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DISTRIBUTION AND BIOLOGY OF THE SPOTTED OWL IN OREGON

by

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FRONTISPIECE. An adult northern spotted owl.

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Abstract: We studied the distribution, habitat, home range characteristics, reproductive biology, diet, vocalizations, activity patterns, and social behavior of the spotted owl (*Strix occidentalis*) in Oregon from 1969 through 1980. Spotted owls were located at 636 sites, including 591 (93%) on federal lands. The range included western Oregon and the east slope of the Cascade Range. Most pairs (97.6%) were found in unlogged old-growth forests or in mixed forests of old-growth and mature timber. No owls were found in forests younger than 36 years old. Paired individuals tended to occupy the same areas year after year and use the same nests more than once. Mean nearest neighbor distances were 2.6 km west of the crest of the Cascade Mountains and 3.3 km on the east slope of the Cascades. From 1969 to 1978, the population declined at an average annual rate of 0.8%. The principal cause of site abandonment was timber harvest.

Home range areas ranged from 549 to 3,380 ha. Seasonal home ranges averaged largest during fall and winter. Home range overlap averaged 68% for paired individuals and 12% for individuals occupying adjacent territories. Old-growth forests were consistently preferred for foraging and roosting by all owls studied. In most cases, use of younger forests was either less than or not significantly different than expected. There was no apparent tendency to concentrate foraging activity in "edge" areas such as along clear-cut boundaries or roadsides. Owls roosted significantly higher in the forest canopy during cold, wet weather than during warm or hot weather.

Of 47 nests located, 30 were in cavities in old-growth conifers and 17 were on platforms of sticks or other debris in mature or old-growth conifers. None of the owls built its own nest. Average nest height was 27.3 m (range = 10.0–55.3 m, SE = 1.67). Forty-two nests were in unmanaged old-growth forests. Canopy closure exceeded 70% in most nest areas.

On the average, 62% of the pairs checked each year attempted to nest; 81% of all nesting attempts were successful. Egg laying began between 9 March and 19 April ($\bar{x} = 2$ April). Average clutch size was 2. Incubation lasted 30 ± 2 days. Eggs hatched between 8 April and 20 May. Females alone incubated and brooded the young. Males provided all food for the female and young until the young were approximately 2 weeks old. The young left the nest at 34–36 days of age. After leaving the nest, owlets were fed by the adults until late August or September. The young became independent and began dispersal in October. Owlet mortality during the first summer of life was 35%. Before they were killed by predators in midwinter, 2 radio-tagged juveniles traveled maximum straight line distances of 10.1 and 16.4 km from their respective natal sites.

The diet varied seasonally and included a variety of mammals, birds, and insects. Mammals comprised 92% of all prey taken. Foraging activity usually began shortly after sunset and ceased shortly before sunrise. Calls given by spotted owls were classified into 13 types. Juveniles did not give adult vocalizations until late September or October of their first year.

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[1] Deceased.

CONTENTS

INTRODUCTION

The spotted owl is a medium-sized, nocturnal owl inhabiting forested areas in western North America (Fig. 1). It occupies a variety of forest types, from humid coniferous forests in the northern part of its range to xeric pine–oak woodlands in the mountains and canyonlands of Mexico and the American Southwest (Bent 1938). It is an extremely tame species, often allowing humans to approach within 2–3 m before flying away.

When the present study was initiated in 1969, the spotted owl was considered a rare or uncommon species in Oregon (Gabrielson and Jewett 1940, Marshall 1969). There were only 24 previous records of the owl in the state, no information was available on nest characteristics, and the only information on the diet was based on an examination of 4 stomachs (Marshall 1942, Maser 1965). Although the species was believed to be threatened by loss of habitat (Marshall 1969), there was no information to confirm this belief. A similar lack of information prevailed throughout the Pacific Northwest and British Columbia.

In the study described in this report the objectives were:

1. To determine the distribution and numerical status of the spotted owl in Oregon and evaluate population trends.
2. To determine the types of habitat occupied by spotted owls in Oregon and evaluate habitat preferences for foraging, roosting, and nesting.
3. To describe the life history of the species, including home range characteristics, reproductive biology, diet, vocal repertoire, activity patterns, and social behavior.

