AN ABSTRACT OF THE THESIS OF

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Title: HABITAT UTILIZATION BY SPOTTED OWLS IN THE WEST-CENTRAL CASCADES OF OREGON

Abstract approved: E Charles Meslow

E. Charles Meslow

Eight adult spotted owls (*Strix occidentalis*) on the west slope of the Cascade Range in Oregon were fitted with radio transmitters and observed for periods ranging from 271 to 383 days. Mean home range size for the owls was 1,177 ha (range = 920-1,376 ha). There was no significant difference between home range size of males and females. On the average, home ranges of individuals occupying adjacent territories overlapped by 12 percent (range = 3-25 percent). Home ranges of paired individuals overlapped by 50 to 73 percent. The size and shape of home ranges varied on a seasonal basis; generally, the largest home ranges were observed during winter. Nest sites were centrally located within the home ranges utilized by the owls.

On the radiotelemetry study area, the mean nearest neighbor distance between nests of adjacent pairs was 2.88 km. On 11 other areas in western Oregon where suitable habitat was available, mean nearest neighbor distances ranged from 1.68 to 3.04 km. The overall mean nearest neighbor distance for the 12 areas was 2.42 km.

Home ranges occupied by the radio tagged owls were so large that consistent defense of the entire home range was impossible. Territorial defense appeared to take the form of a decreasing zone of influence centered around the nest; areas near each nest were defended consistently, but defense became increasingly inconsistent with distance from the nest. Discrete territorial boundaries could not be determined and probably did not exist.

Territorial interactions between individuals of the same sex were much more aggressive than interactions between individuals of opposite sex. Spotted owls may have responded less aggressively toward individuals of the opposite sex because the advantage of allowing potential mate replacements to remain within the territory outweighed other considerations.

Except for a few instances in which 2 of the owls foraged in recently clear-cut areas or in rock talus, virtually all foraging occurred in forests over 30 years old. Old-growth forests, which covered 36 to 64 percent of the area on individual owl home ranges, were strongly preferred for foraging by all of the owls; 92 percent of all foraging occurred in such forests. Utilization of younger forests (30 to 200 years old) was generally either less than or not significantly different than expected, indicating that younger forests were less desirable for foraging than old-growth stands.

Old-growth forests were also preferred for roosting (97 percent of all roosts). Large old trees apparently were preferred for roosting during inclement weather because they provided better overhead protection from rain and snow. Small trees in the understory were

preferred during warm weather because they provided greater protection from high temperatures and solar radiation.

Spotted owls were primarily nocturnal. On the average, they left their day roosts to begin foraging at 14 minutes after sunset and stopped foraging at 21 minutes before sunrise. Diurnal foraging was limited primarily to opportunistic attempts to capture animals that wandered into roost areas. The usual method of foraging was to move from perch to perch at night, watching and listening for potential prey. The average rate of movement while foraging in this manner was 247 m/hr, and the average distance moved per nightly foraging period was 2,782 meters (range = 320-8,895 m).

Seven species of mammals comprised the nucleus of the diet, the northern flying squirrel (*Glaucomys sabrinus*), red tree vole (*Phenacomys longicaudus*), western red-backed vole (*Clethrionomys occidentalis*), deer mouse (*Peromyscus maniculatus*), western pocket gopher (*Thomomys mazama*), snowshoe hare (*Lepus americanus*), and bushy-tailed woodrat (*Neotoma cinerea*). The flying squirrel, the most common animal in the diet, comprised 42 percent of all prey captured. During mid-winter, 85 percent of the prey captured were arboreal mammals. During the rest of the year, terrestrial prey became more abundant in the diet, but the flying squirrel remained the most common animal in the diet.

Mean prey size and dietary composition for male and female spotted owls were not significantly different; this suggested that males and females did not partition the prey resource on the basis of size or species. Estimates of biomass consumed per owl per day on the study area ranged from 77.6 to 164.8 g, but the latter estimate was probably inflated.

Four hypotheses are presented to explain why spotted owls foraged primarily in older forests and avoided recently cutover areas: (1) the biomass of prey preferred by the owls may have been greater in older forests than in cutover areas, (2) switching from arboreal mammals in older forests to terrestrial mammals in cutover areas might have resulted in increased competition with other nocturnal predators, (3) prey may have been less accessible in the dense vegetation that developed on cutover areas, and (4) spotted owls may have been more susceptible to predation in cutover areas where escape cover was absent.

Habitat Utilization by Spotted Owls in the West-Central Cascades of Oregon

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES (Cont.)

LIST OF FIGURES

LIST OF FIGURES (Cont.)

LIST OF FIGURES (Cont.)

HABITAT UTILIZATION BY SPOTTED OWLS
IN THE WEST-CENTRAL CASCADES OF OREGON

INTRODUCTION

When studies by Forsman (1976) and Forsman et al. (1977) indicated that the spotted owl (Strix occidentalis) was most frequently associated with old-growth forests in Oregon and was uncommon or absent in young second-growth forests, the species became a focal point in the controversy over the harvest of old-growth forests. Groups advocating the preservation of old-growth began to cite the owl as an example of why such forests should be preserved while representatives of the commercial forest industry pointed to the occasional pairs of spotted owls located in predominantly second-growth forests as proof that spotted owl populations could exist in second-growth. While it is unlikely that the old-growth controversy will ever be resolved to the mutual satisfaction of all parties, there is a need for more information on the habitat requirements of the spotted owl.

Some aspects of the ecology of the spotted owl in Oregon have been well-documented. Forsman (1976) found that the owl was dependent on large cavities or clumps of deformed limbs in old trees for nesting and that the principle prey utilized by the owl in northwestern Oregon were the flying squirrel (Glaucomys sabrinus) and red tree vole (Phenacomys longicaudus), both of which are arboreal mammals. The heavy dependence upon arboreal mammals as prey indicated that the owls foraged primarily in forested areas rather than in cutover areas where arboreal mammals were absent (Forsman 1976). Because no quantitative data were available on the foraging behavior of the owl, however, Forsman (1976) could only speculate about the relationship between diet and habitat preference for foraging.

The research described in this report was designed to investigate habitat utilization by spotted owls in typical western Oregon forests of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Radiotelemetry was chosen as the principle method of observation because it was the most efficient and accurate method available for collecting data on the movements and habitat use of nocturnal raptors (Fuller 1979, Forbes and Warner 1974, Nicholls 1970). The objectives of the study were to: (1) determine the home ranges utilized by spotted owls on a seasonal and cumulative basis, (2) examine territorial behavior and the spacing of resident pairs, (3) determine which types of vegetation were preferred for foraging and roosting, (4) determine the daily activity pattern of the radio-tagged owls, (5) determine the diet of the owls. Because the opportunity presented itself, I also put radio transmitters on 4 juvenile spotted owls and observed the movements of the juveniles after they became independent of their parents. I expected this research would lead to a better understanding of habitat selection in the spotted owl and would provide forest managers with quantitative data that could be used to design habitat management plans for spotted owls in western Oregon.

STUDY AREAS

Western Oregon and the East Slope of the Cascade Mountains

Between 1972 and 1974 I searched for spotted owls at locations scattered throughout Oregon. Eventually, however, it became apparent that spotted owls did not occur east of the Cascade Mountains and investigations were thereafter restricted to the area between the eastern foothills of the Cascade Mountains and the coast (Fig. 1) (Forsman 1976). This area was dominated by rugged mountains and extensive coniferous forests. The only non-forested areas were the lowland interior valleys which were used for agriculture. For a detailed description of the climate and vegetation of this area refer to Franklin and Byrness (1973).

The Radiotelemetry Study Area

The radiotelemetry study area was located on the west slope of the Cascade Mountains, 8 km northeast of the town of Blue River, Lane County, Oregon. It included the 6,070 ha H. J. Andrews Experimental Forest (HJA) and approximately 5,000 ha of forest land adjacent to the Experimental Forest (Fig. 2). The HJA was eatablished by the U.S. Forest Service in 1948 as an outdoor laboratory for ecological and forest management studies. The climate, topography, and vegetation of the area were typical of forest areas throughout western Oregon. The following description of the topography, climate, and vegetation on the area draws on Waring and Norris (1976), Dyrness et al. (1974) and meteorological

Fig. 1. Outline map of Oregon, indicating the distribution of the spotted owl. Each dot represents a location where a pair of spotted owls was located. Of 636 pairs located between 1969 and 1979, 576 are shown on the map.


COAST RANGE
CASCADE MOUNTAINS
SISKIYOU MTNS.

Fig. 2. Aerial photograph of the H. J. Andrews study area showing harvest patterns. Blue River Reservoir is in lower left-hand corner. Major highway bordering southern edge of study area is U.S. 126. Scale: 1 cm = 1.27 km.

records maintained by the Pacific Northwest Forest and Range Experiment Station, Corvallis, Oregon.

The topography was mountainous with high forested ridges separating several deeply incised drainage systems (Lookout Creek, Blue River, McKenzie River). Elevation ranged from 380 m along U.S. Highway 126 at the southern boundary of the study area to 1,630 m on Lookout Mountain near the eastern edge of the area. With the exception of some relatively flat ridgetops, bench areas and narrow valley floors, mountain slopes were steep with slopes commonly ranging from 40 to 60 percent and occasionally up to 80 percent. A 500 ha reservoir was present on Blue River in the southwest corner of the study area (Fig. 2).

The climate was maritime with wet, relatively mild winters and cool, dry summers. Annual precipitation averaged 239 cm with 72 percent occurring between November and March and only 7 percent between June and September.

Two major forest types or zones occurred in the study area: Temperate Forests (*Tsuga heterophylla* Zone) below about 1,050 m and Subalpine Forests (*Abies amabilis* Zone) above 1,050 m (Dyrness et al. 1974). These forest types overlapped in a broad ecotone at about 1,050 m. In the *Tsuga heterophylla* Zone, old-growth forests of Douglas-fir and western hemlock were the dominant biological feature throughout the northern one-half and much of the southern one-half of the study area (Fig. 3). Overstory trees in these stands were generally 275 to 450 years old, 50 to 70 meters tall, and 100 to 150 cm diameter at breast height (dbh). Species composition varied considerably from dry to moist sites; on very dry sites, Douglas-fir predominated and little western hemlock was present. On more mesic sites, which

Fig. 3. Typical old-growth forest communities on the H. J. Andrews study area. Upper: Mixed association of Douglas-fir and western hemlock in the temperate zone. Douglas-fir predominates in the overstory and western hemlock predominates in the understory. Lower: Mixed association of Douglas-fir, silver fir and western hemlock in the transition area between the temperate and subalpine zones. Overstory is dominated by old-growth Douglas-fir with silver fir and western hemlock predominating in the understory. (Credit: Dyrness et al. 1974 and Waring and Norris 1976).

characterized most of the zone, mixed forests of Douglas-fir and western hemlock predominated. Stand structure in these mixed forests generally was characterized by an overstory layer of large Douglas-fir and a few western hemlock and a lower understory layer(s) of western hemlock (Fig. 3,4). On mesic sites western red cedar (Thuja plicata) commonly occurred with western hemlock and Douglas-fir. Less commonly, western redcedar formed nearly pure stands on seeps or boggy areas. On all but the driest sites within the Zone, western hemlock was considered the climax tree species, thus the designation Tsuga heterophylla Zone (Franklin and Dyrness 1973).

Ecotonal forests in the area of transition between the Tsuga heterophylla and Abies amabilis Zones were characterized by mixed associations of old-growth Douglas-fir and silver fir (Abies amabilis) with understories dominated by silver fir and western hemlock (Fig. 3). On the highest ridges, old-growth Subalpine Forests consisted of mixtures of silver fir and mountain hemlock or nearly pure stands of silver fir or mountain hemlock.

Forests that were 80 to 140 years old were also well represented in both Zones on sites that burned during the mid-1800's. In the Tsuga heterophylla Zone, 80- to 140-year-old stands were mostly uniform forests of Douglas-fir, 40 to 100 cm dbh and 30 to 50 m tall (Fig. 5). Remnant old-growth Douglas-fir trees were sometimes scattered through such stands. In the Abies amabilis Zone, 80- to 130-year-old mixtures of silver fir or mountain hemlock were relatively common, especially on ridge tops where fires had occurred in the relatively recent past. Forests between 30 and 80 years old were not abundant in either Zone

Fig. 4. Distribution of larger trees (over 25 cm dbh) by species and size class on a 16 ha tract of old-growth Douglas-fir and western hemlock on the H. J. Andrews study area. This stand was typical of mixed associations of Douglas-fir and western hemlock on the area. (Credit: Waring and Norris 1976).

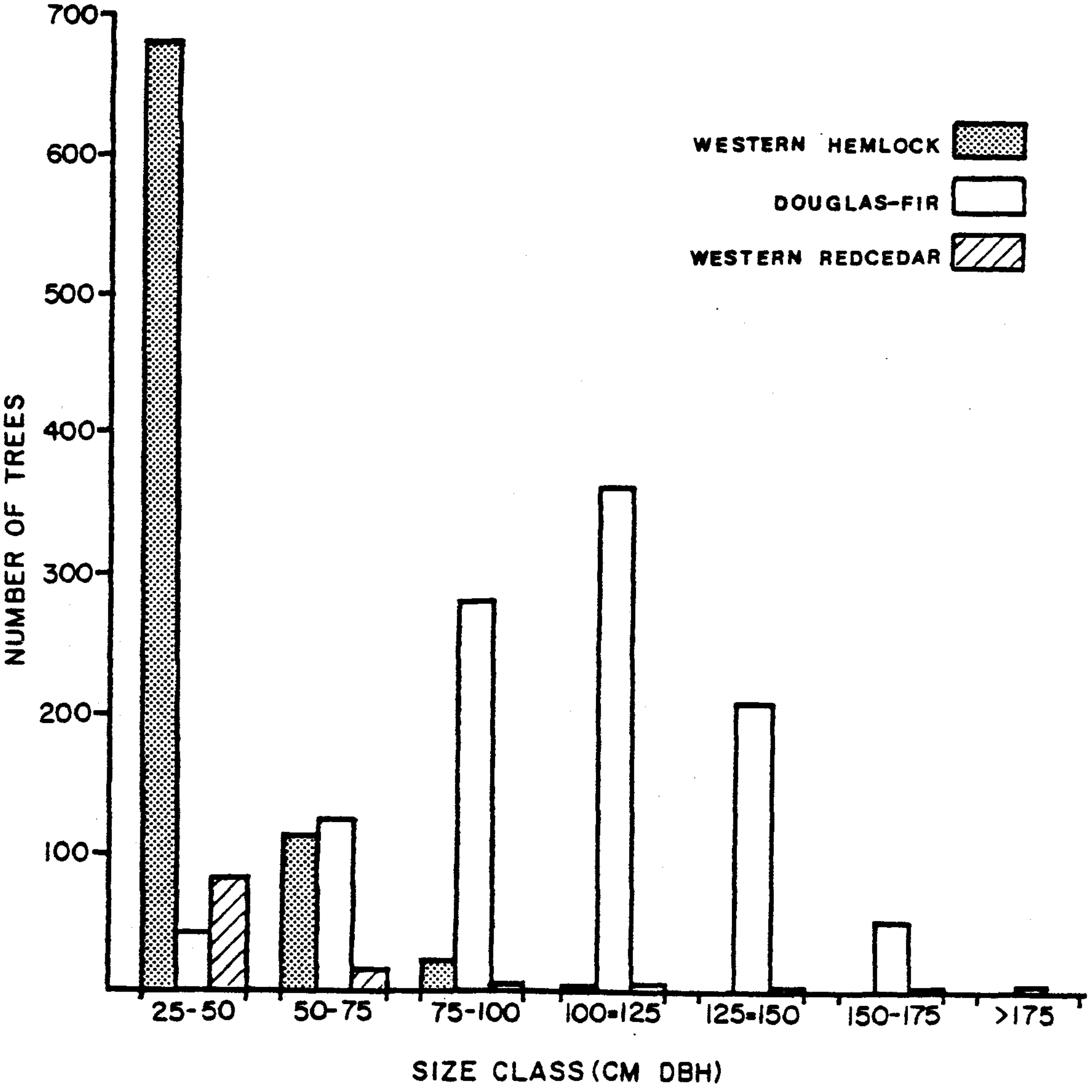
NUMBER OF TREES
700
600
500
400
300
200
100
WESTERN HEMLOCK
DOUGLAS-FIR
WESTERN REDCEDAR
25-50
50-75
75-100
100-125
125-150
150-175
>175
SIZE CLASS (CM DBH)

Fig. 5. Typical mature (130-year-old) stand of Douglas-fir on the H. J. Andrews study area. Note that a few individuals of western hemlock have become established beneath the Douglas-fir overstory. (Credit: Dyrness et al. 1974).

but were present on scattered sites where small fires had occurred within the previous 90 years.

Approximately 25 percent of the forests on the HJA had been clear-cut since the early 1950's. Areas adjacent to the experimental forest had been more heavily clear-cut over, especially the southern third of the study area where approximately 50 percent of the forests had been clear-cut or burned within the previous 30 years (Fig. 3). Vegetation on cut-overs ranged from bare ground or mixtures of herbs and shrubs on recent cuttings to dense stands of 5- to 20-m tall young conifers on the older cut-overs (Fig. 6). Most harvest had been by clear-cutting units of 10 to 20 hectares, although unit size range from 0.5 to nearly 100 ha.

Fig. 6. Typical clear-cut areas on the H. J. Andrews study area. Upper: sparse regeneration of Douglas-fir 12 years after harvest. Many deciduous shrubs and small openings are present. Lower: dense regeneration of Douglas-fir on a north aspect 25 years after harvest. (Top photo credit: J. Franklin).

METHODS AND MATERIALS

Most of the data presented in this report were collected between May 1975 and June 1976, during the radiotelemetry study. However, some information on pair spacing and diet was also collected between 1972 and 1974 and between 1977 and 1978.

Locating Owls, Roost, Nests

To locate spotted owls I imitated their calls in forest areas at night. If owls were present they usually challenged the suspected intruder by calling back, thus revealing their location (Foresman 1976, Foresman et al. 1977). The entire HJA study area was searched several times in this manner during the spring and summer of 1975, until I was confident that all resident pairs had been located. After I obtained a rough idea of pair locations by calling at night I returned to the same areas during the day to locate the owls and attach radio transmitters. During the day I systematically walked the areas where I suspected the owls might be roosting, calling as I walked. Usually, the owls called back from their roosts if they could hear me and I could then home in on their roosts.

