that most units were of the same scale as the nightly foraging move-ments of spotted owls reported by Carey et al. (1989).

Defining Use of Landscape Units. Because behavior varied seasonally, we used seasons (breeding, 1 March to 31 August; nonbreeding, 1 September to 28 February; Carey et al. 1992) as temporal units. Use of landscape units was determined by season by overlaying telemetry locations of pairs of spotted owls on the new landscape coverages. A unit was considered to be selected by a pair in a given season if its relative use (proportion of total relocations) exceeded its availability (unit area divided by MMCP area). We used the MMCP area as the denominator because the MMCP contained relatively little unused area (Carey et al. 1989). Then we examined patterns of use across more than four seasons. We categorized each unit into one of four types: used but not selected; selected spor-adically—in only one season or separated by four seasons; selected intermittently-used at least one seas-on, but <75% of seasons; selected frequently—≥75% of seasons studied. Selected frequently entailed constant to almost constant use; hereinafter, we refer to these areas as constant-use areas. We then produced seasonal maps of usage and examined the maps for consistencies in patterns.

Characterization of Home Ranges. We calculated total area of home ranges by summing the areas of landscape units that were used (A_{TU}) and also summed areas of landscape units selected for use (A_{TS}). We did not include landscape units that were not used even if they were surrounded by or in the path to units that were used because spotted owls are capable of flying over these areas quickly and we did not believe that use of "air space" involved use of unit space. Owls, however, could select travel corridors (R. Gutiérrez pers. comm.), thus our method may be conservative. These new home-range areas differ from the area encom-passed by MCP or MMCP home ranges. Whereas polygon estimates are overestimates of area actually used (because they incorporate unused areas), sum-mation estimates may be underestimates of area actu-ally used (because we only sampled use). If too few nonindependent or variable numbers of relocations are taken, all these indices could be error-laden because of differences in effective sample sizes. Area-used (A_{TU}) and area-selected (A_{TS}) are refined analogs of MCP (area-traversed) and MMCP (area-used) and, as such, are measures of response to both landscape character and prevailing prey base (Carey et al. 1992).

Analysis of Home Range Structure. To further examine the character of the home ranges, we asked how are the home ranges structured on average? We postulated that the structure of home ranges could be dequately described by: (1) the apportionment of home range areas into use categories (selected constantly, selected intermittently, selected sporadically, or used but not selected), (2) the relative (proportional) allocation of area to use categories—expressed as the percentage of the range in each category, (3) the proportional allocation of time or activity to each category—expressed as the percentage of radiotelemetry locations,) the incorporation of the preferred habitat type (old forest, Carey et al. 1992)

Seasonal use pattern

Constant   Sporadic

Intermittent   Used but not selected
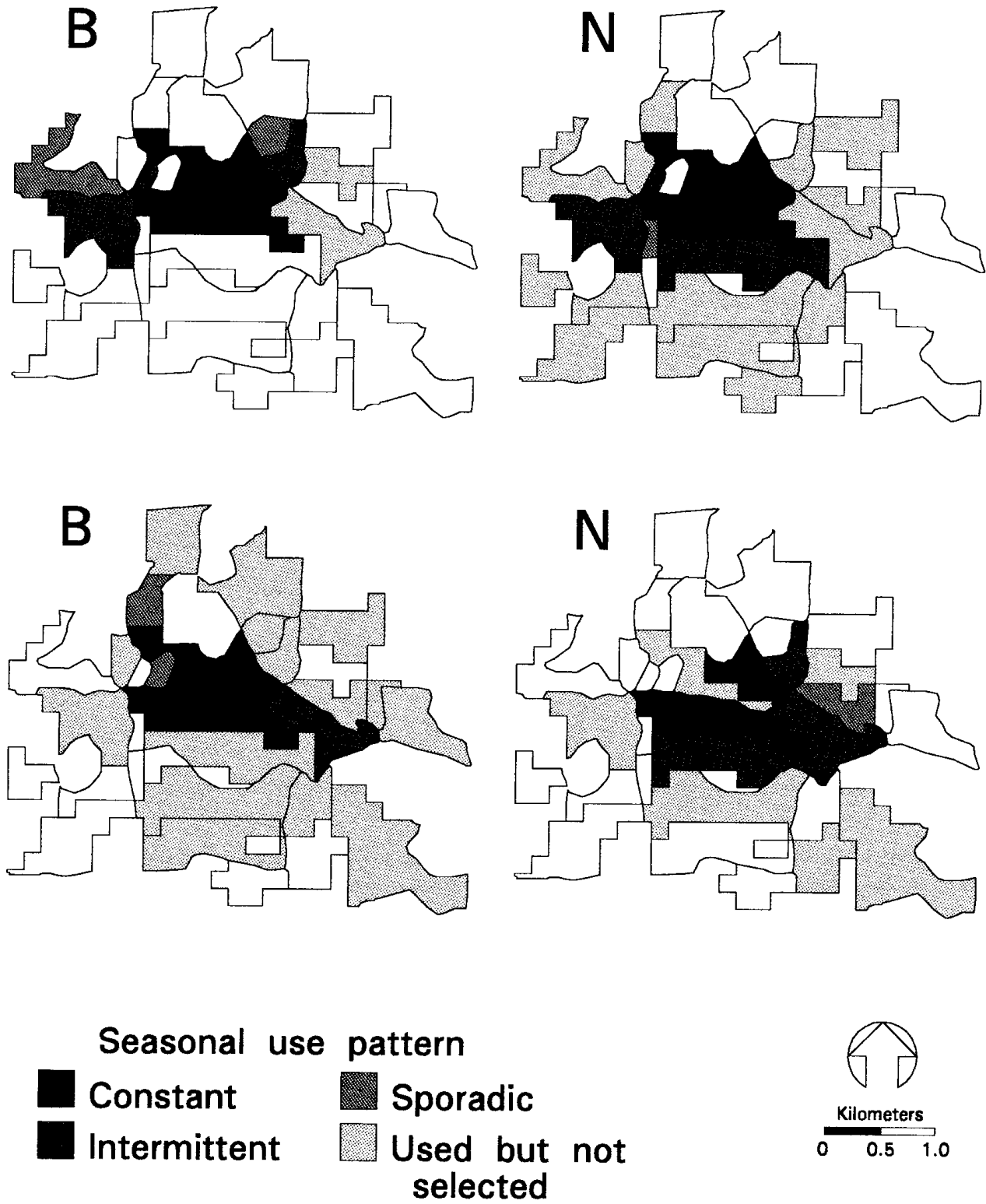
Kilometers
0   0.5   1.0