4. To develop specific management recommendations for the species based on the information obtained.

Acknowledgments.—We are deeply indebted to many biologists and foresters who helped locate spotted owls. These individuals and the agencies with which they were affiliated included: Charles Bruce, James Collins, Robert Mace, Ralph Opp, and Harlan Scott (Oregon Department of Fish and Wildlife); James Harper, Richard King, Wayne Logan, Jerry Mires, Kenneth Munson, William Neitro, Lawrence Scofield, Douglas Smithy, Charles Thomas, and Frank Wagner (Bureau of Land Management); Gerald Astrella, Margaret Bell, Terry Bryan, Warren Current, Jerry Diebert, William Dugas, Stephen English, Edward Harshman, William Heckel, John Hillis, Kirk Horn, Bruce Hotchkiss, Phillip Janik, Paul Moroz, Walter Parker, Richard Reynolds, Gene Silovsky, Robert Summerfield, and Lee Webb (U.S. Forest Service); William Chilcote (Oregon State University); Ron Nussbaum (Michigan State University); Wes Pike (University of Arizona); James Blaisdell (National Park Service); Keith Comstock (Georgia Pacific Lumber Company); and Robert Anderson (Weyerhaeuser Corporation). If we have left anyone out, we apologize.

For their participation in developing a spotted owl management plan for Oregon, we would like to acknowledge the following individuals: Charles Bruce, William Haight, Robert Maben, and Frank Newton (Oregon Department of Fish and Wildlife); Barbara Holder, Kirk Horn, Leon Murphy, Richard Pederson, and Gene Silovsky (U.S. Forest Service); Dave Luman, William Neitro, Douglas Smithy, and Charles Thomas (Bureau of Land Management); and David Marshall and Peter Stein (U.S. Fish and Wildlife Service).

For his support of this study, we would like to thank Jack Ward Thomas of the U.S. Forest Service Pacific Northwest Forest and Range Experiment Station, LaGrande, Oregon (Range and Wildlife Habitat Research Project USDA-FW-PNW-1701). We also acknowledge Andrew Carey and Len Ruggiero of the U.S. Forest Service Pacific Northwest Forest and Range Experiment Station, Olympia, Washington, for their support of ongoing studies of the spotted owl.

Chris Maser of the Bureau of Land Management helped identify mammal remains in pellets and generously provided his unpublished data on body weights of Oregon mammals. Loren Russell of Oregon State University identified most of the

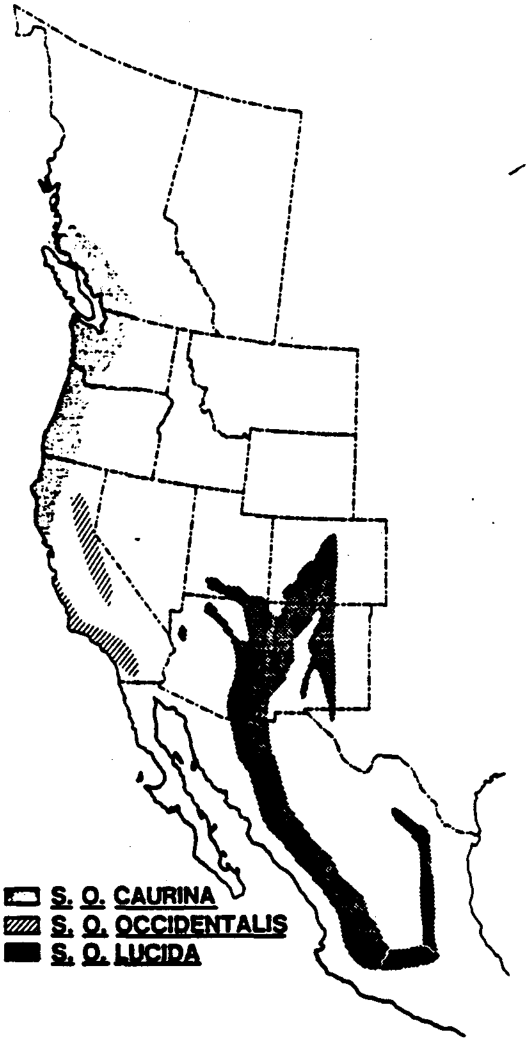

Fig. 1. Distribution of the 3 subspecies of spotted owl in North America. The distribution in Colorado and Mexico is poorly documented. Map compiled from numerous sources in the literature.