Nest trees and roosts of owls equipped with radio transmitters were found by triangulation of radio signals. Other nests and roosts were located by: (1) observing adults during the period of nest site selection, (2) imitating spotted owl calls in suspected nest or roost areas during the day until the owls responded, or (3) tethering live mice on the ground near roosting adults and then watching as the owls captured the mice and carried them to the nest. The last method was effective only after the eggs hatched.

Radiotelemetry Equipment, Data Collection and Analysis

Between 25 May and 14 September 1975, radio transmitters were placed on 8 adults (5 females and 3 males) and 4 owlets. The adults represented 5 pairs occupying adjacent territories on the study area. The two males that were not radio-tagged were seen regularly with their radio-tagged mates, and both participated in nesting. All adults and 2 of the owlets were trapped in mist nets or bow nets placed below their day roosts and baited with live mice. The other 2 owlets were captured in a long-handled dip net. All owlets were trapped and instrumented in August when they were 3 to 4 months old.

The radio transmitters weighed 21 to 22 grams including battery and harness and operated for 271 to 383 days before they either stopped transmitting or were removed from the owls at the end of the study. Transmitters were attached with a back-pack harness of tubular teflon ribbon (Dunstan 1972). The teflon harness material was 6 mm wide and was obtained from Bally Ribbon Mills, Bally, Pennsylvania.

Receiving equipment included a 12-channel portable receiver, a 4-element hand-held yagi antenna and a 4-element yagi mounted in fixed position on a truck. The fixed yagi on the truck was used only to determine when an owl was nearby or was moving or not. Triangulation to establish the location of an individual was done with the hand-held antenna. Because an excellent road system was present on the study area it was often possible to walk quietly to within 50 to 100 m of foraging owls at night and to pinpoint their location to within a few meters. The owls usually made no attempt to move away from the observer as long as they were approached quietly and no closer than 50 m.

Two techniques were used for tracking owls at night. One was to establish the location of an individual and then to move on to the next individual, and so on throughout the night. The sequence in which owls were checked was varied so that all data for a given individual were not obtained at the same time each night. The second technique was to remain with an individual for longer periods (up to 12 hours), obtaining a fix every 15 to 30 minutes if the owl was stationary, or at shorter intervals if it was moving rapidly. Movements could be detected by changes in signal direction and strength. On most nights tracking included a combination of both of the above methods, depending to some extent upon the distribution of individual owls relative to each other and upon uncontrollable factors such as weather. If several owls were in close proximity to each other then I usually tracked them as continuously as possible so as not to miss any social interactions that might occur and to maximize the amount of data collected. When owls were more widely spaced with respect to each other, I either checked them at intervals or continuously tracked 1 individual, depending upon the amount of time lost in driving and walking between owls. As much as possible, I tried to collect equal amounts of data from each individual on a monthly basis, although this became impossible during the winter when roads into areas occupied by some pairs were blocked by snow.

To determine when owls began and ended nightly foraging activity, I either watched them in their day roosts or monitored them remotely, listening until the transmitter signal indicated that an owl had started or stopped moving. Activity during the day was monitored by periodically listening to transmitter signals and by visually checking individuals in their roosts each day. Individual owls were sometimes checked visually several times a day to see if they changed roosts.

Each time an owl was located, I recorded the identity of the individual, the time, date, location coordinates, type of vegetation (cover type) occupied, activity type and a numerical code indicating the accuracy of a fix (a "fix" refers to an owl's location as determined at 1 point in time). Five accuracy codes were used depending upon whether an owl's location was determined visually or via radiotelemetry: (1) visual location, (2) accurate to within 0.5 ha, (3) accurate to within 2.0 ha, (4) accurate to within 7 ha, and (5) accurate to within 20 ha. Fixes in category 4 were used in habitat selection analyses only if the cover type was uniform where the owl was located. Fixes in category 5 were not used for any analyses.

Eight activity types were recognized: (1) foraging, (2) roosting, (3) moving, (4) calling, (5) territorial interaction, (6) incubation/brooding, (7) begging, and (8) unknown. Begging referred to the persistent begging calls given by owlets as they waited for adults to bring them food. At night all fixes where an adult was not calling or moving from one place to another were considered foraging fixes, even if an owl did not move for a long period of time. This approach was adopted because it was extremely difficult to distinguish between foraging and resting behavior at night. An owl might be immobile (i.e., "resting") for some time and yet still be actively watching for prey.

The home range of an individual was defined as the area utilized for foraging, roosting and nesting. In calculating home range areas I excluded one-time-only movements into areas considerably outside an individual's usual area of activity; including such movements would have produced inflated home range estimates in a few instances. The number of fix coordinates eliminated for this reason ranged from 1 to 8 per individual.

To determine if there were seasonal differences in utilization of the home range, data for each owl were subdivided into 2 to 3 month intervals and plotted separately. The number of intervals for each individual depended upon the length of the tracking period.

Home range areas were calculated by plotting all fixes for a given individual on an XY grid system (50 m grid) overlaying an orthophoto mosaic of the study area. Scale of the photomosaic was 6.31 cm/km. The coordinate system divided the area into 0.25 ha blocks and allowed the positioning of fixes to the nearest XY grid intersection with a maximum rounding error of 35 m. The XY coordinates for each fix were entered on computer cards along with codes for time, date, activity, cover type and fix accuracy, and a computer program was used to calculate areas and to plot maps of the movements of each owl. Home ranges were calculated according to the minimum convex polygon and elipse methods described by Jennerich and Turner (1975).

To compare the spacing of spotted owl pairs on the HJA and other areas in Oregon, 14 different areas were searched intensively for spotted owls until all of the resident pairs had been located in each area. The mean nearest neighbor distance was then calculated for each area and used to obtain a rough estimate of the size of defended areas (by calculating the area of a circle with radius equal to 0.5 of the mean nearest neighbor distance).

Cover types on the study area were divided into 19 categories, depending primarily upon the age, structure, and species composition of the vegetation (Appendix 1). Cover types were determined by ground reconnaissance and were plotted as an overlay on an orthophoto mosaic of the study area. Areas of all cover types within the home range of each owl were measured with a dot grid or polar planimeter and were then converted to percentages of the total area. These percentages were then multiplied by the total number of fixes for an owl in order to generate the expected number of fixes in each cover type.

To determine if certain cover types were preferred over others for foraging, chi-square values were calculated for each cover type by comparing the expected and observed number of fixes and then summing the individual chi-square values to obtain a total chi-square for each owl. If this value was significant then a confidence interval was constructed around the observed utilization values with the Bonferroni $\underline{z}$ statistic (Neu et al. 1974). If the expected utilization value for a given cover type exceeded the limits of the confidence interval constructed for that type I concluded that the cover type was not selected randomly.

Variables measured at owl roost sites were: (1) perch height above ground, (2) dbh of roost tree, (3) species of roost tree, (4) distance between owl and nearest tree trunk, (5) amount of overhead perch

protection and (6) approximate age of the roost tree. Overhead perch protection was a ranked variable, indicating whether an owl was roosting under some sort of overhead protection (either close against a vertical tree trunk under overhanging limbs or underneath a leaning tree trunk) or was in a more exposed perch out on limbs away from the tree trunk. Each observation was placed in 1 of 5 different weather categories, depending on the weather conditions on the day that the roost was used: (1) clear, hot day with $T \geq 28^{o}C$, (2) clear, warm day with $10^{o}C < T < 28^{o}C$, (3) clear, cold day with $T \leq 10^{o}C$, (4) overcast day with little or no precipitation, or (5) overcast day with steady or intermittent rain or snow. Roost characteristics were then compared to determine if there was any relationship between weather conditions and the type of roosts selected.

Collection and Analysis of Pellets and Prey Remains

During the radiotelemetry study, pellets were collected from spotted owl roosts during all months of the year (May 1975 to June 1976). In other years, data were collected only during the spring and summer (March-August). Data were also gathered from observations of food brought to young, collections of discarded prey remains, and collections of prey remains found at nests. Prey species in pellets were identified from skulls, bones of the appendicular skeleton, fur, feathers, or scales. Insects were identified from mandibles or other fragments of the exoskeleton. Numbers of vertebrate prey items were determined by counting skulls, pairs of jaws, or other skeletal remains. Biomass of each prey species in the diet was determined by multiplying the number of individuals of a given species by the mean body weight for that species (Appendix 3). In the case of snowshoe hares (Lepus americanus), however, the body weight of each hare was estimated based on the size of skeletal fragments and then summed to obtain total biomass. When snowshoe hare fur occurred in a pellet but no skeletal remains were present, biomass was estimated at 350 g, the approximate mean weight for hares taken during the study (spotted owls rarely captured adult hares).

Chi-square contingency tests were used to determine seasonal or annual differences in dietary composition. Pellets were used for seasonal comparisons only if I knew approximately when the pellets were regurgitated.

To estimate the number and biomass of prey captured and consumed on a daily and seasonal basis, I first determined the mean number of prey per pellet during each of three seasonal periods (fall and winter periods were combined). Only pellets from non-nesting individuals were utilized during the nesting season because I could not be certain that nesting individuals consumed some portion of all prey they captured. After determining the mean number of prey per pellet, the biomass consumption per owl per day was calculated according to the following formula:

$$\text{Mean number of prey per pellet} \times \text{Number of days in period} = \text{Number of prey consumed in period}$$

$$\text{Percent composition of each prey species in diet during period} \times \text{Number of prey consumed in period} = \text{Number of each prey species consumed during period}$$

$$\text{Mean biomass of each species} \times \text{Number of each species consumed during period} = \text{Total biomass consumed during period}$$

Then,

$$\frac{\text{Total biomass consumed during period}}{\text{Number of days in period}} = \text{Biomass consumed per owl per day}$$

One correction factor was introduced into the analysis: because uneaten portions of large prey (e.g., squirrels, woodrats, hares) were often stored and then consumed on the day or night following the night of capture, these large prey frequently were represented in 2 pellets regurgitated 1 day apart. Mice and voles, on the other hand, were usually consumed completely on the night of capture. To correct for the biased representation of larger prey, large prey animals (> 100 grams) found in pellets were counted as 0.5 individuals rather than 1. A basic assumption in the analysis was that the owls regurgitated 1 pellet per day on the average (Smith and Richmond 1972).

To determine if male spotted owls selected different prey than females, I marked roost trees occupied by radio-tagged owls of known sex and returned the nest day to collect pellets. Less frequently, I collected pellets after watching owls regurgitate them. Pellets collected below roosts used jointly by males and females were excluded from this analysis as were pellets from nesting females (most food eaten by nesting females was captured by males). Data on prey selection by females during the nesting period were collected from 2 radio-tagged females that did not nest during 1976; these 2 females foraged for themselves.

The confidence level for statistical tests was 0.95.

RESULTS

Home Range Characteristics

The 5 pairs studied on the HJA were distributed along the 2 major stream drainages (Lookout Creek and Blue River) that crossed the study area (Fig. 7, 8). An intensive search of the area indicated that there were no other pairs occupying areas between the radio-tagged pairs. There were, however, at least 4 other pairs occupying areas immediately adjacent to the study area. The latter pairs were not studied intensively, although some data on their food habits and spacing relative to other pairs were collected.

Between 4 May 1975 when the first transmitter was placed on an owl and 14 June 1976 when the last transmitter was removed, 261 nights were spent tracking owls (Table 1). A total of 4,927 fixes was obtained, excluding fixes that were too inaccurate for home range and habitat selection analyses (Table 2). Of the 8 radio-tagged adults, 6 occupied the same areas for the duration of the study (Fig. 7). The other two individuals (BRR male and female) occupied well-defined home range areas initially, but during the course of the study they began to wander extensively, spending much of their time within areas occupied by neighboring pairs. It appeared that the wandering behavior of the BRR pair may have occurred because they were displaced from their territory by another pair of owls. For purposes of home range analyses, the BRR pair was excluded because the large areas covered in their wanderings (Table 3, Fig. 8) did not conform to the typical pattern of home range use displayed by established spotted owl pairs.

Fig. 7. Home ranges utilized by 4 female and 2 male spotted owls on the H. J. Andrews study area, May 1975 to June 1976. Upper: computer maps illustrating movements of 4 females occupying adjacent territories. Lower: outline maps of home ranges of the same 4 females and 2 males that were paired with 2 of the females. The asterisk within each home range indicates location of the nest site used by each pair during the study or during years before or after the study.

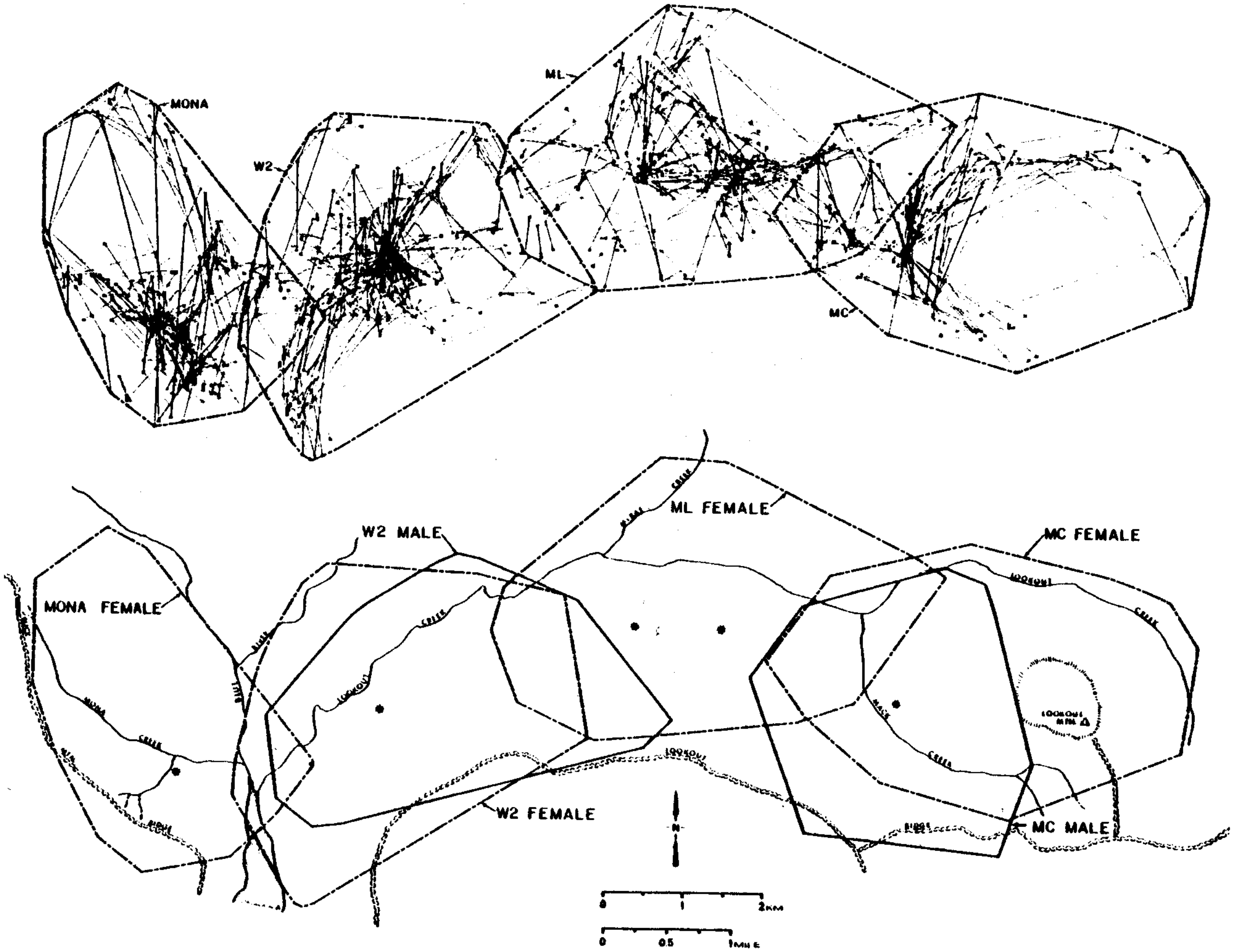
MONA
W2
ML
MC
ML FEMALE
MC FEMALE
W2 MALE
MONA FEMALE
W2 FEMALE
MC MALE
MONA CREEK
LOOKOUT CREEK
LOOKOUT MTN
N
0 1 2 KM
0 0.5 1 MILE

Fig. 8. Principle areas of activity utilized by the BRR male and female on the H. J. Andrews study area, May 1975 to June 1976. Asterisk indicates location of nest area utilized during years before and after the radiotelemetry study.