Figure 1. Representative spatiotemporal use of a home range by a pair of spotted owls by breeding and nonbreeding seasons in a mixed-conifer, clumped old-forest landscape in southwest Oregon.
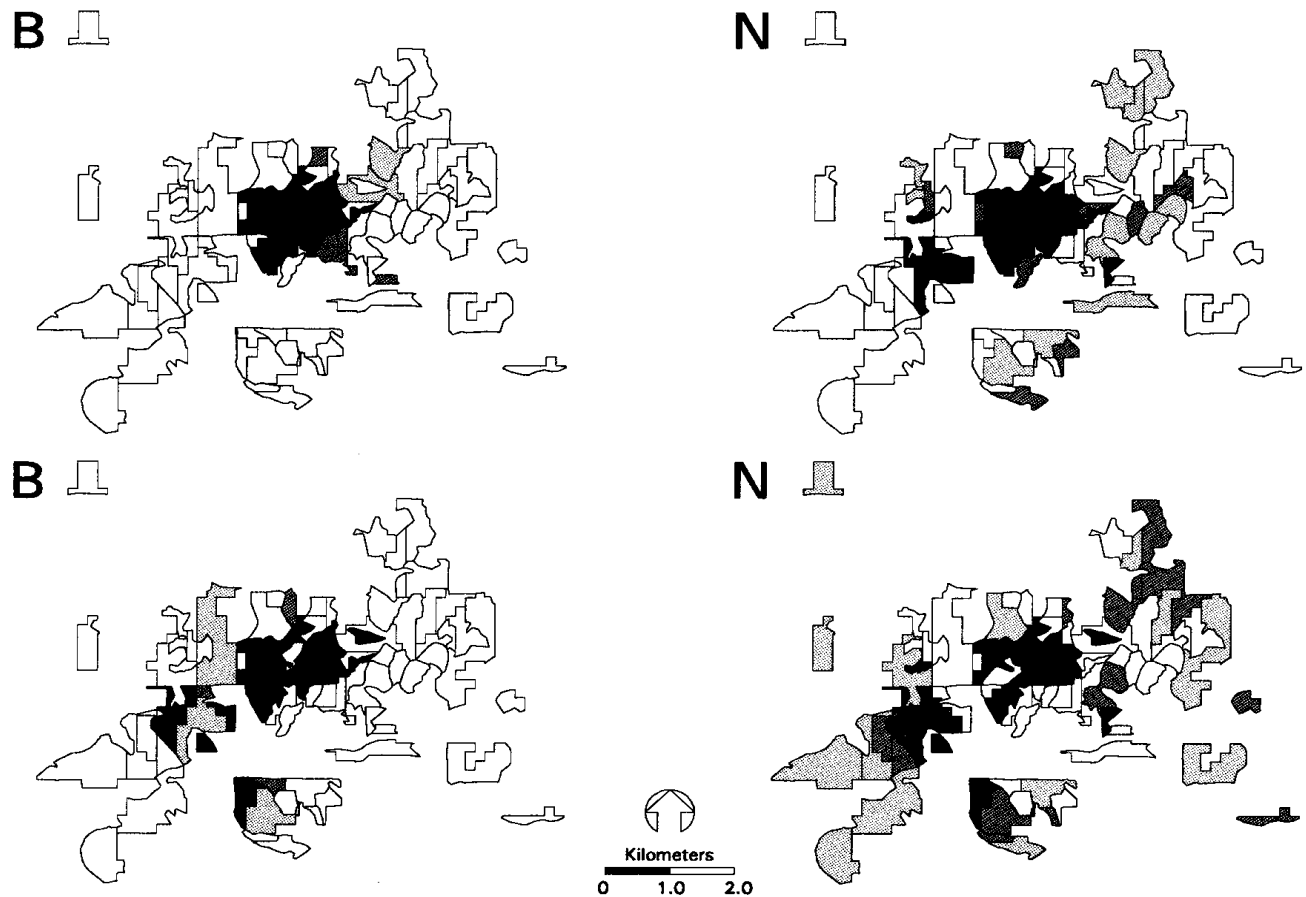
Figure 2. Representative spatiotemporal use of a home range by a pair of spotted owls by breeding and nonbreeding seasons in a mixed-conifer, fragmented old-forest landscape in southwest Oregon. See Fig. 1 for legend.

in each category—the percentage of each that was old forest, and (5) the travel cost of (mean distance to) accessing each category. The cost measure is essential to the interpretation of results because proportional measures of structure could be equivalent but represent markedly different costs. We compared because proportional measures of structure could be equivalent but represent markedly different costs. We compared home range structure (space use) among the three landscapes using summary statistics. Both structure and temporal variation in structure are displayed graphically. Here, we present sample figures for pairs most closely approximating the average values for each landscape (Figs. 1-4). One pair's range spanned two landscape types (DFLUMP and its transition to a mixed-conifer, fragmented old-growth type), and we displayed its range separately.