Fig. 2. Major geographic regions within the Oregon study area (area west of the heavy dashed line). Radiotelemetry study areas are indicated by square symbols.

nonvertebrate prey remains in owl pellets. Monica Forsman contributed to almost every aspect of the study, including trapping and radio tracking owls, caring for captive owls, collecting and dissecting pellets, conducting calling routes, measuring nest trees, and typing manuscripts.

Special thanks are due Charles Thomas of the Bureau of Land Management (BLM) who arranged the funding and logistic support for a radiotelemetry study on BLM lands, His enthusiasm and support were greatly appreciated. John Beuter, Richard Clark, John Crawford, Carl Marti, Richard Reynolds, Thomas Scott, Helen Schultz, Robert Storm, and Jack Ward Thomas reviewed drafts of the manuscript; Alma Rodgers and Charlotte Vickers typed several drafts of the manuscript.

The study was conducted under the auspices of the Oregon Cooperative Wildlife Research Unit: Oregon Department of Fish and Wildlife, Oregon State University, U.S. Fish and Wildlife Service, and the Wildlife Management Institute cooperating. Portions of this study were presented by the senior author in partial fulfillment for the M.S. and Ph.D. degrees in Wildlife Science at Oregon State University. This is Oregon Agricultural Experiment Station Technical Paper 6251.

STUDY AREA

The study area included the western one-third of Oregon (Fig. 2). This area is characterized by rugged mountains and, together with western Washington, comprises the most densely forested region in the United States (Franklin and Dyrness 1973). Based on climate and vegetation, the study area was divided into 3 major subregions: (1) western Oregon (which included the Coast Ranges, Willamette Valley, and west slope of the Cascade Range in Fig. 2), characterized by mild, wet winters and warm, dry summers, (2) the Klamath Mountains (southwestern Oregon), characterized by cool, dry winters and hot, dry summers, and (3) the east slope of the Cascade Range, characterized by cool winters and warm, dry summers. Elevations ranged from sea level to 3,452 m. Most of the area was below 1,500 m.

Vegetation of western Oregon was dominated by extensive temperate forests of Douglas-fir and western hemlock (scientific names of plants are in Appendix 1) (Fig. 3). Other major forest types in this region included a narrow zone of sitka spruce along the coastal headlands and a relatively narrow subalpine forest zone at high elevations on the west slope of the Cascades, where Pacific silver fir and mountain hemlock forests predominated.

In the Klamath Mountains, temperate forests of Douglas-fir and western hemlock were largely replaced by mixed evergreen and mixed conifer forests (Franklin and Dyrness 1973). In the latter forest types, Douglas-fir occurred in mixed

Fig. 3. A typical old-growth forest of Douglas-fir and western hemlock on the H. J. Andrews study area, Oregon.

stands with white fir, grand fir, sugar pine, ponderosa pine, incense-cedar, Port-Oxford cedar, and associated broad-leaved evergreen trees such as tanoak, Pacific madrone, canyon live oak, California laurel, and golden chinkapin. Above 1,500 m in this region, mixed evergreen and mixed conifer forests were largely replaced by forests of white fir and Shasta red fir, with lesser amounts of Douglas-fir, sugar pine, and western white pine. The east slope of the Cascades was characterized by forests of Pacific silver fir, subalpine fir, Shasta red fir, lodgepole pine, or mountain hemlock at higher elevations, mixed forests of white fir, Douglas-fir, ponderosa pine, and incense-cedar at midelevations, and forests of ponderosa pine or lodgepole pine at lower elevations.

In all 3 subregions, extensive areas of old-growth and mature forest had been harvested within the 19th century (Fig. 4). As a result the vegetation was distributed in a mosaic of recent harvest units, young second-growth stands, and residual stands of mature and old-growth timber. Typical old-growth forests were 230–350 years old in the Coast Ranges and 250–500 years old in the Cascades (Franklin et al. 1981).

Radiotelemetry studies were conducted on 2 areas in Lane County in western Oregon (Fig. 5). The H. J. Andrews (HJA) study area was located on the west slope of the Cascade Mountains, 8 km northeast of the town of Blue River. The Bureau of Land Management (BLM) study area was located in the Coast Ranges, 16 km west of the town of Lorane. Both study areas were characterized by mountainous terrain and numerous small streams and rivers. Elevations ranged from 380 to 1,630 m on the HJA study area and 150 to 590 m on the BLM study area. Slope gradients on both areas commonly ranged from 40 to 70% and occasionally up to 100%.