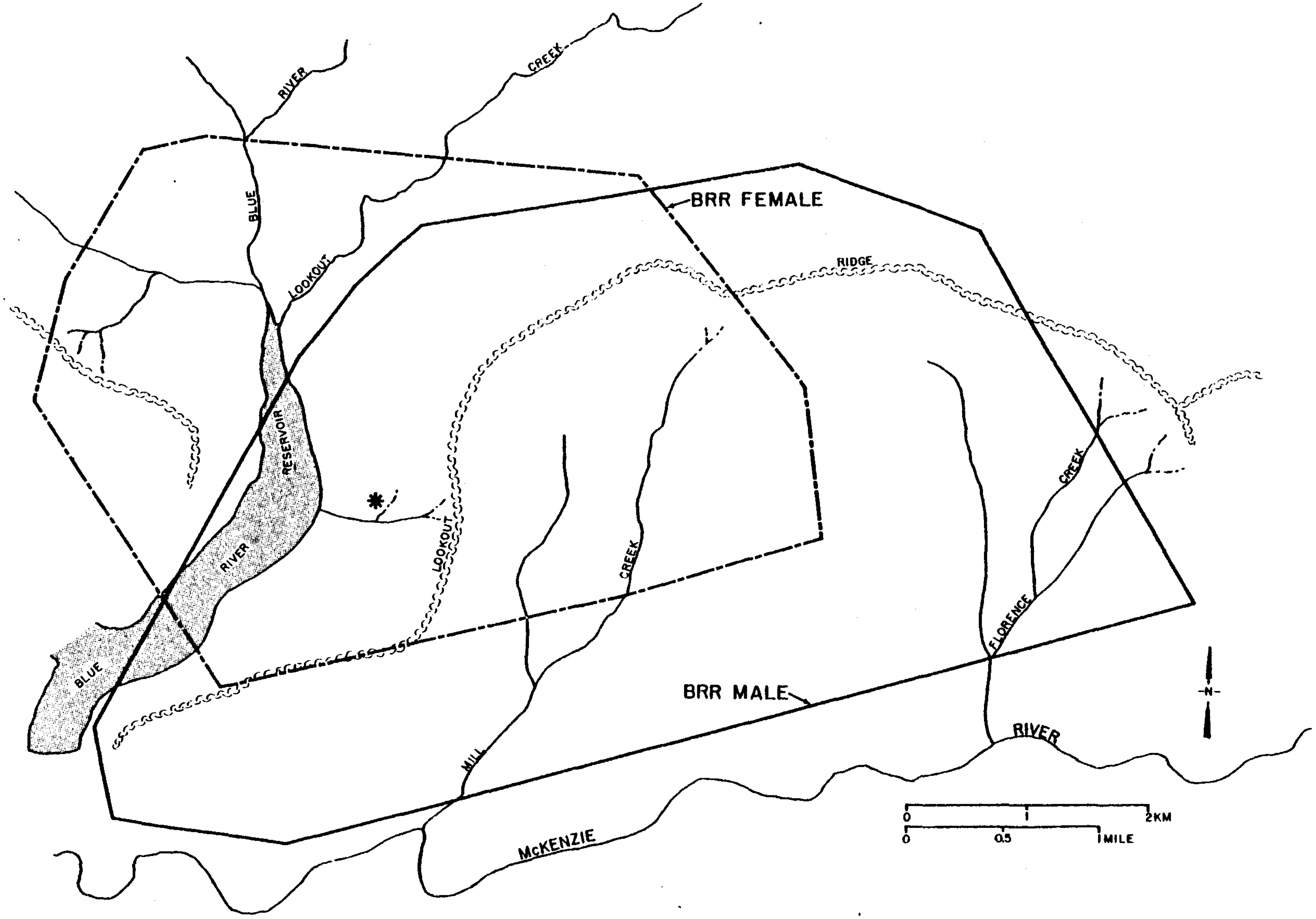
RIVER
CREEK
BLUE
LOOKOUT
BRR FEMALE
RIDGE
RESERVOIR
RIVER
BLUE
LOOKOUT
CREEK
CREEK
FLORENCE
BRR MALE
RIVER
MILL
McKENZIE
N
0
1
2KM
0
0.5
1 MILE

Table 1. Code names and radio-tracking periods for 8 adult spotted owls radio-tagged on the H. J. Andrews study area during summer 1975.

Owl Identification Code	Date transmitter installed	Date when transmitter was removed or stopped transmitting	Number of days[1] in tracking period
Blue River Reservoir (BRR) Male	4 May 1975	5 May 1976	367
Blue River Reservoir (BRR) Female	8 June 1975	14 May 1976	332
Watershed 2 (W2) Male	25 May 1975	3 April 1976	314
Watershed 2 (W2) Female	12 July 1975	3 June 1976	327
Mona Creek (Mona) Female	12 July 1975	9 May 1976	302
McRae-Lookout (ML) Female	26 July 1975	1 June 1976	311
Mack Creek (MC) Male	25 May 1975	11 June 1976	383
Mack Creek (MC) Female	14 September 1975	11 June 1976	271

[1] Owls were observed approximately 5 out of every 7 nights and days during the tracking period.

Table 2. Number of fixes by activity type for 8 adult radio-tagged spotted owls on the H. J. Andrews study area, May 1975 to June 1976[1].

Activity type	BRR male	BRR female	W2 male	W2 female	Mona female	ML female	MC male	MC female	Totals
Foraging	382	364	364	416	345	361	213	161	2,606
Roosting	258	251	301	256	170	167	153	96	1,652
Moving	41	13	26	44	11	37	24	23	219
Calling	17	11	31	53	10	16	15	4	157
Territorial interaction	8	17	5	2	3	1	1	0	37
Incubation/brooding	-	-	-	-	40	80	-	87	207
Unknown	2	3	5	2	3	7	11	16	49
TOTALS	708	659	732	773	582	669	417	387	4,927

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[1] Includes only fixes that were accurate enough to use in determination of home range and habitat utilization.

Table 3. Size of home range areas utilized by 8 radio-tagged adult spotted owls on the H. J. Andrews study area, May 1975 to June 1976[1].

Owl identification	Minimum convex polygon estimate (hectares)	Jennerich and Turner ellipse estimate at the 95% conf. level (hectares)
BRR male	3,254	4,855
BRR female	2,179	3,169
W2 male	1,272	1,156
W2 female	1,220	936
Mona female	920	1,002
ML female	1,376	1,239
MC male	950	684
MC female	1,324	1,173
Means	1,177	1,032
Means for males	1,111	920
Means for females	1,210	1,087

[1] The BRR male and female did not occupy the same home range areas for the duration of the study. The large areas utilized by this pair were not considered typical home ranges and were not used in calculations of mean home range size in table.

Total or Cumulative Home Range Size

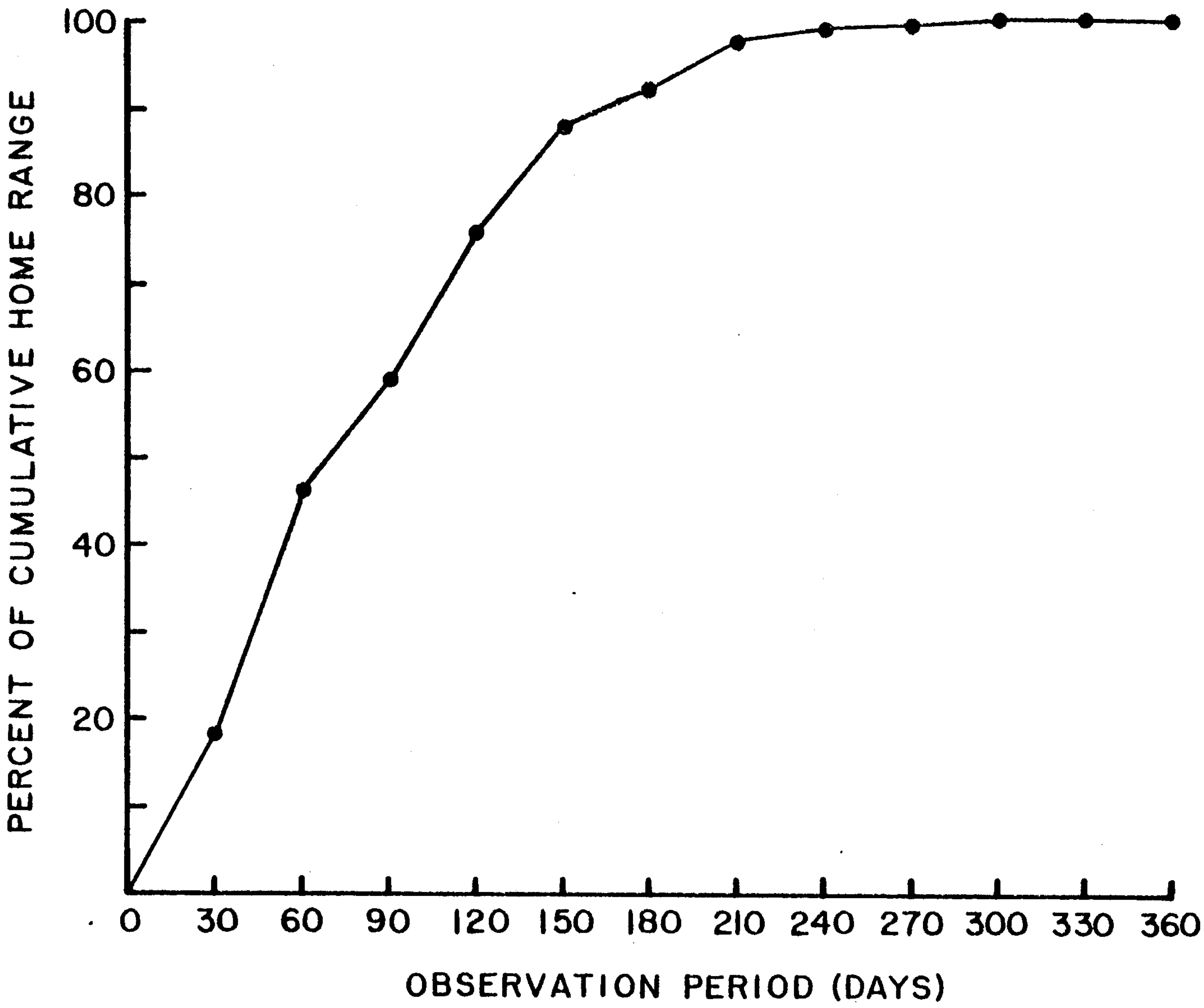
Mean home range size for the 6 owls based on the minimum convex polygon method was 1,177 ha (range = 920-1,375 ha) (Table 3). By comparison, the elipse method produced a mean home range of 1,032 ha at the 95 percent confidence level (range = 684-1,239) (Table 3). Because the minimum convex polygon is conceptually simple and has a long history of use in ecological studies, it is the method that will be used for calculations and comparisons in the following sections.

On the average, 131 days (range = 75-150 days) were required to determine 80 percent of the total home range utilized by each owl and 165 days (range = 105-204 days) were required to determine 90 percent (Fig. 9). After owls had been observed for 5 or 6 months, movements outside the home range boundaries already delineated became uncommon. The relatively long period required to determine total home range size reflected the fact that owls visited some portions of their home ranges infrequently.

Home Range Overlap Between Paired Individuals

The mean home range size for males was 1,111 ha and for females was 1,210 ha (Table 3). These means were not significantly different ($t = 0.435$, d.f. = 4, $0.3 < p < 0.4$). Home ranges occupied by paired individuals overlapped by 50 to 73 percent (Fig. 7). In all cases, the areas of overlap contained the nest area, major roost sites and the areas that were used most intensively for foraging. Collective home range size for the W2 and MC pairs was 1,597 and 1,607 ha, respectively.

Fig. 9. Percent of cumulative home range size for spotted owls on the H. J. Andrews study area as a function of time. Data were averaged for 4 owls (2 owls were excluded from the analysis because they could not be observed regularly during mid-winter). During the observation period owls were observed approximately 5 days out of every week.


PERCENT OF CUMULATIVE HOME RANGE
100
80
60
40
20
0
30
60
90
120
150
180
210
240
270
300
330
360
OBSERVATION PERIOD (DAYS)

Although home range areas used by paired individuals overlapped considerably, plots of foraging activity for paired individuals indicated that the sexes foraged in different areas much of the time and that when they utilized the same general areas they infrequently foraged at the same exact sites. For instance, the W2 male tended to forage most commonly within the eastern 1/2 of the collective home range utilized by the pair while the W2 female foraged most commonly in the western 1/2. Only 10 percent of the coordinates at which foraging occurred overlapped during the fall and winter (September-February) and only 8 percent overlapped during the spring and summer (March-August). Corresponding percentages for the MC male and female were 4 and 7. When paired individuals foraged at or near the same coordinates they rarely did so at the same time. It appeared, therefore, that partitioning of foraging areas by paired individuals occurred on both a spatial and temporal basis. By foraging separately, paired individuals largely avoided interference competition and were able to collectively forage over a larger area.

Home Range Overlap Between Neighboring Individuals

On the average, any 2 owls occupying adjacent territories shared 12 percent of their home ranges (range = 3-25 percent). Shared areas were generally near the periphery of adjacent home ranges where the owls spent a relatively small proportion of their time (Fig. 7). Home range overlap between neighboring individuals did not differ greatly depending upon sex. Average female/female overlap was 11 percent and male/female overlap was 14 percent. Overlap between males could not be calculated because the radio-tagged males did not occupy adjacent territories (Fig. 7).

Total overlap between the home range area of one individual and the combined home range areas of two adjacent pairs could only be calculated for the ML female. She shared a total of 39 percent of her home range with the MC and W2 pairs (Fig. 7).

Seasonal Differences in Home Range Utilization

The size and shape of home ranges varied on a seasonal basis (Table 4; Figs. 10-12). The most noticeable differences in home range utilization occurred between the breeding season (March-August) and the fall-winter period (September-February). Between March and June, nesting males usually roosted near their nests during the day and left the nest area at dusk to forage (Fig. 13). During the night they usually made 2 to 3 return trips to the nest to deliver food. Nesting females did virtually no foraging from the time they laid eggs in early April until mid-May when the young were 2 to 3 weeks old. Thereafter, females began to forage in essentially the same manner as males; plots of foraging activity for both sexes appeared as a series of lines radiating from the nest site to foraging locations up to 2.6 km away (Fig. 13). After the young left the nest in late May or June, adult foraging activity continued to center around the location of the brood until the young left the parental territory in September or October.

When other pairs were nesting or feeding fledged young, non-nesting pairs frequently roosted during the day near the nests that they had used in previous years (Figs. 11, 14). These non-nesting individuals

Table 4. Home range size (in hectares) of 6 radio-tagged adult spotted owls during different periods of the year on the H. J. Andrews study area.

	1975→			1976→		
Owl	6 May-July	Aug.-Sept.	Oct.-Nov.	Dec.-Jan.	Feb.-March	April-10 June
W2 male	661	593	646	824	604	-
W2 female	--	336	1,047	1,048	449	335
Mona female	--	332	695	693	224	--
ML female	--	1,062	911	1,154	318	227
MC male	172	262	386	--	160	834
MC female	--	596	1,054	--	227	810
Means	416	530	790	930	330	552

Fig. 10. Computer maps showing seasonal changes in home range utilization by the Mona female on the H. J. Andrews study area, August 1975 to April 1976. Dashed lines indicate boundaries of seasonal areas utilized and solid lines indicate total home range. The asterisk indicates location of the nest used in 1976.

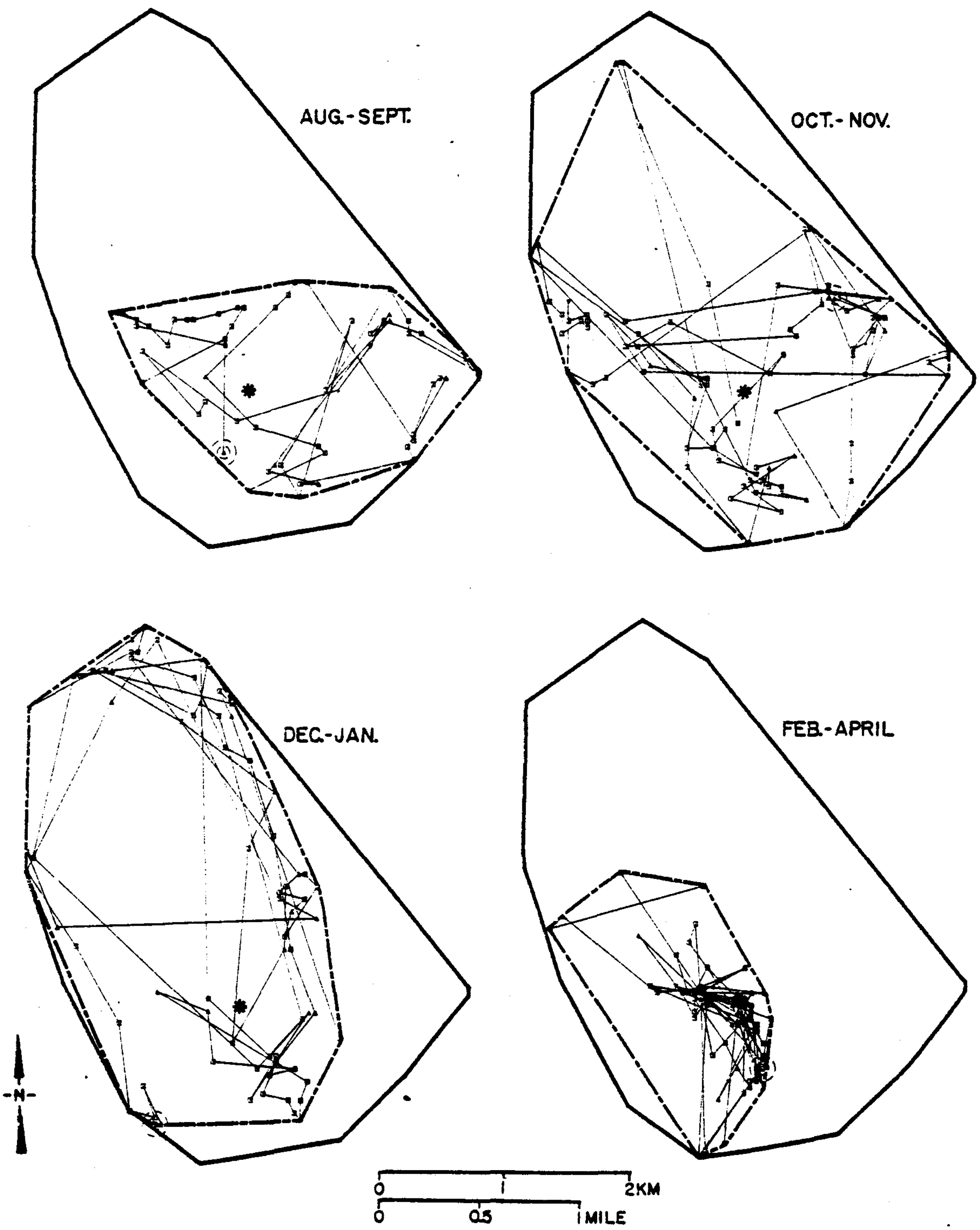

AUG.-SEPT.
OCT.-NOV.
DEC.-JAN.
FEB.-APRIL
N
0
1
2 KM
0
0.5
1 MILE

Fig. 11. Computer maps showing seasonal changes in home range utilization by the W2 male on the H. J. Andrews study area, May 1975 to March 1976. Dashed lines indicate boundaries of seasonal areas utilized and solid lines indicate total home range. The asterisk in each plot indicates the location of the nest. The W2 pair did not nest during the study, but nesting did occur in some years before and after the study.