Ford (1983) analyzed structure by calculating utilization distributions and defining a core area based on utilization-the area that contained 65% of use ($A_{0.65}$). He used the ratio of the core area to the area containing 95% of use ($A_{0.65}/A_{0.95}$) as a measure of the tendency to concentrate use. He used the ratio of the 95% area for a foraging bout to the total area for all bouts ($A_{F0.95}/A_{T0.95}$)

variation reflecting renewal rates. The use of arbitrarily chosen percentiles to truncate utilization distributions began with Jennrich and Turner (1969), and soon became widely adopted (e.g., Ford and Krumme 1979, Schoener 1981). Although we agree with the concept of a core area, we do not agree that the best way to define the core area (or the extended range) is to use arbitrary percentiles or probabilities, especially in patchy environments. We choose to let the animal define its core area by intensity and consistency of use over time-landscape units frequently, almost constantly, used more than their proportional representation (A_C) relative to MMCP area. We define the remainder of the home range by seasonal use-intermittent or sporadically used landscape units still used more than their proportional representation (A_{I+S}). Use of units not selected was assigned to an uncertain status that would include the forays outside the normal range
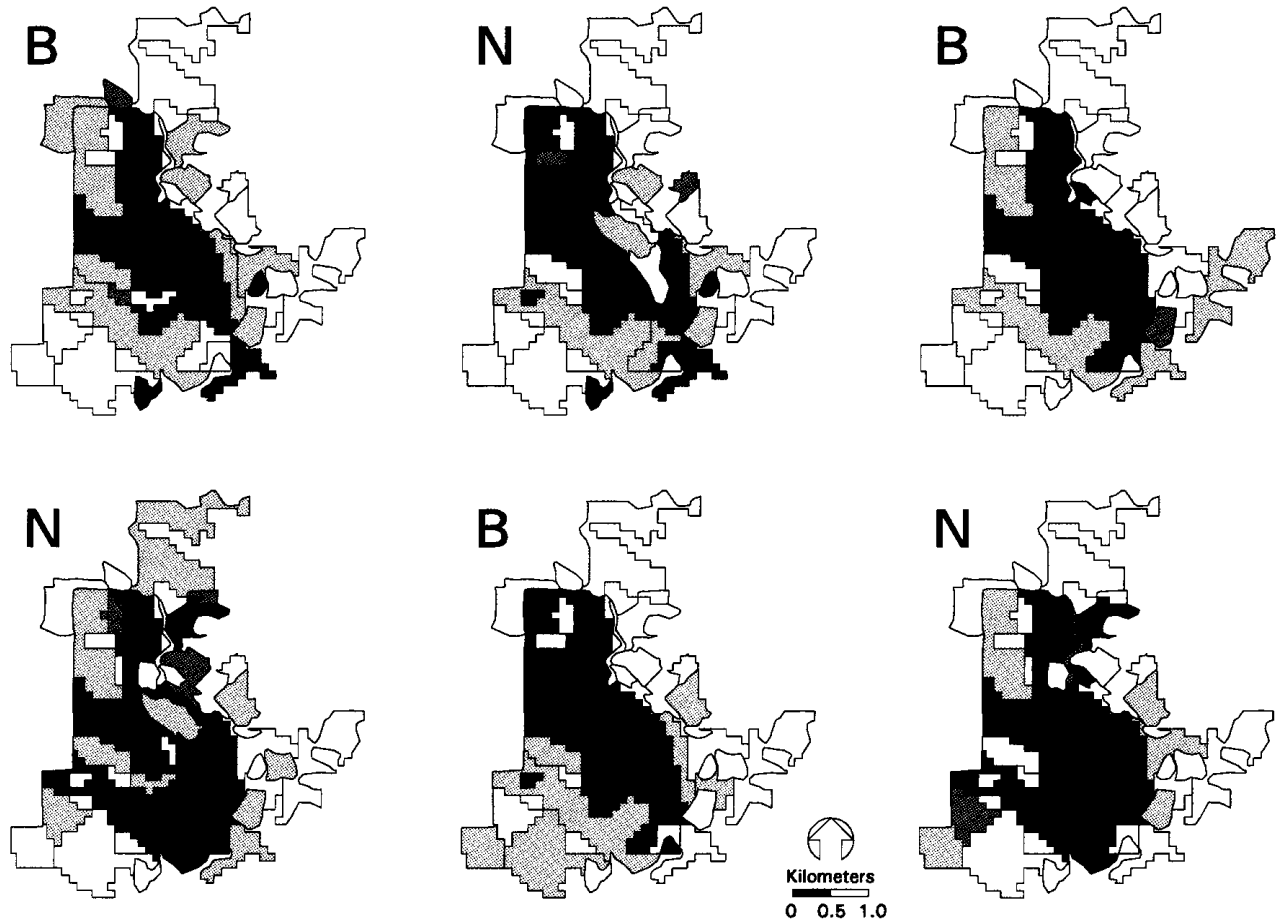
Figure 3. Representative spatiotemporal use of a home range by a pair of spotted owls by breeding and nonbreeding seasons in a Douglas-fir, clumped old-forest landscape in southwest Oregon. See Fig. 1 for legend.