The climate and vegetation of both radiotelemetry study areas were typical of

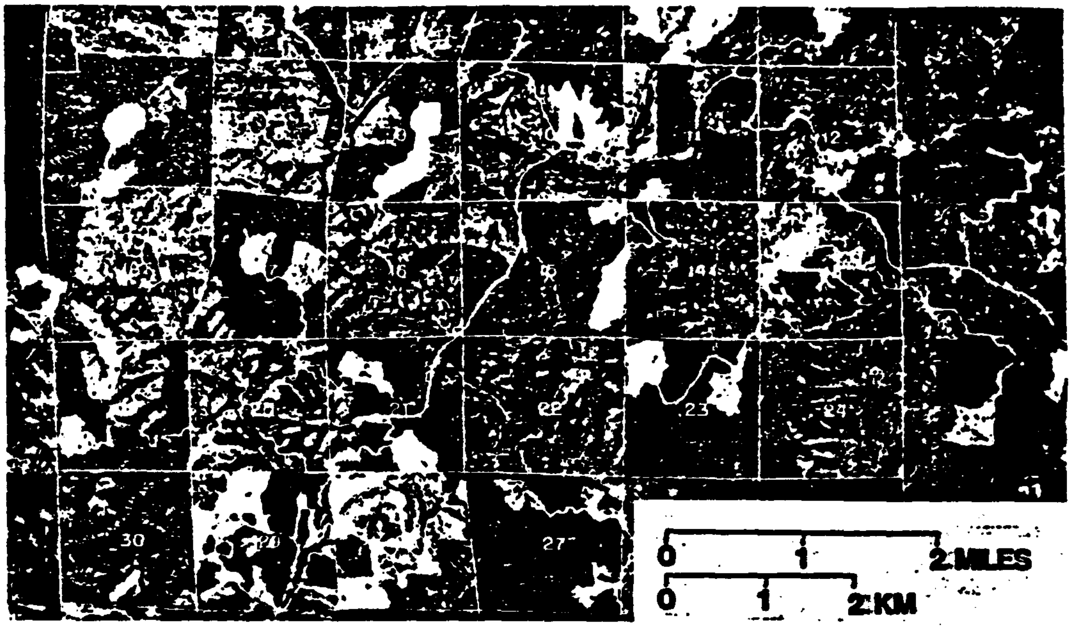

Fig. 4. Aerial photo of the southern half of the BLM study area, illustrating extensive cutover areas and remnant stands of old-growth and mature forest. Asterisks indicate nest sites or major roost areas of 6 pairs of spotted owls located on this portion of the study area.

western Oregon, as described earlier. The 2 areas differed, however, in the amount of harvest that had taken place. On the HJA study area about 55% of the land area was covered by old-growth forests and about 10% was covered by 80–200-year-old forests. The remainder of the area was mostly covered by early successional vegetation on recent clear-cuts (Fig. 6). On the BLM area, about 70% of the land area had been clear-cut within the previous 40 years. The remaining blocks of old-growth forest were widely spaced and covered only about 20% of the land area. A detailed description of vegetative cover types on the HJA and BLM study areas is provided in Appendix 2.

METHODS

Location of Owls

To locate spotted owls we imitated spotted owl calls in forest areas at night, either vocally or with a tape recorder. This incited the resident owls to call and reveal their presence. Most nighttime calling inventories were conducted by driving along forest roads, stopping at 0.3–0.8-km intervals to call and listen for owls. Inventories also were conducted by calling every 15–30 seconds as we walked continuous transects along roads or trails (Forsman et al. 1977). Calling inventories were conducted between March and September when owls were most responsive.

Numerous biologists from federal, state, and private agencies assisted in the ow inventory by conducting calling routes. Because most of these cooperators were federal employees, the greatest inventory effort was concentrated on federal lands. However, BLM and Forest Service biologists also inventoried extensive areas o private land in areas where federal and private lands were intermixed. Mean nearest neighbor distances were determined by measuring between nests or major roost areas of neighboring pairs.