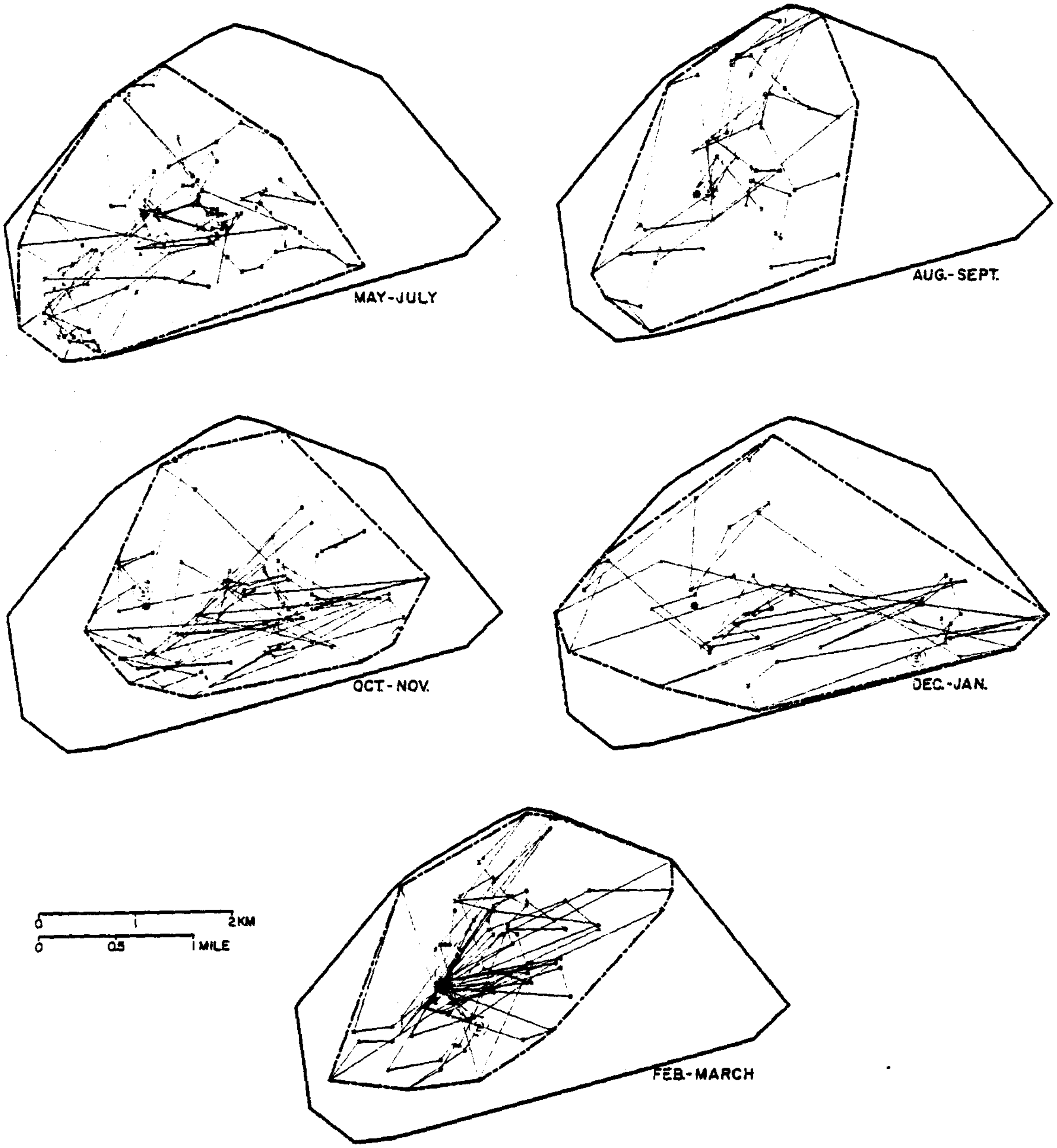

MAY-JULY
AUG.-SEPT.
OCT-NOV.
DEC.-JAN.
0
1
2 KM
0
0.5
1 MILE
FEB.-MARCH

Fig. 12. Computer maps showing seasonal changes in home range utilization by the ML female on the H. J. Andrews study area, August 1975 to June 1976. Dashed lines indicate boundaries of seasonal areas utilized and solid lines indicate total home range. The asterisk on the right in each seasonal plot indicates the location of the nest utilized in 1975 and the asterisk on the left indicates the location of the nest utilized in 1976.

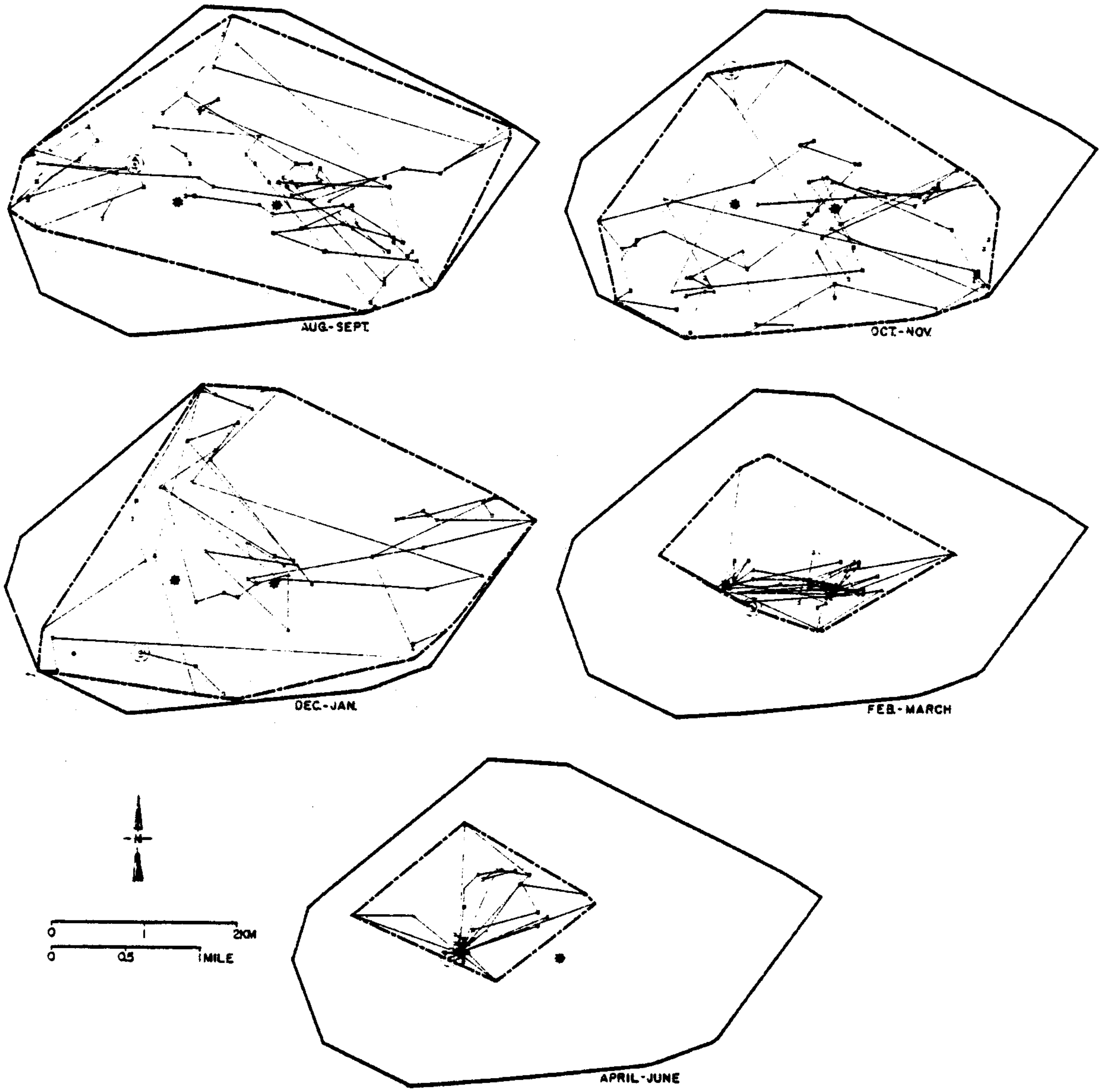

AUG-SEPT.
OCT-NOV.
DEC-JAN.
FEB-MARCH
APRIL-JUNE
N
0
1
2KM
0
0.5
1MILE

Fig. 13. Computer maps showing movements of the MC male and female on the H. J. Andrews study area during the period when they were feeding young at the nest (May-June 1976). Solid lines around computer maps indicate the total home ranges for the 2 owls. The nest was the focus of activity for both adults.

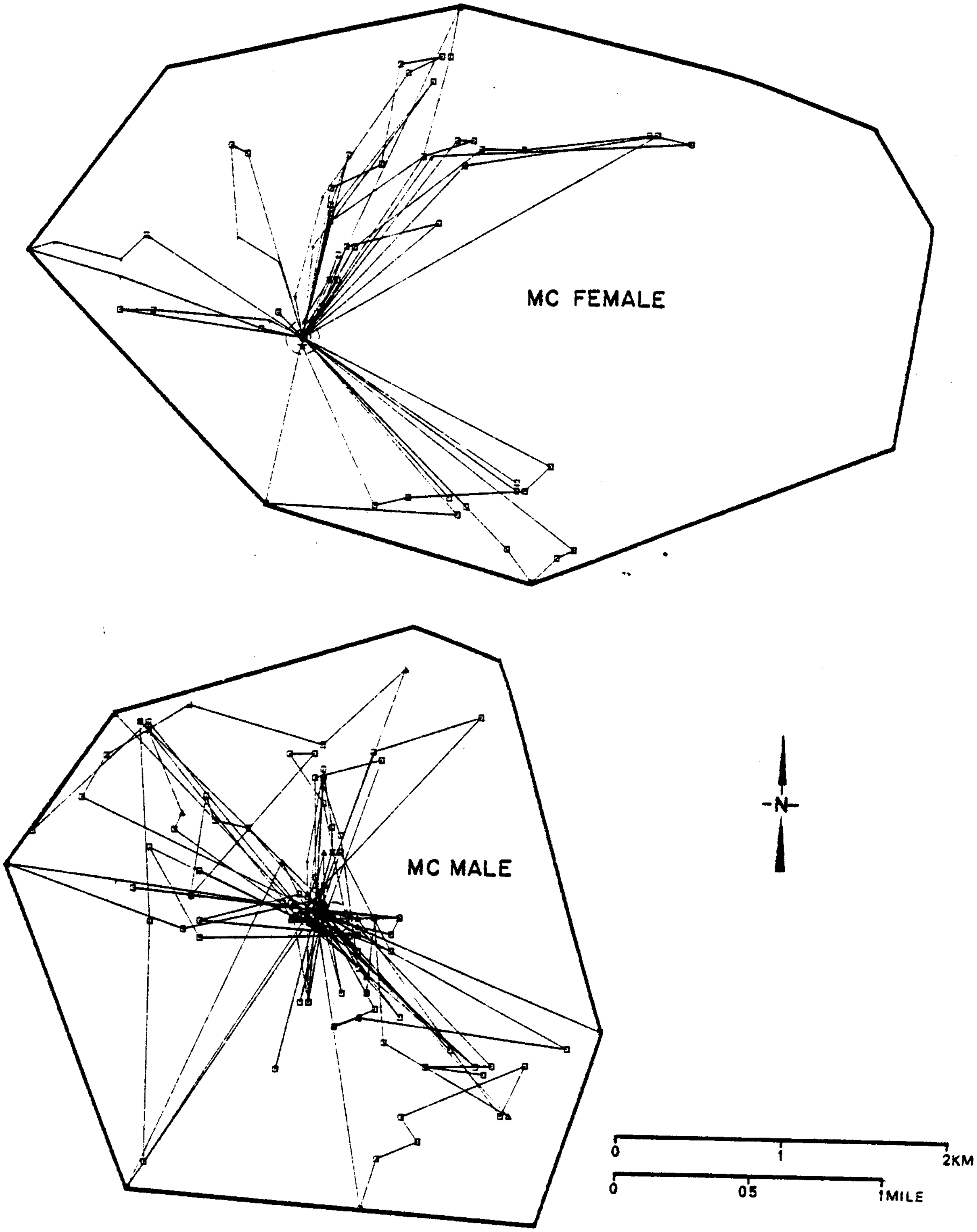
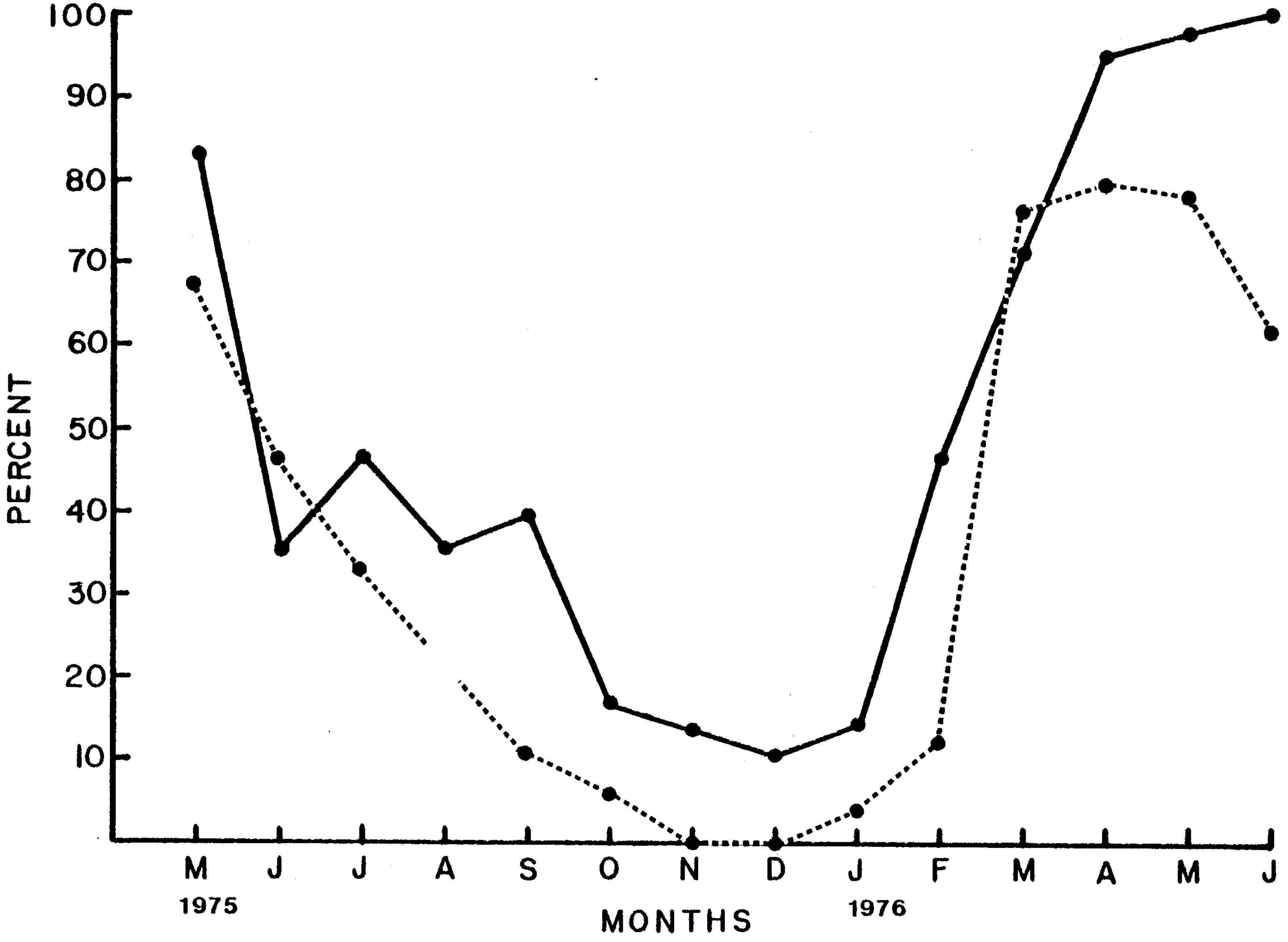

MC FEMALE
MC MALE
N
0
1
2KM
0
05
1MILE

Fig. 14. Percent of days on which adult spotted owls on the H. J. Andrews study area roosted near (within 400 m) their nest trees (solid line) or roosted together as pairs (broken line). Percentages calculated on a monthly basis from May 1975 to June 1976. Data for August 1975 were inadequate to calculate pair association.


100
90
80
70
60
50
40
30
20
10
PERCENT
M
J
J
A
S
O
N
D
J
F
M
A
M
J
1975
1976
MONTHS

separated at dusk to forage and then rejoined again at dawn near the traditional nest area to roost together. This pattern gradually disppeared during late summer as both nesting and non-nesting pair members began to roost apart increasingly often and to roost away from their nest areas.

From late September to mid-February the radio-tagged adults infrequently roosted near their nest areas and rarely roosted together as pairs (Fig. 14). They remained within the same home ranges but roosted wherever they concluded nightly foraging activities. From late October to January they led an essentially solitary existence (Fig. 14). The largest seasonal home ranges were recorded during mid-winter (November to January) when the owls utilized peripheral areas within their home ranges more than at any other time (Table 4, Figs. 10-12). Apparently utilization of these peripheral areas was energetically less profitable during the spring and summer because to reach them, the owls would have had to make longer flights to and from their nest areas. It is also possible that the owls foraged over larger areas during winter in response to gradually declining prey populations.

Influence of Physiographic Features on Home Range Shape

The 3 pairs occupying the Lookout Creek drainage confined nearly all of their activities to that drainage, rarely crossing over Lookout Ridge to forage on the south side of the ridge (Fig. 7). It appeared, therefore, that Lookout Ridge formed a natural home range boundary along the southern edge of the Lookout Creek drainage where the ridgetop elevation ranged from 800 to 1600 m. The only pair that regularly crossed over Lookout Ridge was the Blue River Reservoir pair (Fig. 8). The principle area of activity of the latter pair was along Blue River Reservoir near the southern end of Lookout Ridge where the ridgetop elevation was only 500 to 800 m. Lookout Mountain, at the eastern end of Lookout Ridge, strongly influenced the shape of the home range areas utilized by the MC male and female, both of which utilized "C"-shaped home range areas around the lower flanks of the mountain (Fig. 7). Their home range areas coincided with the old-growth forests of Douglas-fir and western hemlock that occurred below about 1,350 m on the mountain. Neither individual was observed in the brushfields or rock cliffs that occurred higher on the mountain.

Another high ridge system that appeared to function as a home range boundary was Buck Mountain Ridge along the western edge of the home range occupied by the Mona female (Fig. 7). The Mona female crossed this ridge only at its southern end where the elevation of the ridge was below 900 m. Except for the major ridge systems described above, the many small ridge and valley systems within the study area appeared to have little influence on home range shape.

Another physiographic feature that strongly influenced owl movements was Blue River Reservoir. This reservoir was 250 to 300 m wide for most of its length and the 3 pairs that occupied home ranges adjacent to the reservoir rarely crossed it except near its upper end where it was less than 150 m wide (Figs. 7, 8).