(Burt 1943), and that represent natural tendencies for exploration, preparation for invasion of depopulated areas, spatial and social orientation (Stickel 1954), and monitoring prey abundance. Ratios of areas of constant use (core areas) to areas of intermittent use (A_C/A_I) or to intermittent and sporadic use (A_C/A_{I+S})can serve the same comparative function as ratios of arbitrarily defined areas ($A_{0.65}/A_{0.95}$), that is as a measure of the tendency to concentrate use (Ford 1983). We choose to use A_C / A_{I+S} instead of A_C/A_{C+I+S} because the former could also approximate the ratio of the area of high prey abundance and quick renewal to the area of easily depleted prey and low renewal; the latter seems to best represent the tendency to concentrate use when prey are uniformly abundant and renewal rates are fast. Similarly, mean area selected for use on a seasonal basis can be compared to cumulative total area selected for use (A_{SS}/A_{TS}) as a measure reflecting overall renewal rates, analagous to $A_{F0.95}/A_{T0.95}$ (Ford 1983). Landscape units, however, must be of the same spatial scale as foraging patches or calculated areas would have little meaning.

Analysis of Movements. Movements within a home range are influenced by breeding behavior (courtship, pair bonding, reproduction) and other social interactions (defense of nest groves, monitoring neighbors) that limit movements and by travel to peripheral hunting areas, foraging, and monitoring prey levels that require movement. Movements can incorporate an economic strategy to ensure efficient use and protection of resources. The more limited resources are, the more efficient must be the exploitation to achieve net benefits. The larger the area that must be traversed, the less effective is defense of resources. If individuals are constrained by pair-bonding, breeding, and parenting to returning regularly to a center of activity, then efficiency is necessarily compromised during the breeding season, when the female is
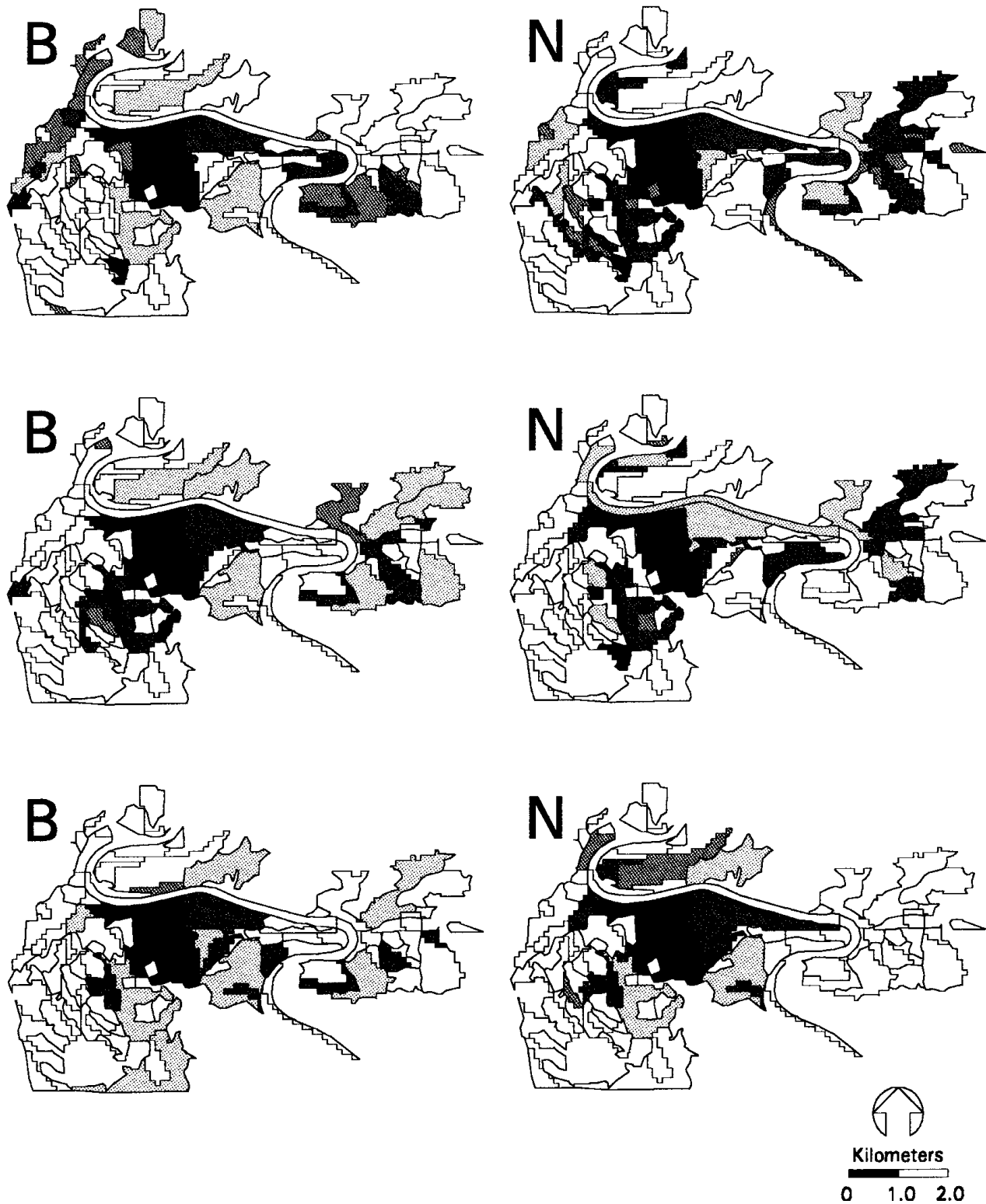
Figure 4. Spatiotemporal use of a home range by a pair of spotted owls by breeding and nonbreeding seasons in a Douglas-fir, clumped old-forest landscape with an eastward extension to a mixed-conifer zone forest with dense populations of bushytailed and dusky-footed woodrats. See Fig. 1 for legend.