Daytime roosts were found by homing in on radio-tagged owls. Roosts of un

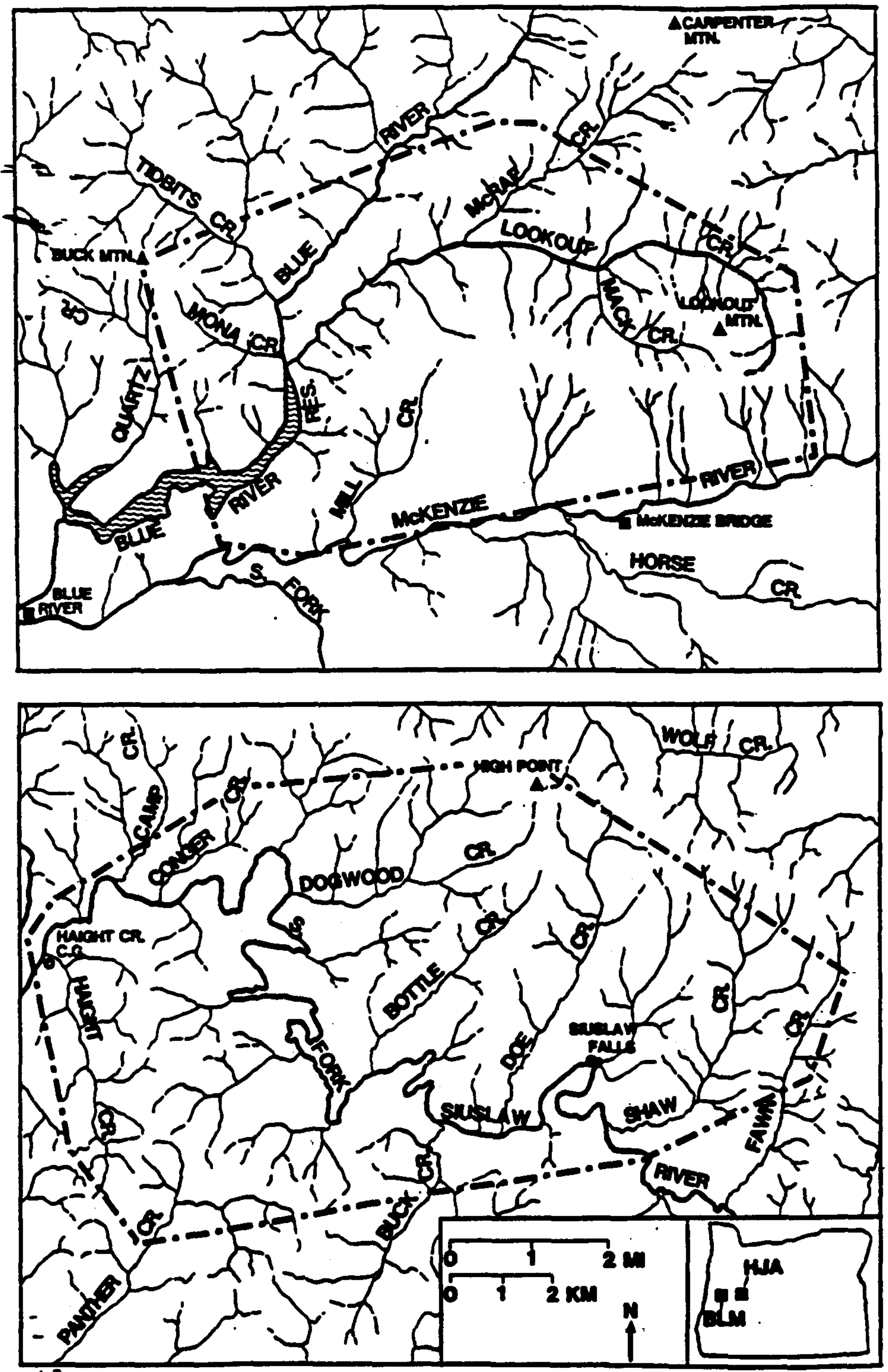

Fig. 5. H.J. Andrews (top) and BLM (bottom) radiotelemetry study areas in western Oregon.

Fig. 6. A typical 12-year-old clear-cut on the H. J. Andrews study area. (Photo by Jerry Franklin).

marked owls were found by calling during the day in areas where owls had been located at night. When owls responded, they were approached on foot and visually located in their roost trees.

Nest trees were located during the day by (1) homing in on radio-tagged individuals, (2) observing adults during the period of nest site selection, (3) imitating spotted owl calls in suspected nest areas until females left their nests to confront the suspected intruder, or (4) tethering live mice on the ground in view of roosting adults and then watching as the owls captured the mice and carried them to the nest. The latter method also was effective for locating owlets after they left the nest. As we became familiar with individual pairs, it became easier to relocate them each year because the same nest and roost areas were often used year after year. Observations on behavior during the day were made by sitting or standing quietly near occupied roosts or nests and watching owls with binoculars or spotting scope. The owls were so unafraid of humans that concealment was unnecessary.