Location of Nest Sites Within Home Ranges

Nest sites usually were centrally located within owl home ranges (Figs. 7, 10-12). At least 1 individual changed nest sites during the study; from the nest she utilized in 1975 the ML female moved 1.1 km west to a new nest in 1976 (Fig. 12). Both nest sites were centrally located within the boundaries of the home range. It also appeared that the MC pair moved to a new nest site in 1976; during spring and summer 1975 this pair did not nest but frequently roosted together in an area that I suspected was a traditional nest site. When the same individuals rejoined for the 1976 nesting season they initially roosted in the area that was used so frequently in summer 1975; then, about 20 days before the female laid eggs, both birds abruptly moved to a new roost area about 0.6 km south of the 1975 roost and subsequently nested there. Again, both the new nest and the suspected site of the old nest (1975 roost area) were located near the center of the home range areas utilized by both pair members (Fig. 7).

In both cases where new nest sites were chosen, the owls first returned to the old nest site and behaved as if they were going to nest there again. In the case of the ML female in 1976, for instance, she began to roost each day near the old (1975) nest beginning on 14 February and continued to do so until 20 March, approximately 17 days before she laid eggs. Then she abruptly moved to the new nest site where she eventually nested.

Spacing of Resident Pairs

On the HJA and surrounding areas, the mean nearest neighbor distance between nest areas of resident pairs was 2.88 km (Table 5). In 11 other areas in western Oregon that were searched intensively for spotted owls, mean nearest neighbor distances ranged from 1.68 to 3.04 km, with an overall average of 2.40 km (Table 5). The shortest distance between 2 active nests was 1.41 km. On all of the above areas old-growth and mature forests were either relatively continuous or were distributed in discontinuous tracts interspersed among cutover areas. In general, if tracts of old-growth forest were fairly large (at least 80 ha) and were spaced not more than 1.5 km apart, then pair spacing was about the same as occurred in more continuous forests (Table 5).

The spacing of spotted owl pairs in western Oregon was similar to spacing patterns described for spotted owls in California and the southwestern U.S. by Marshall (1942). Marshall found that pairs of spotted owls were usually spaced 1.6 to 3.2 km apart in areas where suitable habitat was available.

Estimates of defended areas derived from the mean nearest neighbor distances in western Oregon ranged from 222 to 726 ha ($\bar{x}$ = 465 ha) (Table 5). Although the closest pair spacing was observed in the Coast Range (Table 5), the overall mean nearest neighbor distances for the Coast Range and western Cascades (2.34 km in the Coast Range and 2.49 km in the western Cascades) were not significantly different ($t = 0.62$, d.f. = 10, $0.25 < p < 0.30$).

In nearly all areas where spotted owls were found on the east slope of the Cascade Range, pairs were widely spaced compared to areas west of

Table 5. Spacing between spotted owl pairs in 14 different areas in Oregon.

Location name	Lat.-long.	Number of pairs	Mean nearest neighbor distance (km)	Range of nearest neighbor distances (km)	Estimated size of defended area based on mean nearest neighbor distance (ha)
		West slope of the Cascade Mountains			
Hills Creek	44°42'-122°21'	5	2.19	1.91-2.51	376
Bagby Spring	44°55'-122°10'	5	2.41	2.21-2.61	456
Steamboat	43°29'-122°45'	7	2.22	1.76-2.72	388
H.J. Andrews	44°14'-122°15'	8	2.88	2.41-3.31	654
Mosby Creek*	43°35'-122°52'	10	2.74	1.61-5.13	589
		Coast Range and Siskiyou Mountains			
Smith River*	43°45'-123°24'	5	2.01	1.71-2.31	318
Tyee Rookery*	43°27'-123°30'	4	2.38	1.91-2.82	445
Radar Creek*	43°26'-123°38'	14	2.31	1.41-3.77	420
Lorane Area*	43°51'-123°24'	10	2.78	2.26-4.52	606
Mary's Peak	44°31'-123°30'	3	2.19	1.86-2.51	376
Secret Creek	42°27'-123°41'	5	1.68	1.41-2.21	222
Mt. Emily*	42°14'-124°07'	5	3.04	1.76-3.77	726
		East slope of the Cascade Mountains			
Lake of the Woods*	42°22'-122°14'	24	3.09	1.58-4.31	749
Abbot Butte*	44°35'-121°43'	3	4.90	3.42-6.39	1887

Average nearest neighbor distances

Coast Range and Siskiyou Mountains = 2.34 km
West slope of the Cascades = 2.49 km
East slope of the Cascades = 3.99 km

*Locations where suitable habitat was distributed in discontinuous blocks as opposed to areas in which habitat was relatively continuous.

the Cascade crest (Table 5). The wider spacing of pairs on the east slope of the Cascades appeared to result from the patchier distribution of suitable habitat on the east slope.

Territorial Behavior

During 261 nights of observation on the HJA, I observed only 12 territorial interactions. The paucity of territorial interactions was apparently due to the wide spacing of pairs and the fact that the owls were relatively quiet when away from their nest areas. At night during the spring and summer all of the owls called occasionally while away from their nest areas, but if there was no response they usually became silent after calling only a few times. Home range areas were so large that neighboring birds frequently were not within hearing distance even if one or the other did call, and as a result, no interaction occurred. If another territory holder was within hearing, however, it would usually respond by calling. The nature of the subsequent interaction was dependent upon the sex of the individuals involved and the location of each individual relative to its home range area. In general, if 2 individuals were of the same sex and if 1 individual was outside its usual home range area, then the latter individual would retreat from the former and stop calling. If the interaction occurred in an area of home range overlap and both birds were of the same sex, they usually approached each other and then chased each other from tree to tree as they called back and forth at close range. One interaction of this type between the BRR male and an unmarked male lasted 132 minutes. Territorial interactions between birds of the same sex did not always escalate into encounters at close range. On at least 1 occasion, the Mona pair and the BRR female called from opposite sides of Blue River Reservoir without ever approaching closer than 300 meters.

Territory holders did not appear nearly as aggressive in rebuffing members of the opposite sex encountered on or within the home range. Three interactions were observed that involved a male and female from adjacent home ranges and in all 3 cases the owls did not retreat from each other, even when 1 individual had wandered well inside the home range of the other. Instead, the owls called rather excitedly and then remained near each other for some time before eventually moving apart. In addition to these male-female interactions the W2 female was found roosting within 50 m of males other than her regular mate on 2 occasions during the winter and the BRR male was found roosting near females other than his regular mate on 3 occasions.

The defense of home range areas did not appear to fit the classical concept of a defended territory with relatively discrete boundaries (Howard 1920). Home ranges were so large that they could not be defended consistently, and as a result territorial defense appeared to take the form of a decreasing zone of influence around each nest area during the reproductive season. Areas near each nest were defended fairly consistently, but with increasing distance from the nest it became increasingly difficult for the resident pair to detect intruders, and defense became increasingly inconsistent. It was common, for instance, for one individual to trespass well inside the home range of another without being detected simply because the other owl was out of sight and hearing. None of the owls regularly patrolled their entire home range areas; to do so would almost certainly have resulted in the aggressive neglect (Ripley 1961) of other duties. Rather than distinct boundaries between territories, therefore, there appeared to be broad areas of overlap contested occasionally by all parties, but defended consistently by none.

Territorial behavior and social behavior in general declined during winter and increased during spring and summer. During mid-winter (November-January) when the owls were largely solitary, they called infrequently, and territorial interactions were uncommon (1 occurrence). After the resident male and female on each territory began to roost togehter again in late February or March, they became more vocal, and began to interact more frequently with neighboring pairs. The increased level of territorial activity continued through the summer, and then declined again in October.

Changes in Territory Holders

During the radiotelemetry study 1 of the radio-tagged pairs was apparently displaced from its territory by another pair. When the study began, the BRR male and female occupied a relatively discrete home range area along the eastern shore of Blue River Reservoir and extending east about 3 km (Fig. 8). The pair did not nest in 1975, but that did not seem unusual because 3 of the other 4 pairs studied also did not nest that year. The BRR pair behaved unusually, however, in that they roosted together infrequently during the summer; by fall of 1975 both birds began to spend much of their time wandering over extensive areas, including the home ranges occupied by the W2 and Mona pairs. The reason for this rather erratic behavior was unknown. The BRR pair returned to the traditional nest area in 1976, but again did not nest, and roosted together only occasionally. At the same time an unmarked female appeared in the area. This new female had white-tipped retrices, indicating that she was 1 to 2 years old (see Forsman 1976 for age determination). On the evening of 10 April the BRR female and male and the unmarked female were involved in an extremely vocal and aggressive dispute near the traditional nest area. Instead of retreating, the juvenile female flew around in the forest canopy with the BRR female as both called excitedly. Both females were diving at each other and several times it sounded as if they actually struck each other. While the females were chasing each other, the male perched nearby and called excitedly but never joined in the chasing behavior. The chasing behavior stopped after about 13 minutes but all 3 owls continued to call in the area for another 50 minutes. For several days following this encounter the BRR male was found roosting with the new female near the traditional nest area. The BRR female, on the other hand, left the traditional nest area and spent the remainder of the study period wandering within the home range areas of the Mona pair and an unmarked pair just outside the study area. After a few days the BRR male also began to wander again and on 18 May the unmarked female was found roosting with an unmarked 1- to 2-year-old male about 400 m from the traditional BRR nest site. The study ended before I could determine what happened to the BRR pair but in 1977 and 1978 the BRR nest area was occupied by a pair other than the original BRR pair. It appeared, therefore, that the original BRR pair was permanently displaced.

The expulsion of an established adult pair by a pair of juveniles seemed unusual because it contradicted the generally accepted belief that territory holders have a psychological advantage over individuals attempting to enter the territory. I suspected, therefore, that the outcome of the interaction between the BRR pair and the unmarked juvenile pair was unusual.

Habitat Selection for Foraging

Chi-square values obtained by comparing the number of observed and expected fixes in the different cover types indicated that all of the radio-tagged owls used the available habitat within their home range areas in a manner significantly different from expected. Therefore, the Bonferroni $\underline{z}$ statistic was used to determine which cover types were preferred or avoided. The following discussion summarizes the results for each owl and each cover type on the study area. A list of cover types on the study area is included in Appendix 1, and results of habitat preference tests for each owl are shown in Appendix 2; Table 6 summarizes the data from Appendix 2.

Old-Growth Conifer Forest (Cover Type 0100)

Old-growth conifer forests were the most abundant cover type on all home range areas and were the preferred foraging habitat for all of the radio-tagged owls (Table 6, Appendix 2). For the habitat selection analysis I did not distinguish between the different old-growth species associations on the study area because they integrated to such an extent that it was usually impossible to accurately map were 1 type stopped and

Table 6. Utilization of cover types for foraging by 8 radio-tagged adult spotted owls on the H. J. Andrews study area, May 1975 to June 1976[1].

Cover type	Proportion of cover within owl owl home ranges	Proportion of fixes occurring in cover type	No. of owls using type sig. less than expected	No. of owls using type in proportion to occurrence	No. of owls using type sig. more than expected
0100	0.358-0.636	0.851-0.986	0	0	8
0115	0.006-0.028	0-0.044	4	2	0
0200	0.013-0.083	0-0.042	3	3	0
0300	0.020-0.183	0-0.115	3	1	1
0400	0.006-0.099	0-0.018	2	3	0
0500	0.009-0.017	0-0.008	2	1	0
0600	0.025-0.187	0-0.005	7	0	0
0700	0.023-0.127	0	5	1	0
0800	0.019-0.084	0	7	0	0
0900	0.013-0.099	0	6	0	0
0809	0.056-0.099	0-0.065	8	0	0
1000	0.013-0.024	0	2	0	0
1100	0.003	0.051	0	0	1
1200	0.014-0.021	0-0.003	4	0	0
1300	0.021	0.017	0	1	0
1700	0.016-0.057	0	4	0	0
1900	0.022	0	1	0	0
Other	0.007-0.031	0-0.009	5	3	0

---

[1] All 8 owls were not tested for each cover type because some cover types did not occur in all home ranges or were so uncommon in some home ranges that statistical testing would not have been meaningful. In the latter case, the cover type was added to the "other" category.

another started. However, my subjective impression was that the owls did not prefer any particular old-growth association over the others.

Old-growth associations of Douglas-fir and western hemlock that had been selectively thinned (cover type 0115) covered 1 to 3 percent of individual home range areas (Table 6). Most thinnings in this type were confined to the removal of dead or damaged trees adjacent to roads; the effect of this type of harvest was to reduce canopy closure slightly and to reduce the number of fallen trees and standing dead trees. In all cases, utilization of the 0115 Cover Type was either not significantly different than expected or significantly less than expected (Table 6). It appeared, therefore, that although owls utilized thinned old-growth forests for foraging they did not prefer them if unthinned old-growth stands were available.

Mature Forest (Cover Types 0200 and 0300)

This category included mixed forests of Douglas-fir and western hemlock or silver fir and mountain hemlock between 80 and 200 years old (Fig. 5). These stands were subdivided into cover type 0200 (121- to 200-year-old stands) and cover type 0300 (81- to 120-year-old stands). Stands of this age were most common on the higher ridges where fires had occurred in the 1800's. They were also common at lower elevations in some areas, especially within the home range occupied by the Mona female. Development of understory trees and shrubs varied considerably between stands; some stands consisted mostly of tall straight trees with little understory development while others included well developed understories of western hemlock or silver fir, or both. For the habitat analysis no attempt was made to differentiate among stands with different amounts of understory development or with slightly different species composition. Stand composition and understory development within and among stands was so variable that any attempt to further subdivide the stands would have made the analysis too complex. Furthermore, the expected number of fixes in the 0200 and 0300 cover types was so small that further subdivisions of the types would have precluded statistical testing in some instances.

In all cases, utilization of the 0200 cover type was either not significantly different than or significantly less than expected. Similar results were obtained for the 0300 cover type except that one owl (BRR male) used this type significantly more than expected (Table 6). The considerable individual variation in utilization of the 0200 and 0300 cover types allowed no clear conclusions about preference for foraging except that mature forests were generally not preferred foraging habitat relative to old-growth forests.

Second-growth Forests (Cover Types 0400 and 0500)

Cover type 0400 (61- to 80-year-old forests) was characterized by stands of Douglas-fir trees that were 30 to 40 m tall and relatively uniform in diameter. Stands in cover type 0500 (31- to 60-year-old forests) were typically composed of Douglas-fir saplings or pole-sized trees 15 to 40 m tall and 20 to 60 cm dbh. Canopy closure and density in 31- to 60-year-old forests varied considerably from dense stands on north aspects to moderately dense pole stands on drier south aspects.

Neither of these cover types was particularly abundant on the study area and, as a result, expected utilization values were too small in some cases to conduct statistical tests for preference. In those instances where tests could be made the results were similar to those observed for mature forests (Cover Type 0200). Utilization was either not significantly different or significantly less than predicted, indicating that the 0400 and 0500 cover types were not preferred foraging habitat relative to old-growth forests (Table 6).

Clear-cut Areas and Recent Burns

Vegetation on clear-cut or burned areas ranged from grass-forb associations on newly harvested areas to dense stands of 20- to 28-year-old Douglas-fir saplings on the older clear-cut units and burns (cover types 0600, 0700, 0800, 0900, 0809, 1000, 1200). Most owls did not use these cover types for foraging (Table 6), although they did occasionally fly across cutover areas enroute from one stand of older forest to another. The only exception to this pattern was the occasional utilization of 5- to 14-year-old shrub -conifer associations (cover type 0809) by the W2 male and W2 female (Table 12). The W2 male foraged in the latter type on 4 different nights (27 fixes) during June and July 1975. All but one of the fixes for the W2 male in this cover type were in Watershed 1, a 96 ha area that had been clear-cut between 1964 and 1966. At the time of the study, vegetation on Watershed 1 consisted of a mixture of deciduous shrubs, ferns, scattered 5- to 8-year-old Douglas-fir trees, and openings with sparse herbaceous vegetation (Fig. 6). Trunks of fallen trees left after logging operations were scattered among the regenerating trees and shrubs. The W2 female foraged in the 0809 cover type on two occasions (6 fixes). In both instances she utilized clear-cut units where the vegetation was similar to that on Watershed 1. Although the W2 pair did use the 0809 cover type occasionally, they used it significantly less than expected, indicating that like the other owls studied, they usually avoided this type. It appeared, therefore, that clear-cut or burned areas provided little foraging habitat for at least 30 years following harvest.

Deciduous Riparian Forest (Cover Type 1300)

In a few areas along Lookout Creek there was a 100- to 150-m-wide corridor of mature and old-growth riparian forest dominated by bigleaf maple (Acer macrophyllum) with variable amounts of western hemlock, red alder (Alnus rubra), western redcedar and Douglas-fir (cover type 1300). Within the home range of the ML female, where this cover type was most abundant (2 percent of the area) there was no significant difference between observed and expected utilization values for this type, indicating that it was neither avoided nor preferred as a foraging habitat (Table 6). Forests of this type in the home range areas of the other radio-tagged owls were so uncommon that meaningful preference tests could not be made.

Alder Brushfields

Dense stands of shrub-like sitka alder (Alnus simulata) occurred in a few areas on the higher ridges and mountainsides where winter snow accumulations were heavy. These sitka alder communities were lumped with other shrub cover types (cover type 0900). No foraging was observed in sitka alder communities although some owls did forage in the mature and old-growth forests of silver fir, mountain hemlock, western hemlock and Douglas-fir that bordered the alder brushfields.

Talus Outcrops and Rockslides (Cover Type 1100)

Natural talus outcrops and rockslides below road cuts were a preferred foraging habitat for the W2 male between June and September 1975 when pikas (Ochotona princeps) were active in the rocky rubble (Table 6). On at least 8 different nights during this period the W2 male was observed perched in trees or on stumps or fallen logs overlooking rocky hillslides. Pikas were common in rockslides and were apparently the stimulus for foraging in such areas. Foraging in rock talus ceased entirely after about 15 October, probably because pikas sharply curtailed their above-ground activities during the winter months. The other owls studied did not demonstrate a preference for rockslides, although the BRR male did forage in this type on at least two occasions. With the exception of the W2 male, however, this evaluation of preference for the rock talus cover type was necessarily subjective; so little rock talus was present within the home range areas of the other owls that statistical tests for preference could not be made.