Table 2. Sample sizes for analysis of spatiotemporal use of home ranges by spotted owls in the Douglas-fir, clumped (DFLUMP), mixed-conifer, clumped (MCLUMP), and mixed-conifer, fragmented (MCFRAG) landscapes near Roseburg, Oregon, 1987-89.

	NUMBERS OF			TOTAL RELOCA-TIONS
LANDSCAPE	PAIRS	SEASONS	RELOCATIONS[a]	
MCLUMP	3	4	332–438	1138
MCFRAG	7	4–5	363–533	3221
DFLUMP	4	5–6	304–756	2516

[a] Relocations per pair.

sedentary and the male must return to feed her and the young. However, few of our pairs bred successfully during the study period. Thus, the influence of raising young could not be addressed. Efficiency of movement can be reduced also by efforts to reduce risk of predation (R. Ford pers. comm.).

To examine individual movements as a strategy for efficient use of resources, we calculated the mean distance between subsequent independent foraging locations of individual birds (MDSL). The MDSL can be interpreted as the equivalent of the mean of the distribution of shortest distances between sites at which prey is simultaneously available (Waser and Wiley 1979), assuming availability as judged by the owl (i.e., based on knowledge of the home range) and that the owl is foraging optimally. Because, distances moved must, in part, reflect prey density and are not independent of home-range size, we calculated the mean distance from the center of activity in the constant-use (core) area to all locations of the pair in landscape units selected for use (MDCS) as a referent for MDSL. The MDCS was assumed to represent what MDSL would be if movements were systematic or random instead of economically deterministic. In other words, the MDCS would be a measure of the round-trip travel time (Orians and Pearson 1979) if the owls, as central-place foragers, returned to the central place after each foraging bout. They do not (Carey et al. 1989, 1992). Efficient exploitation of the prey base would entail MDSL less than MDCS and could represent the male and female partitioning their range. Efficient defense and monitoring of the prey base could be emphasized where prey density was high (and home ranges small) and would entail MDSL more than MDCS, but with costs (mean MDSL) less than costs where efficiency of exploitation was maximized.

Table 3. Mean areas used by pairs of spotted owls as determined by modified minimum convex polygons (MMCP), sums of areas of landscape units that were used (ATTJ), and sums of landscape units used more than would be expected based on their area relative to MMCP area (ATS) for the Douglas-fir, clumped (DFLUMP), mixed-conifer, clumped (MCLUMP), and mixed-conifer, fragmented (MCFRAG) old-growth landscapes near Roseburg, Oregon, 1987-89.

	AREA (ha)			
LANDSCAPE	MMCP MEAN (SE)	A_{TU} MEAN (SE)	A_{TS} MEAN (SE)	A_{TS} %M-MCP
MCLUMP	561 (79)	847 (69)	398 (64)	71
MCFRAG	1919 (311)	1453 (26)	788 (114)	41
DFLUMP	2727 (956)	1909 (369)	1251 (309)	46

RESULTS

Redefinition of Landscape Units. Redefinition of landscape units based on seral stage and aspect increased the number of units four- to five-fold for old-forest units and two- to three-fold for younger units. Mean unit size was reduced from 82-108 ha to 1921 ha for old forest and from 36-48 ha to 15-18 ha for younger forest. Mean landscape unit size decreased from 51-59 ha to 16-19 ha. Redefinition resulted in >67% of landscape units in each landscape being <20 ha (Table 1), effectively (in our opinion) ameliorating analytical problems associated with coarse environmental grain, but not affecting arrangement and composition of natural units as determined by aspect, forest fragmentation, and disturbance history.

Redefinition of Home Ranges. We analyzed 6875 telemetry locations of 14 pairs of owls in the three landscapes for four to six seasons (Table 2). Home range sizes (A_{TU} and A_{TS}) differed significantly among the landscapes with MCLUMP < MCFRAG < DFLUMP (Table 3; Fs = 4.6 and 4.1, respectively; Ps < 0.05). The 95% confidence interval for the mean for MCFRAG overlapped those of MCLUMP and DFLUMP. A_{TU} were 70-76% of the multi-season MMCP estimates in the DFLUMP and MCFRAG where ranges were large (and unused units were incorporated in the MMCP). In the MCLUMP, where ranges were small and habitat was concentrated, A_{TU} was 1.5 times the MMCP, reflecting the parts of landscape units outside MMCP boundaries. Areas preferentially selected (ATS) were only 41-46% of the MMCP in the DFLUMP and MCFRAG but 71% of the MMCP

Table 4. Structural attributes of home ranges of spotted owls in the mixed-conifer, clumped (MCL), mixed-conifer, clumped (MCL), mixed-conifer, fragmented (MCF), and Douglas-fir, clumped (DFL) landscapes near Roseburg, Oregon, 1987-89.

Use Category	% Home Range			% Use			% Old Forest			Mean Distance[a] (m)		
	MCL	MCF	DFL	MCL	MCF	DFL	MCL	MCF	DFL	MCL	MCF	DFL
Constant	20	18	18	66	59	60	57	92	97	477	639	702
Intermittent	14	10	23	15	20	26	61	81	77	838	1462	1664
Sporadic	13	25	22	9	15	8	34	51	63	905	2107	2171
Total sel.	46	53	64	90	94	94	51	70	75	579	1048	1093[b]

[a] Mean distance form center of constant-use telemetry locations to individual locations.
[b] Weighted (by % use) mean distance.

in the MCLUMP.