In addition to observations on free-ranging owls, we raised 2 female spotted owls in captivity and recorded information on their development, molt, and behavior (Forsman 1981*b*). One of the captive owls laid eggs every year from 1975 to 1980. Vocalizations were recorded on a Uher 4000L tape recorder and analyzed on a Kay 6061A sonograph.

Habitat Evaluation

In all habitats occupied by spotted owls, we recorded species composition of overstory and understory trees and stand age. Stand age was determined from core samples or by counting annual growth rings on stumps in harvested areas adjacent to stands occupied by spotted owls. Variables measured at nest sites included percent slope, aspect, canopy closure, and distance to the nearest stream or spring. Canopy closure at nests was estimated at 4 points around the nest tree and averaged. The 4 points were determined by walking a random number of steps (1–9) away from the nest tree along north, south, east, and west compass bearings.

Radiotelemetry Data Collection and Analysis

To capture owls we set mist nets or bow nets near the roosting owls during the day and baited the nets with live mice. The owls almost invariably attempted to capture any small prey placed near their roosts and were thus easily captured. Radio transmitters were placed on 8 adult spotted owls (5 females, 3 males) on the HJA study area in 1975 and 6 adults (3 females, 3 males) on the BLM study area in 1980. Each of the radio-tagged owls was a resident that occupied an area with its mate. In 6 cases transmitters were placed on both members of a pair. In 2 cases, we put transmitters on females but were unable to capture the males with which they nested. In addition to the 14 adults radio-tagged, 4 owlets were radio-tagged in August 1975.

Radio transmitters were attached with a backpack harness of tubular teflon ribbon (Dunstan 1972). Transmitters weighed 18–22 g including battery and harness and operated for 111–383 days before they either stopped transmitting or were removed. Transmitter frequency was 164 Mhz. Signal pulse rate was 56–120 ppm.

Radio receiving equipment included an AVM Model LA 12 receiver, a whip antenna mounted on a vehicle, and a hand-held 4-element yagi antenna. To determine the location of an owl by triangulation, the observer obtained a bearing with the hand-held yagi, then moved down the road or trail to obtain at least 2 additional bearings. If the owl moved before at least 3 bearings were determined, a new series of bearings was obtained as soon as movement ceased. Movement could be detected from fluctuations in signal strength and changes in signal direction relative to the observer. The problem of owls moving before a location could be accurately determined was relatively minor because of the manner in which the owls foraged. Except for occasional periods of movement, the owls usually spent considerable time at each foraging location, permitting the observer to obtain numerous bearings before movement occurred.

The accuracy of locations generally declined as the distance between the observer and signal source increased. For this reason we always moved as close as possible to radio-tagged owls before triangulating (in most cases we were able to get within 400 m). Locations that were not sufficiently accurate to determine the type of cover occupied were not used in habitat utilization analyses.

Locations were plotted on a cartesian coordinate system overlaid on an orthophoto of the study area. Coordinates were then recorded on Fortran computer sheets along with the time (Pacific Standard Time), date, activity type, and type of cover occupied.

Seven types of activity were recognized: foraging, roosting, moving, calling, territorial interaction, incubation or brooding, and unknown. At night when adults were not calling or moving from 1 place to another, they were considered to be foraging even if they did not move for long periods of time (except, of course, for incubating or brooding females). This approach was adopted because it was extremely difficult to distinguish between foraging and resting behavior at night. For example, an owl might be immobile (i.e., "resting") for some time and yet still be actively watching for prey. When tracking owls we always tried to stay within hearing distance so that we could detect calling activity or territorial interactions. On both study areas, owls were tracked an average of 5 nights/week. On the HJA study area we attempted to locate each owl at least once each night. This "spot check" method was alternated with continuous tracking sessions in which 1 or 2 individuals were observed continuously for up to 12 hours at a time. During continuous tracking sessions, locations were reported every 15–30 minutes. Between November and February on the HJA area, deep snow limited access to the home ranges of 3 owls at higher elevations, and we were forced to concentrate observations on 5 individuals. During this period the 3 individuals at high elevations were located at least once each week.