Miscellaneous Cover Types

Miscellaneous cover types included Blue River Reservoir, 7 small rock quarries, a golf course, a forested public campground, a cleared strip beneath a powerline, bare rock outcrops, a small cleared agricultural field and a 9.4 ha area of old-growth Douglas-fir that had been harvested by the shelterwood method (see Appendix 2). All trees on the latter area had been harvested except for scattered old-growth trees spaced 20 to 30 m apart. Douglas-fir seedlings were planted on the cutover area but the ground was otherwise bare except for scattered grasses, forbs and shrubs. Foraging was observed in the miscellaneous cover types on only two occasions--once when the W2 male foraged in a small rock quarry and once when the Mona female foraged within the public campground. Although Blue River Reservoir was partially drained during the winter, exposing extensive mudflats and gravel bars, foraging was never observed within the exposed area or on the grassy slopes bordering the reservoir. Except for the reservoir, expected utilization values for all miscellaneous cover types were too small for statistical preference tests.

Roads

Narrow secondary gravel roads were common on the study area. These roads were not treated as a separate cover type. When a road occurred within a cover type, the area of the road surface was treated as if it were part of the cover type within which it occurred. Assuming that roads were equally common in all cover types, this approach should not have influenced the habitat utilization analysis.

All of the radio-tagged owls regularly foraged in forests bordering roads. It did not appear, therefore, that these secondary roads greatly affected habitat quality. Vehicle traffic also did not appear to interfere with foraging activity. On numerous occasions when vehicles were driven past owls that were foraging 10 to 50 m from the edge of a road, the owls continued to forage in the same area.

Seasonal Differences in Habitat Selection

Seasonal differences in habitat selection for foraging were relatively small. During all seasons, foraging was essentially limited to forested areas, especially old-growth forests. During mid-winter (December-February), when approximately 85 percent of the diet consisted of arboreal mammals (see Food Habits) the owls foraged almost totally in forested areas. During the rest of the year, rock talus and recent clear-cuts were used occasionally but over 90 percent of foraging still occurred in forests over 30 years old.

Habitat Selection for Roosting

Of 1,098 roost sites located during the study, 97 percent were in old-growth forests, indicating that all of the owls preferred such forests for roosting. The 27 roosts located in cover types other than old-growth included 26 in forests that were between 30 and 200 years old and 1 in a dense stand of 20- to 30-year-old trees (Table 7). The owls usually roosted on limbs in trees or rarely on uprooted stumps or other debris on the ground (Table 8). With the exception of incubating or brooding females, no owls were observed roosting in cavities in trees.

Although roosting usually occurred in old-growth forests, the type of roost utilized varied with weather conditions. Perch height averaged significantly lower on hot summer days than during overcast, cold or wet weather (Table 8). On warm or hot days the owls usually roosted low in the forest understory in small second-growth trees whereas when it was cold, overcast, raining or snowing, the owls preferred to roost in the forest overstory in large trees (Table 14). In addition, when it was

Table 7. Utilization of cover types for roosting by adult spotted owls on the H. J. Andrews study area, May 1975 to June 1976.

	Number of roosts located in different cover types									
Cover type	BRR male	BRR female	W2 male	W2 female	Mona female	ML female	MC male	MC female	Total	Percent
0100	148	164	167	194	114	113	101	63	1,064	96.9
0115	0	4	1	0	0	2	0	0	7	0.7
0200	0	0	1	0	0	0	1	0	2	0.2
0300	6	1	0	2	3	0	0	0	12	1.1
0400	4	0	0	2	0	0	0	0	6	0.5
0500	6	0	0	0	0	0	0	0	6	0.5
0600	0	1	0	0	0	0	0	0	1	0.1
TOTALS	164	170	169	198	117	115	102	63	1,098	100.0

[1] Cover types are described in text and Appendix 1.

Table 8. Characteristics of roost perches utilized by adult spotted owls under different weather conditions on the H. J. Andrews study area, May 1975 to June 1976.

	Weather conditions				
Variable measured	Clear and hot ($T \geq 28^{\circ}C$)	Clear and warm ($10^{\circ}C<T<28^{\circ}C$)	Clear and cold ($T < 10^{\circ}C$)	Overcast with little or no precipitation	Overcast with steady or intermittent rain or snow
Number of roosts examined	12	78	69	69	103
Mean perch height (m)	3.6	10.1	20.4	18.7	23.5
Mean distance between owl and nearest tree trunk (cm)	100	78	85	71	30
Mean dbh of roost trees (cm)	18	45	88	85	115
Percent of roosts in trees older than 250 years	0	15.4	55.1	52.2	77.7
Percent of roosts in trees between 80 and 250 years old	0	0	4.3	1.4	3.9
Percent of roosts in trees younger than 80 years old	100.0	83.3	40.6	43.5	18.4
Percent of roosts not in trees	0	1.3	0	2.9	0
Percent of roosts in perch[1] category A	100.0	98.7	92.8	76.8	41.7
Percent of roosts in perch category B	0.0	1.3	7.2	23.2	58.3

[1] Perch categories A and B refer to the amount of overhead protection provided by the roost against rain and snow. Category A included roosts in which owls perched out on limbs away from the trunk where they were not protected by an overhanging trunk or by large overhanging limbs. Category B included roosts in which owls either roosted close against the trunk under overhanging limbs or roosted on the underside of a leaning tree trunk.

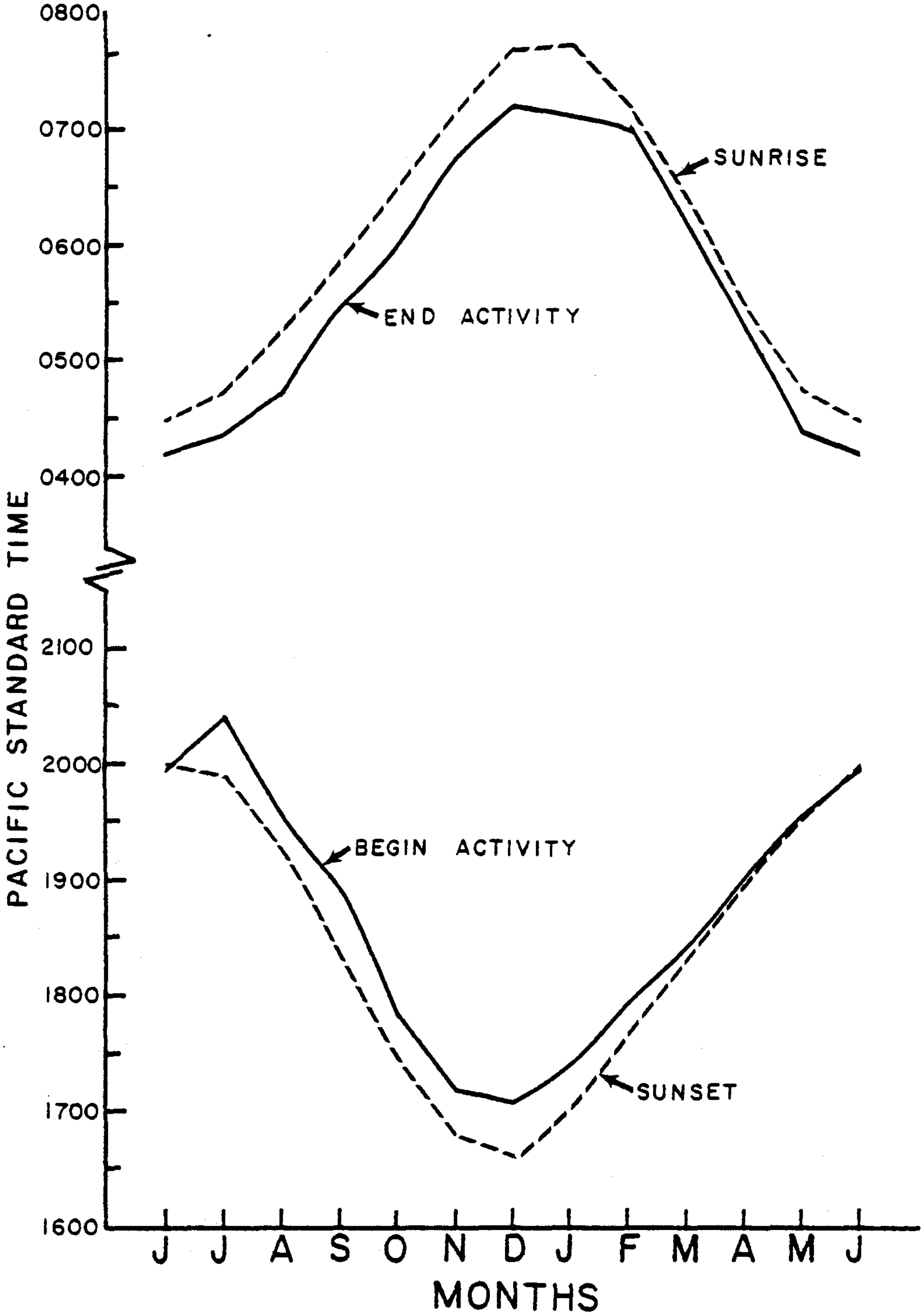
raining or snowing the owls tended to roost closer to the trunk of the perch tree and under some sort of overhead cover such as a leaning tree trunk or overhanging limbs (Table 14).

Roost selection appeared to be influenced by thermoregulatory considerations, as suggested by Forsman (1976) and Barrows and Barrows (1978). In old-growth forests on the HJA, temperatures in the understory averaged more than 1°C cooler than in the overstory during all seasons of the year (W. C. Dennison pers comm. 1979). By roosting in the shade of the understory during warm weather, the owls reduced their exposure to high temperatures and solar radiation (Forsman 1976, Barrows and Barrows 1978). By roosting in the overstory during cold or wet weather, the owls apparently avoided lower temperatures near the ground and increased their exposure to solar radiation. Both strategies should have reduced the metabolic energy expenditure required for thermoregulation.

Diel Activity Patterns

Spotted owls on the HJA were primarily but not entirely nocturnal. On the average, they left their day roosts to begin foraging at 14 min after sunset (range = -54 to +60 min) and stopped foraging at 21 min before sunrise (range = -45 to +6 min) (Fig. 15). Activity generally began earlier (in relation to sunset) during the spring and early summer than during fall and winter (Fig. 15), a response that may have been due to greater energy requirements during the nesting period. After selecting a roost at dawn, the owls usually remained in the same tree until sunset. Some diurnal activity did occur, however. On 9

Fig. 15. Diel (24 hour) activity pattern of spotted owls on the H. J. Andrews study area, June 1975 to June 1976. The average time when owls began and ended activity was calculated for each month (solid lines). Dashed lines indicate average time of sunset and sunrise by month.


0800
0700
0600
0500
0400
2100
2000
1900
1800
1700
1600
PACIFIC STANDARD TIME
SUNRISE
END ACTIVITY
BEGIN ACTIVITY
SUNSET
J
J
A
S
O
N
D
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F
M
A
M
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MONTHS

different occasions I saw spotted owls leave their day roosts to attempt to capture diurnal or crepuscular mammals in the vicinity of a day roost. The longest distance moved during one of these diurnal foraging flights was about 60 m. I also found that spotted owls would readily leave their day roosts to capture live mice tethered on the ground beneath roost trees. They also made occasional short flights during the day to retreive stored prey or to bathe in springs or streams near their roosts or to join a mate roosting in a nearby tree. The longest distance moved during 1 day for any type of activity was approximately 250 m; this occurred when I called in an occupied territory and the resident female flew across a forested canyon to intercept the suspected intruder. All types of diurnal activity increased during the spring and summer when the owls were paired.

The relative infrequency of diurnal foraging activity was also indicated by the low occurrence of diurnal animals in the diet (see Food Habits). Only 4.5 percent of the prey captured on the HJA were diurnal animals and I suspected that many of these were captured either at night or during periods of crepuscular activity. The percent of diurnal prey in the diet varied only between 4 and 6 percent by season, indicating that seasonal differences in the amount of diurnal foraging were negligible.

Rate of Movement While Foraging

The owls foraged at night by moving from perch to perch, apparently watching and listening for potential prey. Time spent at individual perches ranged from only a few seconds to over 6 hours. The average rate of movement while foraging in this manner was 247 m/hour (range = 0-1,086 m) (Table 9). The average distance moved each night was 2,782 m (range = 320-8,895 m). All estimates of distance moved were considered minimums because it was impossible to detect all of the short flights that owls made while foraging.

Rate of movement while foraging was highest during the spring and summer and lowest during the fall and winter (Table 9). Reproduction and the behavior associated with it appeared to have the greatest influence on rate of movement during different seasons; the average distance moved per hour by nesting individuals between May and June (when they were feeding nestlings) was 593 m, compared to only 206 m between October and February. Once their eggs hatched, nesting birds (except for brooding females) were almost constantly moving between foraging areas and nest sites during the night. For non-nesting individuals, the increase in rate of movement during the spring was not as pronounced but was still apparent (345 m/hour during spring as opposed to 206 m/hour during winter). Regardless of their nesting status owls had less time to forage during the short spring and summer nights than during fall and winter and may have compensated by spending less time resting at night during spring and summer.

On the average, owls moved less during periods when it rained or snowed (Table 9). However, when the data were examined on a seasonal basis the only consistent relationship between weather and movement was that movement ceased almost altogether when heavy rains were accompanied by strong winds (Table 9). I concluded, therefore, that seasonal

Table 9. Average rate of movement (in m/hour) of spotted owls while foraging under different weather conditions and during different seasons on the H. J. Andrews study area[1].

	Period				
Weather conditions	March-April	May-June	July-Sept.	Oct.-Feb.	Means
Clear, no precipitation	203	532	283	197	304
Overcast, no precipitation	-	530	316	192	329
Intermittent rain or snow	286	297	312	231	244
Steady rain or snow	178	302	345	194	242
Rain or snow and strong winds (>32 km/hour)	-	-	-	32	-
Means	209	488	293	206	247

[1] Data compiled from 8 adults.

weather patterns were responsible for little if any of the seasonal differences in rate of movement.

In contrast to the regular seasonal trends in rate of movement, nightly patterns of movement were unpredictable. For instance, at any time of the night it was common for individuals to stop moving and stay in one small area (radius < 50 m) for several hours. On 2 occasions, owls remained almost stationary for over 24 hours. These quiescent periods did not seem to fit any recurring pattern, possibly because 2 of the major variables affecting movement at night (prey encounters and prey capture) occurred on an unpredictable schedule. When owls captured large prey animals (e.g., squirrels, woodrats, hares), they commonly stored what they could not eat and remained in the vicinity until the prey was consumed; this response to prey capture was verified on several occasions when owls stopped moving in the middle of the night and were found roosting the next morning near a stored prey animal. The capture of prey probably did not occur at regular times each night and, as a result, periods when owls stopped moving were unpredictable.

Food Habits

In 3 years between 1972 and 1976, 753 prey items were identified from pellets or kills of spotted owls on the HJA. Mammals comprised 93.3 percent of all prey taken and birds and insects comprised 3.0 and 3.6 percent, respectively (Table 10). Seven species of mammals comprised the nucleus of the diet, the flying squirrel (Glaucomys sabrinus), red tree vole (Phenacomys longicaudus), western red-backed vole (Clethrionomys occidentalis), deer mouse (Peromyscus maniculatus),

Table 10. Composition of the diet of spotted owls on the H. J. Andrews study area during 1972, 1975, 1976.

Prey[1] species	Percent of prey in diet 1972 (n=182)	Percent of prey in diet 1975 (n=99)	Percent of prey in diet 1976 (n=472)	Total numbers N	Total numbers Percent	Total biomass Grams	Total biomass Percent
MAMMALS							
Glaucomys sabrinus	27.5	32.4	50.0	318	42.2	36,570	57.3
Phenacomys longicaudus	12.1	12.1	13.4	97	12.9	2,619	4.1
Clethrionomys occidentalis	1.7	7.1	11.9	66	8.8	1,518	2.4
Peromyscus maniculatus	17.0	10.0	5.1	68	9.0	1,496	2.3
Thomomys mazama	6.0	10.1	1.7	29	3.9	2,523	4.0
Lepus americanus	4.9	6.1	0.8	19	2.5	9,930	15.6
Neotoma cinerea	2.2	2.0	2.1	16	2.1	4,240	6.6
Eutamias townsendi	0.6	3.0	1.1	9	1.2	720	1.1
Microtus oregoni	3.3	1.0	1.5	14	2.0	266	0.4
Sorex spp.[2]	6.0	1.0	2.1	22	2.9	220	0.3
Unidentified mouse or vole	1.7	3.0	3.4	22	2.9	550	0.9
Other mammals	4.4	8.1	1.5	23	2.9	1,968	3.1
BIRDS							
Small diurnal birds	3.9	0.0	2.1	17	2.3	616	1.0
Small owls	1.1	1.0	0.4	5	0.7	536	0.8
INSECTS	7.1	3.0	2.3	27	3.6	16	T[3]
REPTILES							
Thamnophis spp.	0.5	0.0	0.0	1	0.1	50	0.1
TOTALS	100.0	100.0	100.0	753	100.0	63,838	100.0

[1] Common names of prey are given in Appendix 3.

[2] Prey not specifically identified in table are listed in Appendix 3.

[3] Trace

western pocket gopher (Thomomys mazama), snowshoe hare (Lepus americanus) and bushytailed woodrat (Neotoma cinerea) (Table 10). In all years the principle prey in terms of numbers and biomass was the flying squirrel, a nocturnal arboreal mammal.

Dietary composition differed significantly between years (Chi-square = 112.6, d.f. = 20, $p < 0.005$) (Table 10). Fluctuating prey populations may have been responsible for some of the differences between years, but much of the variability was probably due to seasonal differences in the periods of data collection. Data were collected between March and September in 1972, between May and December in 1975 and between January and June in 1976. Comparisons of data collected during different seasonal periods may have introduced seasonal variation into the analysis as will become apparent in the next section.

Seasonal Changes in Diet

The percent composition of the flying squirrel in the diet changed considerably during the year, apparently in response to seasonal changes in prey abundance and vulnerability (Table 11). In general, arboreal mammals were less common in the diet during the late spring and summer (May-August) when other sources of food became available and increased in the diet during fall and winter (September-February) as alternative sources of food became less abundant (Table 11).

With the onset of cold, wet weather in October, insects became less active and by mid-November chipmunks (Eutamias townsendi) were in hibernation. Snowshoe hares were very uncommon in the diet after September as juvenile hares produced during the spring and summer

Table 11. Percent frequency of major prey species in the diet of spotted owls during different seasons on the H. J. Andrews study area, May 1975 to June 1976.