Home Range Structure. Despite marked differences in home range size, A_c averaged 18-20% of the home range and received 59-66% of use (Table 4; A_{TS} constituted 46-64% of the ranges and received 90- 94% of use. The coincidence of these percentiles with those suggested by Ford (1983) was fortuitous but suggested that the arbitrary percentiles may, in this case, have biological relevance. Compared to owls in the MCLUMP, owls in the DFLUMP and MCFRAG (1) maintained a greater proportion A_{TS} relative to A_{TU} and used the selected units more intensively, (2) maintained more of the A_{TU} in A_I and A_S, and (3) made proportionally greater use of old forest (75% and 70%, respectively, vs. 51 %). Compared to owls in the

Table 5. Relative structure of home ranges of spotted owls in mixed-conifer, clumped (MCLUMP), mixed-conifer, fragmented (MCFRAG), and Douglas-fir, clumped (DFLUMP) landscapes near Roseburg, Oregon, 1987-89; MCLUMP provides the baseline with values equal to 1.

Relative Measure[a]	Landscape		
	MCLUMP	MCFRAG	DFLUMP
Selected stands			
Total area	1	2.0	3.1
Area of old forest[b]	1	2.8	4.9
$A_C : A_{I+S}$	1	2.8	3.9
$A_C : A_I$	1	1.1	0.6
Effort expended	1	1.8	1.9

[a] A_C = constant-use area; A_{I+S} = intermittent-use area + sporadic-use area. Effort expended is the weighted mean distance between the center of activity in C and telemetry locations in C, I, and S.
[b] Mean total area of the old-forest landscape units that were used by spotted owls; MCLUMP = 197 ha; MCFRAG = 548 ha; DFLUMP = 961 ha.

DFLUMP maintained more of their ranges in intermittently-used stands and apportioned more use to these areas. Seasonal usage means, assumed to vary with renewal rates (A_{SS}/A_{TS} X 100), were 46 (SE = 2) and 46 (SE = 5) in the DFLUMP and MCFRAG, respectively, but 61 (SE = 0) in the MCLUMP. Second-year increases in A_{TS} were 20% in the DFLUMP, 18% in the MCLUMP, and 29% in the MCFRAG. Second-year increases in A_{TU} were 29-37%. Ranges in the DFLUMP expanded 10-11% in the third year.

Even though the MCFRAG old forests had greater prey biomass than the DFLUMP old forests, the effort expended in using home ranges was equal (Table 5). Fragmentation by early seral stages was accompanied by sporadic use of distant older units at a cost (Table 5) equivalent to the benefit of the addition of a major prey species (the dusky-footed woodrat) to the mixed-conifer forest.

Contrasts of home ranges and use of home ranges based on ratios improve clarity of the relationships (Table 5). DFLUMP owls used three times more area than MCLUMP owls and 1.5 times more area than MCFRAG owls. They selected five times the area of old forest and maintained four times more area in intermittently and sporadically used areas than MCLUMP owls. MCFRAG owls were intermediate in these values. Yet, distance traveled (energy expended) by MCFRAG and DFLUMP owls did not differ and was twice that of MCLUMP owls. The lack of difference between MCFRAG and DFLUMP owls appears to be due to a proportionately greater use of distant, sporadically used stands and distant stands, in proportion to their area, on the part of the MCFRAG owls.

Table 6. Mean (SE) distances (in meters) between subsequent, independent telemetry locations of individual spotted owls (SL) and mean distance from center of activity to all disproportionately selected landscape units (AC) in clumped, mixed-conifer old forest (MCLUMP), fragmented, mixed-conifer old forest (MCFRAG), and clumped, Douglas-fir old forest (DFLUMP) landscape, 1987-89.

LANDSCAPE		FEMALES		MALES	
		BR S[a]	NB S	BR S	NB S
MCLUMP	SL	621 (78)	742 (80)	657 (67)	681 (51)
	AC	550 (60)	638 (45)	550 (60)	638 (45)
MCFRAG	SL	925 (62[b])	1186 (69)	1003 (70)	1185 (65)
	AC	736 (70)	1198 (40)	736 (70)	1198 (40)
DFLUMP	SL	995 (84)	1206 (103)	1085 (52)	1161 (34)
	AC	1028 (102)	1343 (47)	1028 (102)	1313 (47)

[a] BR S = breeding season; NB S = nonbreeding season.
[b] Indicates significantly different pairs, SL versus AC ($P < 0.05$).

In summary, MCLUMP owls use smaller ranges and concentrated use in constant-use stands (Fig. 1), used less old forest and more mixed-age young forest (26% of core area) and young forest (16% of core area), and possibly expended 45% less effort in travel than DFLUMP and MCFRAG owls. Intermittent use was restricted to areas adjacent to core areas. MCFRAG owls maintained large ranges and apportioned use more equally among distant intermittently and sporadically used areas (Fig. 2) than owls in the less fragmented landscapes, and emphasized use of old forest stands. The marked fragmentation of old forest and the use of distant landscape units is apparent in Fig. 2. Owls in the DFLUMP maintained the largest ranges, made greatest use of intermittently used stands at intermediate distances (Fig. 3), and placed the greatest emphasis on old forest. There was heavy emphasis on intermittently used units (24% of the range) and large core areas in DFLUMP. Some owls, however, extended their range to take advantage of areas with high prey biomass (Fig. 4). This pair extended its range from the DFLUMP to nearby mixed-conifer forest. This eastward extension made use of exceptionally high numbers of bushy-tailed woodrats and dusky-footed woodrats in young forest along Bottle Creek (Carey et al. 1992). Even so, the range was characterized by heavy emphasis on intermittent use of landscape units.