Species	May-Aug. (Summer) n = 206	Sept.-Nov. (Fall) n = 20	Dec.-Feb. (Winter) n = 66	Mar.-Apr. (Spring) n = 282
Glaucomys sabrinus	34.5	60.0	66.7	50.3
Phenacomys longicaudus	11.6	5.0	18.2	13.5
Clethrionomys occidentalis	6.3	0.0	3.0	17.0
Peromyscus maniculatus	12.6	5.0	1.5	3.2
Other mammals, birds, insects	35.0	30.0	10.6	16.0
TOTALS	100.0	100.0	100.0	100.0
	Chi-square = 77.4, d.f. = 12[1]			

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[1] Chi-square computed from numbers of prey in diet. $P < 0.005$.

became too large for the owls to capture easily. Between December and February, a permanent snowpack developed over much of the area. This snowpack probably made terrestrial and subterranean mammals such as deer mice, red-backed voles, gophers, pikas, creeping voles (Microtus oregoni), shrew moles (Neurotrichus gibbsii) and shrews (Sorex spp.) less vulnerable to predation because these animals spent considerable time tunneling beneath the snow. Birds became less abundant as migrants left the area in late summer. As a result of these supposed changes in prey availability the number of species in the diet declined during the late fall and winter. When snow covered the ground between December and February, 85 percent of the prey consisted of flying squirrels and red tree voles (Table 11).

During spring and summer (March-August), the number of species in the diet increased and the number of arboreal mammals in the diet declined (Table 11). The increased number of species in the diet appeared to reflect several factors, notably recruitment among small mammals and birds, increased above-ground activity by subterranean and terrestrial mammals, emergence of hibernators and insects, and the return of migrant birds.

Although never taken in large numbers, the snowshoe hare became an important part of the diet in terms of biomass during the late spring and summer. The pattern of predation upon the snowshoe hare was directly related to its reproductive cycle. Juvenile hares appeared in the owl diet in April, soon after the first hares of the year were born. Thereafter, predation upon juvenile hares continued through the summer and then practically ceased by the end of September. Of the snowshoe hares captured by owls during the study, 74 percent weighed less than 600 grams and 84 percent weighed less than 900 grams. The largest hare captured weighed approximately 1,500 grams.

Seasonal and Daily Food Requirements

Calculated separately for 3 seasons, the mean biomass consumed per owl per day on the H. J. Andrews ranged from 77.6 to 164.8 g ($\bar{x}$ = 109.2 g) (Table 12). The estimates of 77.6 and 85.4 g per owl per day for winter and early spring, respectively, indicated a rate of food intake within the range reported for other small or medium-sized owls (Table 13) (Graber 1962). However, the estimate of 164.8 g per owl per day obtained for the summer period indicated an unreasonably high rate of food intake. I believe that small sample size may have resulted in an inflated estimate of the mean number of prey per pellet during the summer period; as a result, food consumption was overestimated.

The seasonal estimates of prey consumed on the HJA indicated that a typical individual consumed 479 prey per year and that a typical non-nesting pair consumed 958 prey per year of which 46 percent were flying squirrels and 13 percent were red tree voles (Table 14). Data for nesting pairs during the period when they were feeding young were inadequate to estimate biomass consumed per day; assuming, however, that a pair with 2 young required twice as much food as a non-nesting pair between May and August (the period when young were being fed), then the nesting pair would have captured 1,468 prey per year, including 620 flying squirrels (Table 14). All of the above estimates of annual

Table 12. Estimated daily, seasonal and total biomass consumed by an adult spotted owl on the H. J. Andrews study area.

	Sept.-Feb. (Fall-Winter)	Mar.-Apr. (Spring)	May-Aug. (Summer)
Average number of prey per pellet	0.7	1.05	2.07
Number of days in period	182	61	123
Number of prey consumed	158	65	256
Total biomass consumed (gm)	14,121	5,210	20,273
Biomass consumed per day (gm)	77.6	85.4	164.8

Table 13. Comparison of body weight and food consumption in 4 species of owls[1].

Owl Species	(A) Body Weight (grams)	(B) Biomass Consumed (grams)	(B)/(A)[2]
Saw-whet owl (*Aegolius acadicus*)	M = 75 F = 91	13, 18[3]	14.3-24.0
Long-eared owl (*Asio otus*)	M = 245 F = 279	51	18.2-20.8
Short-eared owl (*Asio flammeus*)	M = 315 F = 378	53	14.0-16.8
Spotted owl	M = 582 F = 637	78, 85, 165[4]	12.2-28.3

[1] Estimates of biomass consumed by saw-whet, long-eared and short-eared owls were derived from data on free living owls presented in Graber (1962). Mean adult weights are from Earhart and Johnson (1970).

[2] For simplification, I assumed that males and females consumed equal biomass.

[3] Data on the saw-whet owl were from 2 different roosts, thus 2 estimates.

[4] Data represent estimates for 3 seasonal periods.

Table 14. Estimated number of prey consumed on a seasonal and total basis by spotted owls on the H. J. Andrews study area.

Prey species[1]	Number captured per season per individual			No. captured per year per individual	No. captured per year per non-nesting pair	No. captured per year per nesting pair
	Sept.-Feb. (fall-winter)	Mar.-Apr. (spring)	May-Aug. (summer)			
Glaucomys sabrinus	101	33	88	222	444	620
Phenacomys longicaudus	23	9	30	62	124	184
Clethrionomys occidentalis	4	11	16	31	62	94
Peromyscus maniculatus	4	2	32	38	76	140
Neotoma cinerea	4	1	6	11	22	34
Thomomys mazama	0	T[2]	20	20	40	80
Lepus americanus	0	1	9	10	20	38
Eutamias townsendi	2	1	3	6	12	18
Tamiasciurus douglasii	0	0	1	1	2	4
Microtus oregoni	0	T	8	8	16	32
Neurotrichus gibbsii	0	T	1	1	2	4
Avicola richardsoni	0	T	0	1	2	2
Scapanus orarius	0	T	0	1	2	2
Ochotona princeps	0	T	4	4	8	16
Zapus trinotatus	2	T	1	3	6	8
Sorex spp.	0	1	9	10	20	38
Unidentified voles and mice[3]	15	2	10	27	54	74
Small birds	2	2	6	10	20	32
Insects	1	1	11	13	26	48
TOTALS	158	65	256	479	958	1,468

[1] Common names of all prey species are given in Appendix 3.

[2] T means that on the average, less than 1 individual was captured per seasonal period.

[3] Most of the unidentified mice or voles were probably *Phenacomys longicaudus*, *Peromyscus maniculatus* or *Clethrionomys occidentalis*.

food consumption should be viewed as maximums because the estimated rate of food intake during the summer period was most likely inflated.

Prey Selection by Male and Female Spotted Owls

Comparison of 128 prey captured by males and 93 captured by females indicated no significant difference in prey size selection, on total or seasonal bases (Table 15). There was also no significant difference in dietary composition (Table 16). Males took slightly larger prey than females during all seasonal periods and on an overall basis. The range of prey sizes taken by males and females was the same except that the only snowshoe hare captured by a female weighed approximately 900 g, whereas the largest prey in the male sample was a snowshoe hare weighing approximately 500 g (remains of snowshoe hares weighing up to 1,500 g were found in pellets below roosts used jointly by male and female owls). These results suggested that prey partitioning between male and female spotted owls did not occur on the study area, at least not on the basis of prey size or species.

Behavior of Juveniles After They Became Independent

Four owlets were radio-tagged during the study, 2 on the HJA and 2 on the east slope of the Cascade Mountains near the Metolius River, Jefferson County, Oregon. All were radio-tagged in August 1975 when they were 3 to 4 months old. Before dispersal began, a transmitter failed on 1 of the owlets near the Metolius River and 1 of the owlets on the HJA study area died. Movements of the other 2 owlets are described below.

Table 15. Seasonal comparison of mean prey weights for male and female spotted owls on the H. J. Andrews study area[1].

Season period	Mean weight of prey in grams and number of prey identified (in parentheses)		t values for differences between means
	Males	Females	
Sept.-Feb. (fall-winter)	108.4(18)	90.6(52)	$t = 1.46$, d.f. $= 68$ $(.05 < p < 0.1)$
March-April (spring)	99.7(58)	84.5(21)	$t = 1.40$, d.f. $= 77$ $(.05 < p < 0.1)$
May-August (summer)	75.6(52)	74.6(20)	$t = 0.03$, d.f. $= 70$ $(p < 0.5)$
Overall average	91.1(128)	84.7(93)	$t = 0.57$, d.f. $= 219$ $(0.2 < p < 0.3)$

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[1] Unidentified prey included in the analysis included 3 mice or voles taken by males and 5 mice or voles taken by females. These unidentified mice or voles were assigned a mean weight of 25 grams each.

Table 16. Prey selection by male and female spotted owls on the H. J. Andrews study area May 1975 to June 1976[1].

Species[2]	Males		Females	
	N	Percent	N	Percent
Glaucomys sabrinus	70	56.0	48	54.5
Phenacomys longicaudus	14	11.2	11	12.5
Clethrionomys occidentalis	5	4.0	8	9.1
Peromyscus maniculatus	11	8.8	8	9.1
Other mammals	19	15.2	5	5.7
Birds/Insects	6	4.8	8	9.1
TOTALS	125	100.0	88	100.0

Chi-square = 7.9, d.f. = 5[3]

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[1] Eight unidentified prey were excluded from the analysis, 3 mice or voles taken by males and 5 mice or voles taken by females.

[2] Common names of mammals are given in Appendix 3.

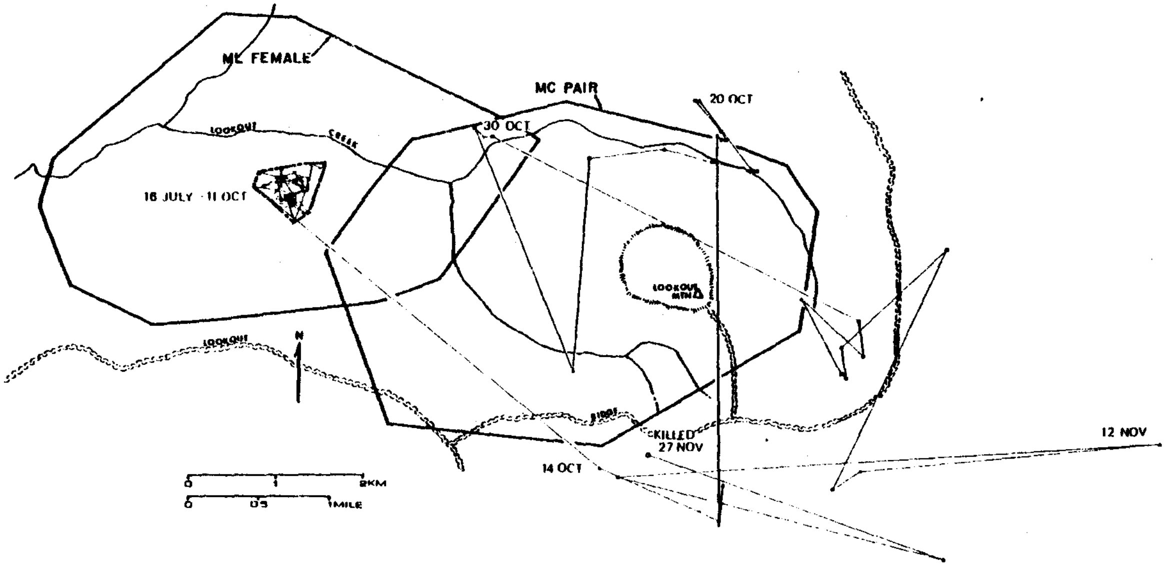
[3] $0.10 < P < 0.20$

After leaving the nest in June both owlets remained in the vicinity of their respective nests and were fed by their parents until late September or early October. The owlet on the HJA study area spent the entire summer within a 35 ha area around the nest (Fig. 16). The owlet near the Metolius River was only checked at 2 to 3 week intervals during the summer, so the full scope of its movements was unknown. Each time I visited the area during the summer, however, the owlet was found within 300 m of the nest tree so I assumed that it did not travel far from the nest area.

On 12 October the owlet on the HJA study area suddenly left the parental nest area and within 2 days moved 4.4 km to the southeast (Fig. 16). For the next 45 days it wandered about over an area of approximately 2,900 ha, sometimes moving away from and sometimes towards the parental territory. The farthest distance traveled from the nest site was 10.1 km. During its wanderings the owlet crossed the territory occupied by the MC pair several times and also ventured into a territory occupied by an unmarked pair just north of the MC pair (Fig. 16). On 26 November the owlet was killed, apparently by a great horned owl (Bubo virginianus). I found the remains of the owlet in a large owl pellet under a tree near the radio transmitter.

I was unable to determine exactly when the owlet on the Metolius River began dispersal but on 18 October it was located 16.4 km from the nest site. It was in a dense forest of old-growth Douglas-fir, white fir (Abies concolor) and ponderosa pine (Pinus ponderosa) and had apparently traveled across some extensive areas of open ponderosa pine forest to arrive at this location. When I checked this owlet again on

Fig. 16. Movements of the ML owlet on the H. J. Andrews study area between 7 August and 26 November 1975. Before it became independent from its parents the owlet confined its activities to a 35 ha area around the parental nest (area inside dashed line). After it became independent it wandered over a large area. The home ranges of the ML female and MC pair are indicated by solid lines.


ML FEMALE
MC PAIR
20 OCT
30 OCT
LOOKOUT CREEK
16 JULY - 11 OCT
LOOKOUT MTN
N
LOOKOUT RIDGE
KILLED
27 NOV
14 OCT
12 NOV
0
1
2KM
0
0.5
1MILE

6 December it had been eaten by a predator. Its remains were found 12.0 km from the parental nest site.

Observations on the 2 owlets described above were too limited to draw any conclusions about dispersal except that mortality during dispersal was high. However, the relatively short distances moved by both owlets during the first 2 months of independence did not appear unusual in light of the relatively short dispersal distances that have been documented for other sedentary owl species (Southern 1970, Houston 1978).

DISCUSSION, SPECULATION AND CONCLUSIONS

The home ranges utilized by spotted owls on the HJA were larger than home ranges utilized by most of the radio-tagged barred and great horned owls studied by Fuller (1979). This result does not support the general theory that raptor body size and home range size are positively correlated (Schoener 1968). The factors influencing home range size in raptors are probably too complex to allow prediction of home range size from a simple straight line relationship with body size.

Because interactions between male and female spotted owls from adjacent territories did not appear to involve the aggressive chasing and retreating behavior characteristic of interactions between individuals of the same sex it was not clear whether male-female interactions should be called "territorial" or not. A possible explanation for the apparent non-aggressiveness of male-female interactions was that conflicting tendencies existed in this type of interaction that did not exist in interactions between individuals of the same sex. For instance, there might have been a tendency to drive all other individuals (except the mate) out of the territory in order to reduce competition for food, but it might also have been an advantage if individuals of the opposite sex were allowed to remain within the territory so that mate replacements would be readily available if a mate was lost.

If defense of the food resource was an important function of territories defended by spotted owls on the HJA, then paired individuals should have excluded all other individuals from the territory regardless of sex. Because this did not appear to be the case, it seemed possible that the principle function of territorial behavior was not to defend a food resource but to exclude potential competitors for mates.

It was not clear whether spotted owls formed a permanent pair bond extending beyond a single breeding season or whether mate constancy from year to year occurred because males excluded other males from the home range while females excluded other females. This pattern of territorial defense, combined with the tendency of residents to remain within a traditional home range, made it virtually certain that the same individuals re-paired each spring, as long as each individual was able to exclude other members of its sex from the home range. Mate constancy, therefore, may have been more a function of the attachment to a traditional home range than attachment to a particular mate.

Radiotelemetry studies of other supposedly nocturnal owls have indicated activity patterns both similar to and noticeably different than observed for spotted owls in this study. The activity cycle of a saw-whet owl studied by Forbes and Warner (1974) was virtually identical to that of spotted owls on the HJA. On the average, the saw-whet began activity 22 min after sunset and ended activity 18 min before sunrise. The mean activity period for spotted owls for the same time period (29 October to 17 November) was from 23 min after sunset to 27 min before sunrise. During the day the saw-whet was relatively inactive.

The timing of activity by great horned owls studied by Fuller (1979) also was similar to the pattern exhibited by spotted owls except that the great horned owls appeared slightly more active during the day than spotted owls. Usually, however, the great horned owls began activity within 30 minutes of sunset and ended activity within 30 minutes of sunrise.

Barred owls (Strix varia) studied by Nicholls (1970) and Fuller (1979) were most active during the night, but considerable activity also occurred during the day, including some long distance foraging flights. Diurnal activity increased considerably when the owls were feeding young. Like spotted owls, both great horned and barred owls were active for longer periods during winter than summer.

The behavior of a female spotted owl studied by Miller (1974) appeared to differ from that of spotted owls on the HJA. According to Miller (1974:115) the female "foraged at all hours of the day or night" when feeding young. I believe, however, that the apparent differences between the female studied by Miller and the owls on the HJA were more semantic than real because Miller did not differentiate between opportunistic attempts to capture prey in roost areas and long distance foraging flights away from roost areas. If the diurnal foraging described by Miller was limited to the vicinity of the day roost, then the pattern of behavior was not much different than that observed on the HJA.

The fact that male and female spotted owls on the HJA utilized the same kinds of prey did not support the theory that sexual size dimorphism evolved in raptors because it allowed males and females to utilize different kinds of prey (Storer 1966, Snyder and Wiley 1976, Reynolds 1972, Selander 1966). Studies of several other raptors, including the American kestrel (Falco sparvarius) (Balgooyen 1976), Montagu's harrier (Circus pygargus) (Schipper 1973), and pygmy owl (Glaucidium gnoma)

(Earhart and Johnson 1970) also indicated that male and female diets were similar or nearly identical. The only raptors in which prey partitioning between males and females has been conclusively demonstrated are species in which males are considerably larger than females, such as hawks in the genus Accipiter (Storer 1966, Snyder and Wiley 1976), and some harriers (Circus cyaneus and C. aeruginosus) (Schipper 1973). The fact that prey partitioning by males and females did not occur in several of the less dimorphic raptors such as the spotted owl and American kestrel suggests that size dimorphism may have evolved in response to selective factors other than prey partitioning. If this is the case, prey partitioning in highly dimorphic raptors may be a result rather than the initial cause for the evolution of size dimorphism.