Habitat Use. Old-forest units comprised a grea-ter percentage of selected units in the Douglas-fir forest than in mixed-conifer forests; 97% of Douglas-fir core units were old forests (Table 4). But the percentage of young-forest units increased with decreasing consistency of use, possibly repre-sentting low renewal rates for maximum densities in young forests. In the mixed-conifer landscape,

great emphasis was placed on old-forest units where young-forest units were rare (MCFRAG), but still there was a high proportion of young-forest units in sporadically used units. Where young-forest units were relatively abundant (MCLUMP), their percentages of core- and intermittent-use areas were similar to old-forest percentages and were higher than old-forest percentages in sporadically used areas. Non-forest, clear-cuts, and sapling units were ≤6% of the selected areas.

Movements. Males and females did not differ in MDSL; only one of 14 pairs had statistically significant differences (paired $t = 3.33$, $P = 0.03$) and in no landscape did mean male MDSL differ statistically from mean female MDSL (Table 6). Breeding season movements did not differ from nonbreeding season movements for males (paired $t = 0.38$, $P = 0.72$) or females (paired $t = 1.22$, $P = 0.28$) in the MCLUMP. All movements in the MCLUMP were substantially less than even breeding-season movements in the other two areas (Table 6). Both males and females moved less during the breeding season than during the nonbreeding season in the MCFRAG (females, 261 m less, paired $t = 2.74$, $P = 0.02$; males 224 m less, paired $t = 1.83$, $P = 0.09$). In the DFLUMP, females moved 19% less ($x = 218$ m, SE = 94, paired $t = 2.32$, $P = 0.04$) in the breeding season than in the nonbreeding season; MDSL of males did not differ (paired $t = 1.67$, $P = 0.13$). These male movements were the greatest of the three areas (Table 6). However, on average over pairs, breeding and nonbreeding season movements did not differ for males and females in the MCLUMP and DFLUMP. In the MCFRAG, females moved 260 m less ($t = 2.81$, $P = 0.04$).

The MDSL exceeded the MDCS in the MCLUMP, suggesting emphasis on monitoring and

defense. In the MCFRAG, the breeding season MD-SL > MDCS and the nonbreeding season MDSL = MDCS. In the DFLUMP, the nonbreeding season MDSL < MDCS, suggesting emphasis on optimal foraging. Males' breeding season MDSL > MDCS, and females' breeding season MDSL = MDCS. An interpretation of these data based on optimal foraging theory would be that MCLUMP owls were inefficiently exploiting the prey base (perhaps maximizing protection and monitoring), MCFRAG owls demonstrated restricted use in the breeding season, and DFLUMP owls exhibited efficient use in the nonbreeding season.

Dicussion

Examination of space use by animals in real-world (versus computer-simulated) environments is difficult and complex. Variability in the real world can be great and, with wide-ranging predators, hard to measure, As in any field study, our ability to measure anything biological is limited not only by logistical considerations, but also by unpredictable and uncontrollable events (for example, whether or not breeding will be successful and whether or not a patch of young forest will be colonized/ occupied by dusky-footed woodrats) including human events (timber harvests, accidents, and illness). Particularly lacking in our study are data that would allow contrasts of tactics used by owls while successfully rearing young with tactics used in nonbreeding years. Similarly, our study was not a prospective experimental test of formal hypotheses. Rather, it was a retrospective examination of how well theory, and hypotheses drawn from theory, could be supported by field data. Fitness in owls is a multistage process: (1) survival to reproductive age, (2) formation and maintenance of pair bonds and home ranges, (3) survival and maintenance of pair bonds and ranges in nonbreeding years, and (4) occasional successful reproduction that results in some young fledging, dispersing, maturing, and breeding. It may not ever be possible to measure everything necessary to completely model animal foraging behavior. Animals are faced with the same complexity and variability and it is unlikely that they can measure, integrate, and optimize all the pertinent information. Owls necessarily must respond to proximate factors such as habitat type and fragmentation with tactics (foraging site selection, spatiotemporal apportionment of effort) conditioned be learning (familiarity with the home range). Tactics can only be effective on average; achievement of true optimality would be unlikely.

Methodology. Our goal was to develop methodology (1) that would be more useful and more defensible in analyzing home range data than methods now being used, (2) that was based on well-developed theories of space use and optimal foraging, and (3) that could be used to interpret more heuristically the results of field studies. Our simple indexes, based on ratios, can be taken (but not proven) to represent both responses to ultimate factors (prey abundance) and tactics–responses to proximate factors conditioned by knowledge of an ultimate factor such as past history of prey abundance, exploitation of the prey base, and likelihood of current high prey levels. One potential impact of extreme forest fragmentation is that separation of members of pairs and increased overlap among adjacent home ranges (Carey et al. 1992) may contribute to uncertainty and inability to track resources. In the less fragmented environments analyzed here, A_{TS} represents the response to prey abundance. Area-of-old-forest represents habitat type selection based on landscape composition and relative abundances of prey in different habitat types. The seasonal proportion (A_{SS}/A_{TS}) can be interpreted as a response to renewal rates. Ratios of constant to intermittent use (A_C/A_I and A_C/A_{I+S}) can be used as measures of tactics of avoidance of prey depletion (or depleted prey) related to diversity and total biomass of prey. Annual increases in A_{TS} (18-29%) and A_{TU} (29-37%) were less than the 4043% increases in MMCP ranges reported by Carey et al. (1992). The increase in A_{TS} may reflect a strategy of avoidance of prey depletion and is a nonrandom change in foraging behavior; the difference between the increases in A_{TS} and A_{TU} could be considered random variation in foraging behavior. The difference between the increases in A_{TS} and MMCP reflect methodology, particularly the incorporation of apparently unused area by the polygon method. Ratios of landscape values (Table 5) allowed us to examine adaptations for space use in response to prey abundance, degree of fragmentation of the preferred habitat type, and type of fragmentation.