The strong preference exhibited by spotted owls on the HJA for old-growth forests for roosting and foraging suggested that such forests were the environment to which the owls were best adapted and, therefore, best able to compete with other species. It is appropriate to ask, therefore, what were the competitive relationships and morphological or physiological characteristics that caused the owls to select for older forests?

Some factors affecting habitat selection seemed relatively obvious. For instance, the owls required a cavity or platform in a tree for nesting. Cavities or platforms large enough for nesting by spotted owls were common in old-growth forests, but were uncommon or absent in younger forests. Not surprisingly, therefore, all nests located on the HJA were in old-growth stands.

For roosting, the owls required trees that provided protection from high ambient temperatures during summer and inclement weather during winter. Cutover areas provided virtually no roost cover until the regenerating trees were at least 30 years old, and stands of second-growth trees (30 to 80 years old) did not provide the same degree of protection from rain and snow as did stands of large old trees with leaning trunks, large clumps of limbs and other deformities under which the owls could roost. Not surprisingly, therefore, most roosting occurred in older forests.

Because of its size, the spotted owl appears ideally suited for pursuit of medium-sized nocturnal mammals such as flying squirrels, small lagomorphs and woodrats. It appeared that the foraging strategy of spotted owls on the HJA was to search selectively for these medium sized mammals. The only sympatric raptor that appeared likely to compete with spotted owls for medium-sized nocturnal mammals was the great-horned owl, a species approximately twice as large as the spotted owl. Virtually all studies of the diet of the great-horned owl have indicated it to be a predator primarily on terrestrial mammals (Marti 1974, Bent 1938, Rusch et al. 1972, Fitch 1947, Errington et al. 1940, Maser and Brodie 1966). By foraging for flying squirrels in the forest canopy, therefore, spotted owls were probably exploiting a prey resource that was not heavily utilized by other owls. If spotted owls had responded to clear-cutting by switching to the terrestrial mice and voles that were common in cutover areas, they might have encountered much greater competition from the great-horned owl as well as from 3 species of smaller owls that occurred on the study area, the saw-whet owl, pygmy owl and screech owl (_Otus asio_).

It is also possible that the biomass of nocturnal prey within the size range most frequently utilized by spotted owls (20 to 300 g) was greater in older forests than in areas clear-cut within the previous 30 years. Although some nocturnal mammals (notably deer mice and Microtines) increase on cutover areas during early stages of succession (Hooven 1972, Gashwiler 1959, Tevis 1956), it is not clear whether this increase makes up for the reduction in biomass resulting from the elimination of mammals such as flying squirrels, red tree voles and red-backed voles. I would like to stress that the comparison being made here is not between total mammalian biomass in old-growth and cutover areas but between the biomass available to a spotted owl (i.e., small or medium sized nocturnal mammals). Unfortunately, no data were available on the density of arboreal mammal populations on the study area, so a quantitative comparison of biomass of nocturnal small mammals on cutover and old-growth areas was not possible.

Even if populations of terrestrial mammals increased in cutover areas, reduced prey detectability may have caused the owls to avoid such areas. Although some recently cutover areas were only sparsely vegetated, many of the 15- to 25-year-old clear-cuts were so densely covered by brush and small conifers that access to the ground must have been difficult for the owls (Fig. 6). Not surprisingly, the latter areas were not utilized at all for foraging.

Spotted owls may also have avoided recently cutover areas because they were more susceptible to predation by great horned owls in open areas where escape cover was absent. Great horned owl predation on juvenile spotted owls that had reached adult size indicated that great horned owls were probably capable of capturing adult spotted owls.

The harvest of old-growth forests on the HJA reduced the amount of cover preferred for foraging, roosting and nesting. It could be inferred, therefore, that clear-cutting reduced the quality of the environment for spotted owls. The extent to which the area of older forest could be reduced without reducing the productivity or density of spotted owl pairs was not determined; there is certainly no universal answer to this question because no 2 areas occupied by spotted owl pairs are exactly the same. Based on the results of this study, however, I concluded that the best method of managing spotted owl populations in Douglas-fir and western hemlock forests was to preserve the maximum amount of old-growth and mature forest possible and to avoid the creation of large cutover areas.

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APPENDICES

Appendix 1. Cover type codes used for analysis of habitat utilization on the H. J. Andrews.

Cover Type Code	Description
0100	Old-growth (250-500 years old) mixed associations of *Pseudotsuga menziesii* and *Tsuga heterophylla* or *Abies amabilis*, *Pseudotsuga menziesii* and *Tsuga heterophylla*. Multi-layered stands.
0115	Same as 0100, except that some removal of dead and damaged trees has occurred, resulting in a slight reduction in canopy closure.
0200	140- to 200-year-old mixed forests of *Pseudotsuga menziesii* and *Tsuga heterophylla* or *Abies amabilis*, *Pseudotsuga menziesii* and *Tsuga heterophylla*. Multilayered stands.
0300	80- to 140-year-old forests dominated by mature *Pseudotsuga menziesii*. Trees typically 30-50 m tall and 40-100 cm dbh.
0400	61- to 80-year-old forests dominated by *Pseudotsuga menziesii*. Trees typically 30-40 m tall and relatively uniform in diameter.
0500	31- to 60-year-old forests dominated by *Pseudotsuga menziesii*. Trees typically 15 to 40 meters tall and 20-60 cm dbh.
0600	Dense stands of 21- to 30-year-old *Pseudotsuga menziesii* and *Tsuga heterophylla* growing on areas clear-cut or burned in the early 1950's or late 1940's.
0700	Dense stands of 15- to 20-year-old *Pseudotsuga menziesii* and *Tsuga heterophylla* growing on areas clear-cut or burned between 1952 and 1958.
0800	Dense stands of 5- to 14-year-old *Pseudotsuga menziesii* and *Tsuga heterophylla* growing on areas clear-cut between 1958 and 1968.
0900	Clear-cut areas or natural openings overgrown by mixtures of woody shrubs, especially *Acer circinatum*.

0809	Clear-cut areas covered by mixtures of cover types 0800 and 0900. Small patches of bare earth or low herbaceous vegetation were often intermixed with woody shrubs and young conifers.
1000	Grass-forbe associations on recent clear-cuts or other early succession areas.
1100	Rock talus slopes. Included natural accumulations of rocky rubble below rock outcrops as well as artificial accumulations of rocky rubble that were created to support road surfaces on steep slopes.
1200	Bare ground on areas clear-cut during the study or within the previous year.
1300	Mature riparian mixture of hardwoods (*Acer macrophyllum*, *Alnus rubra*) and conifers (*Thuja plicata*, *Pseudotsuga menziezii*, *Tsuga heterophylla*).
1400	Rock quarry.
0015	Numerical suffix added to primary cover type codes to indicate a stand in which very light overstory removal-has been conducted
1600	Shelterwood Harvest Unit. In a mixed stand of old-growth *Pseudotsuga menziesii* and *Tsuga heterophylla*, all trees had been harvested except for individual stems of old-growth *Pseudotsuga menziesii* spaced approximately 20-30 m apart. Soil on the harvested unit was bare.
1700	Blue River Reservoir and the grassy slopes forming a narrow border around the reservoir.
1800	Blue River Reservoir Campground. A mixed stand of *Pseudotsuga menziesii*, *Acer macrophyllum*, *Thuja plicata* and *Tsuga heterophylla* that had been thinned to open up campsites and parking areas.
1900	Tokatee Golf Course. This area bordered the southern edge of the study area, and fell within the boundaries of the area utilized by the BRR male.
2000	Cleared area beneath a high voltage powerline along the southern boundary of the study area.

Appendix 2. Utilization of cover types for foraging by eight radio-tagged spotted owls on the H.J. Andrews study area (May 1975-June 1976).

Cover type	Proportion of total home Range	Proportion of fixes in cover type	Conf. interval on proportion of occurrence	Level of[1] Significance
ML female (No. fixes = 361)				
0100	0.636	0.936	$0.895<p_1<0.978$	.99 +
0115	0.028	0.044	$0.009<p_2<0.079$	NS
0600	0.027	0	$0.000<p_3<0.011$	.99 -
0700	0.127	0	$0.000<p_4<0.011$	.99 -
0800	0.037	0	$0.000<p_5<0.011$	.99 -
0900	0.013	0.003	$0.000<p_6<0.011$	.99 -
0809	0.104	0	$0.000<p_7<0.011$	.99 -
1300	0.021	0.017	$0.000<p_8<0.038$	NS
Other	0.007	0	$0.000<p_9<0.011$	NS
	1.000	1.000		
MC Male (No. fixes = 213)				
0100	0.577	0.958	$0.914<p_1<1.000$	.99 +
0200	0.083	0.042	$0.000<p_2<0.086$	.95 -
0400	0.066	0	$0.000<p_3<0.019$	.99 -
0600	0.035	0	$0.000<p_4<0.019$	.99 -
0800	0.030	0	$0.000<p_5<0.019$	.99 -
0809	0.181	0	$0.000<p_6<0.019$	.99 -
Other	0.028	0	$0.000<p_7<0.019$	.99 -
	1.000	1.000		
MC Female (No. fixes = 161)				
0100	0.636	0.975	$0.936<p_1<1.000$	.99 +
0200	0.050	0.025	$0.000<p_2<0.064$	NS
0400	0.099	0	$0.000<p_3<0.026$	.99 -
0700,0800	0.035	0	$0.000<p_4<0.026$	.99 -
0900	0.099	0	$0.000<p_5<0.026$	.99 -
0809	0.062	0	$0.000<p_6<0.026$	.99 -
Other	0.019	0	$0.000<p_7<0.026$	NS
	1.000	1.000		

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[1] A plus sign after the level of significance figure indicates that a cover type was used significantly more than expected. A minus sign indicates that the cover type was used significantly less than expected.

Appendix 2. (continued)

Cover Type	Proportion of total home range	Proportion of fixes in cover type	Conf. interval on proportion of occurrence	Level of[1] Significance
		Mona female (No. fixes = 345)		
0100	0.571	0.965	$0.932<p_1<0.998$	.99 +
0115	0.012	0.003	$0.000<p_2<0.011$	.95 -
0300	0.199	0.023	$0.000<p_3<0.050$	.99 -
0500	0.016	0	$0.000<p_4<0.013$	.99 -
0600	0.025	0	$0.000<p_5<0.013$	.99 -
0800	0.050	0	$0.000<p_6<0.013$	.99 -
1900	0.024	0	$0.000<p_8<0.013$	.99 -
0809	0.056	0	$0.000<p_7<0.013$	.99 -
1200	0.016	0	$0.000<p_9<0.013$	.99 -
1700	0.018	0	$0.000<p_{10}<0.013$	.99 -
Other	0.011	0.009	$0.000<p_{11}<0.026$	NS
	1.000	1.000		
		W2 Female (No. fixes = 364)		
0100	0.537	0.953	$0.916<p_1<0.990$	.99 +
0115	0.022	0.006	$0.000<p_2<0.020$	.99 -
0200	0.029	0	$0.000<p_3<0.012$	.99 -
0300	0.020	0.011	$0.000<p_4<0.029$	NS
0400	0.003	0.014	$0.000<p_5<0.035$	NS
0600	0.044	0	$0.000<p_6<0.012$	.99 -
0700	0.035	0	$0.000<p_7<0.012$	.99 -
0800	0.032	0	$0.000<p_8<0.012$	.99 -
0900	0.017	0	$0.000<p_9<0.012$	.99 -
0809	0.199	0.016	$0.000<p_{10}<0.038$	.99 -
1000	0.013	0	$0.000<p_{11}<0.012$	.99 -
1200	0.021	0	$0.000<p_{12}<0.012$	.99 -
1700	0.016	0	$0.000<p_{13}<0.012$	.99 -
Other	0.012	0	$0.000<p_{14}<0.011$	.95 -
	1.000	1.000		

Appendix 2. (continued)

Cover type	Proportion of total home range	Proportion of fixes in cover type	Conf. interval on proportion of occurrence	Level of Significance
		W2 Male (No. fixes = 416)		
0100	0.554	0.858	$0.801<p_1<0.914$	.99 +
0115	0.026	0.002	$0.000<p_2<0.009$	.99 -
0200	0.015	0.005	$0.000<p_3<0.015$	NS
0300	0.024	0.007	$0.000<p_4<0.020$	.99 -
0600	0.069	0.-05	$0.000<p_5<0.016$	.99 -
0700	0.119	0	$0.000<p_6<0.009$	.99 -
0800	0.019	0	$0.000<p_7<0.009$	.99 -
0900	0.022	0	$0.000<p_8<0.009$	.99 -
0809	0.131	0.065	$0.053<p_9<0.077$	.99 -
1100	0.003	0.051	$0.040<p_{10}<0.062$	.99 +
Other	0.018	0.007	$0.000<p_{11}<0.020$	NS
	1.000	1.000		
		BRR Male (No. fixes = 382)		
0100	0.358	0.851	$0.790<p_1<0.912$	.99 +
0115	0.006	0	$0.000<p_2<0.012$	NS
0200	0.015	0.005	$0.000<p_3<0.017$	NS
0300	0.062	0.115	$0.060<p_4<0.170$	.95 +
0400	0.009	0.018	$0.000<p_5<0.041$	NS
0500	0.009	0.008	$0.000<p_6<0.023$	NS
0600	0.187	0	$0.000<p_7<0.012$	.99 -
0700	0.060	0	$0.000<p_8<0.012$	.99 -
0800	0.058	0	$0.000<p_9<0.012$	.99 -
0900	0.031	0	$0.000<p_{10}<0.012$	.99 -
0809	0.096	0	$0.000<p_{11}<0.012$	.99 -
1200	0.014	0	$0.000<p_{12}<0.012$	.99 -
1700	0.046	0	$0.000<p_{13}<0.012$	.99 -
1900	0.022	0	$0.000<p_{14}<0.012$	.99 -
Other	0.027	0.003	$0.000<p_{15}<0.012$	.99 -

Appendix 2. (continued)

Cover type	Proportion of total home range	Proportion of fixes in cover type	Conf. interval on proportion of occurrence	Level of significance
		BRR Female (No. fixes = 364)		
0100	0.497	0.986	$0.965<p_1<0.986$	.99 +
0115	0.009	0	$0.000<p_2<0.009$	.95 -
0200	0.013	0	$0.000<p_3<0.009$	.99 -
0300	0.025	0	$0.000<p_4<0.009$	.99 -
0400	0.-06	0.003	$0.000<p_5<0.009$	NS
0500	0.017	0.003	$0.000<p_6<0.009$	.99 -
0600	0.080	0.005	$0.000<p_7<0.017$	.99 -
0700	0.023	0	$0.000<p_8<0.009$	.99 -
0800	0.084	0	$0.000<p_9<0.009$	.99 -
0900	0.015	0	$0.000<p_{10}<0.009$	.99 -
0809	0.123	0	$0.000<p_{11}<0.009$	.99 -
1200	0.020	0.003	$0.000<p_{12}<0.009$	.99 -
1700	0.057	0	$0.000<p_{13}<0.009$	.99 -
Other	0.031	0	$0.000<p_{14}<0.009$	.99 -
	1.000	1.000		

Appendix 3. Weights of prey species used to compute biomass consumed by spotted owls on the H. J. Andrews study area.

Species		Number of Specimens	Mean Weight (grams)	Source of Data
Scientific Name	Common Name[1]			
Mammals				
Lepus americanus	Snowshoe Hare	—	150–1,500	estimated from skeletal size
Neotoma cinerea	Bushy-tailed Woodrat	24	265	C. Maser unpublished
Tamiasciurus douglasii	Douglas' Squirrel	61	208	C. Maser unpublished
Ochotona princeps	Pika	11	158	C. Maser unpublished
Glaucomys sabrinus	Northern Flying Squirrel	33	115	C. Maser unpublished; OSU[1]
Thomomys mazama	Western Pocket Gopher	24	87	C. Maser unpublished
Eutamias townsendii	Townsend's Chipmunk	48	80	C. Maser unpublished
Arvicola richardsoni	Water Vole	27	70	C. Maser unpublished
Scapanus orarius	Coast Mole	34	53	C. Maser unpublished
Mustela erminea	Ermine	8	41	OSU[2]
Phenacomys longicaudus	Red Tree Vole	17	27	C. Maser unpublished
Peromyscus maniculatus	Deer Mouse	98	22	C. Maser unpublished
Clethrionomys occidentalis	Western Red-backed Vole	66	23	C. Maser unpublished
Zapus trinotatus	Pacific Jumping Mouse	10	24	OSU[2]
Microtus oregoni	Creeping Vole	90	19	C. Maser unpublished
Sorex bendirii	Pacific Water Shrew	42	18	C. Maser unpublished
Neurotrichus gibbsii	Shcrew-mole	31	9	C. Maser unpublished
Sorex pacificus	Pacific Shrew	79	12	C. Maser unpublished
Sorex trowbridgii	Trowbridge's Shrew	92	5	C. Maser unpublished
	Squirrel-size mammal	—	100	Estimated average
	Unidentified mouse or vole	—	25	Estimated average
	Unidentified shrew	—	10	Estimated average
Birds				
Otus asio	Screech Owl	—	140	Estimated
Cyanocitta stelleri	Steller's Jay	?	107	Kilgore (1971)
Aegolius acadicus	Saw-whet Owl	45	83	Earhart and Johnson (1970)
Glaucidium gnoma	Pygmy Owl	52	67	Earhart and Johnson (1970)
Hesperiphona vespertina	Evening Grosbeak	?	64	Kilgore (1971)
Sphyrapicus varius	Yellow-bellied Sapsucker	?	46	Kilgore (1971)
Nuttallornis borealis	Olive-sided Flycatcher	?	34	Kilgore (1971)
Troglodytes troglodytes	Winter Wren	?	9	Kilgore (1971)
Parus rufescens	Chestnut-backed Chickadee	—	10	Estimated
	Small Owl	—	90	Estimated Average
	Small Birds	—	90	Estimated Average
	Medium-sized Birds	—	70	Estimated Average
Reptiles				
Thamnophis spp.	Garter Snake	?	50	R. Nussbaum unpublished
Insects-Spiders				
Cyphoderris spp.		—	2	Estimated
Ergates spiculatus		—	2	Estimated
	All other insects	—	0.5	Estimated
	Unidentified spiders	—	0.5	Estimated

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[1] Specimens in Oregon State University collections, collected in Oregon.

[2] Common names of mammals conform to Jones et al. (1973).