Analyses of intensity of use and movements allowed us to estimate relative costs of fragmentation and simplified prey bases. Examination of space-use patterns in the context of the theory of space use contributes to our understanding of why spotted owls do what they do–a major step beyond reporting empirical data. The existence of plausible explanations of empirical patterns lends confidence to conservation efforts that incur substantial societal costs.

Our redefinition of landscape units and characterization of ranges by unit use allowed us to take a closer look at foraging site selection. We were able to detect the selection and use of young forest not apparent using larger units and MCP estimates of home-range size and resource availability. The spatiotemporal analyses support the hypothesis that spotted owls in Douglas-fir forests with low-to-moderate prey abundance follow a strategy to avoid depletion of prey and areas in which prey has been depleted. Of course, this analysis would not have been possible without the empirical documentation of patterns of prey abundance across our study areas by Carey et al. (1992) and Carey (1995a,b). Thus, the expansion of home-range size (and amount of old forest used) between years most likely reflects a need for additional resources as opposed to random movement. Our closer examination of foraging activity further demonstrated the great impact of forest fragmentation on spotted owls—in our case, it was equivalent to losing a species of prey that occurs in relatively high density. But our analysis also showed that all fragmentation was not equal; fragmentation by early seral stages was clearly much more detrimental than by young forest. The impact of fragmentation varies with biotic region-in the Douglas-fir forests, where dusky-footed woodrats were not present, the impact of fragmentation by young, stem-exclusion stages would be less distinguishable from the impact by early, stand-initiation stages.

Our refined analysis also clarifies aspects of habitattype selection defined on the basis of use versus availability. In most studies (Thomas et al. 1990), the only habitat type selected by spotted owls was old forest. Young forests were used in proportion to their occurrence in the home range. Early seral stages were avoided. Changing the scale of examination did not affect our conclusions about the owls' preference for old forest. However, it did become apparent that use in proportion to occurrence can mask selection taking place over time and as a function of proximity to the preferred habitat type.

Some authors (e.g., Rosenberg and Anthony 1992, Zabel et al. 1993, Rosenberg et al. 1994), despite evidence of proportional use, have concluded that young forests do not have a structure suitable for foraging by the spotted owl. Carey (1995a) provided a counter argument to these claims. Carey et al. (1992) reported that spotted owls will forage in most habitat types, and that young forests in which spotted owls foraged and roosted had a structure similar to that in old forest. Carey (1995b) identified understory development and snag abundance as determinants of flying squirrel abundance in young

stands, albeit with thresholds beyond which no increase was seen. Simply, some young stands have more old-growth legacies than other stands, some develop faster than others, and some are colonized by potential prey faster than others (Carey 1995b). Here, we found the owls were capable of selecting from among the young stands and using some of them consistently and intensively. This conclusion offers support for habitat restoration efforts as part of a strategy for the recovery of the spotted owl.

Theoretical Predictions. The spotted owls we studied behaved as predicted by our combination of the general theory of space use and optimal foraging theory. Home-range size (A_{TS}) and core area (A_C) decreased with increasing abundance of medium-sized prey. Ranges in mixed-conifer forests (with diverse prey and high prey biomass) were less than ranges in Douglas-fir forests (with fewer prey and lower prey biomass). Ranges in mixed-conifer old forest fragmented by young forests (which still provide foraging habitat) were less than ranges fragmented by clearcuts (which are normally avoided by owls). Ranges in Douglas-fir forests contained more intermittently and sporadically used units than ranges in mixed-conifer forests, as would be expected if simple prey bases are more subject to depletion than complex prey bases. Fragmentation of mixed-conifer old forests by clearcuts was accompanied by increased intermittent use of landscape units as would be expected if discrete (bordered by clearcuts) patches were more subject to predation pressure and prey depletion than patches of high prey density in the context of patches with lower prey density. Seasonal usage of the home ranges (proportion used in any one season) decreased with prey density and with decreased postulated (assumed) renewal rates; we hypothesized a value of 0.50 for areas with prey bases simplified by few species or by fragmentation; our measured mean rates were 0.46 (SE = 0.2) and 0.46 (SE = 0.5), respectively, and not significantly different from 0.50. We hypothesized a proportion >0.50 and <1.0 for areas with complex prey bases and we measured a mean rate of 0.61 (SE = 0) that met both boundaries. We found activity was concentrated in old forest and nearby young forest where prey densities would be most easily monitored (MCLUMP); in the other areas, old forest was emphasized. As predicted, owls preferentially used units of young forest near their core areas when dusky-footed woodrats were present but only used young forests from time to time when flying squirrels were the primary prey. Finally, home ranges conformed to the pattern of old forest as determined by forest, fragmentation and were extended

to incorporate unusually high concentrations of prey in young forest. We conclude that the owls we studied were foraging optimally in accordance with the general theory of space use, and changing tactics to adapt to zoogeographically determined differences in prey bases and to anthropogenic changes in the landscapes. Adapting to anthropogenic changes was costly, and in MCFRAG perhaps only possible because of the addition of a species of medium-sized prey; in areas of simple prey bases, fragmentation may result in unstable populations (Carey et al. 1992).

ACKNOWLEDGMENTS

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