On the BLM study area a different observation schedule was followed. Each night 1 pair of owls was observed from early evening until midnight, and another pair was observed from midnight until dawn. When both pair members could not be tracked simultaneously, we either tracked 1 member of the pair continuously or alternated between the 2 individuals at intervals of 1–2 hours. Locations were determined at 5-minute intervals instead of 15–30-minute intervals. A rotating schedule was established so that observations were distributed equally with respect to pairs and time of night. The observation schedule used on the BLM study area was initiated because it produced more data per unit time and provided a more continuous record of owl movements than the method used on the HJA area.

The minimum convex polygon and ellipse methods (Jennerich and Turner 1969) were used to calculate home range areas.

Maps of owl movements were generated on a computerized plotter. The home range was defined as the area used by an owl for foraging, roosting, and nesting.

Based on the age, structure, and species composition of the vegetation, we recognized 16 cover types on the HJA study area and 10 cover types on the BLM study area (Appendix 2). Cover types were determined by ground reconnaissance and were plotted as overlays on orthophotos of each study area. The area of each cover type within the home range (minimum convex polygon method) of each owl was determined with a dot grid or polar planimeter. The preference analysis described by Neu et al. (1974) was used to determine which cover types were preferred for foraging.

To determine when spotted owls were active, we either watched them in their day roosts or monitored them remotely, listening until the transmitter signal indicated that movement had begun or ceased. When possible, owls were located visually or via triangulation in the morning, then relocated in the late afternoon to see if they had changed roost areas.

Roost site characteristics were determined by visually locating 1–6 radio-tagged individuals in their roosts each day. Variables recorded at roosts on the BLM study area were: stand age, perch height above ground, dbh of roost tree, species and age of roost tree, aspect, distance to nearest spring or stream, and overhead perch protection. Overhead perch protection was a ranked variable, indicating whether an owl was roosting under some sort of cover where it could avoid getting wet during rainstorms or was roosting in a position where it was not well protected from rainfall. Variables measured at roost sites on the HJA study area were the same as on the BLM study area except that aspect was not recorded.

Data collected at roosts were divided into 5 categories, depending on the prevailing weather conditions on the day of use: (1) clear, hot day with temperature >28 C, (2) clear, warm day with temperature between 10 and 28 C, (3) overcast day with little or no precipitation, (4) overcast day with steady or intermittent rain or snow, or (5) clear, cold day with temperature <10 C. Roost characteristics were then compared to determine if roost selection was influenced by weather conditions.

Dietary Analysis

The diet of spotted owls was determined from prey remains in regurgitated pellets. Freshly killed prey stored in or near roost trees were also recorded. Pellets collected during each visit to a roost were combined in a single sample, unless some pellets were markedly older than others, in which case samples were further subdivided into "old" vs. "recent" pellets. Vertebrate prey in pellets were identified from skeletal remains, fur, feathers, or scales (see Appendix 3 for scientific names and weights of prey species). Insects were identified and enumerated from mandibles and fragments of the exoskeleton. Numbers of vertebrate prey were determined by counting skulls, pairs of jaws, or other skeletal remains (whichever gave the highest count) in each sample. The biomass of each prey species in the diet was estimated by multiplying the number of individuals times the mean body weight of the species. In the case of snowshoe hares, brush rabbits, and mountain beavers, however, the body weight of each individual was estimated based on the size of skeletal fragments and then summed to obtain total biomass.

To determine seasonal and sexual differences in prey selection on the radiotelemetry study areas, we marked roost trees occupied by individual owls of known sex and then returned to those roosts the next day to collect any pellets that had been regurgitated. Less frequently, pellets were collected after we saw radio-tagged owls regurgitate them. If pellets were collected several days in a row from the same owl, those pellets were combined into a single sample. This was done because remains of a single large vertebrate often appeared in different pellets regurgitated 1 or more days apart. Pellets collected under roosts occupied by more than 1 owl were not used to compare sexual differences in prey selection. Also, pellets regurgitated by nesting females were not used to compare sexual differences in prey selection, because nesting females received most of their food from males. However, some radio-tagged pairs did not nest during the radiotelemetry studies; we were able to compare sexual differences in prey selection in those pairs during the spring and summer.

For all statistical tests the maximum probability accepted for statistical significance was $P = 0.05$. Probabilities below $P = 0.01$ were considered highly significant.

RESULTS

Distribution and General Habitat Characteristics

Spotted owls were found at 636 locations during the study (Fig. 7). At 322 locations both a male and female were observed. Single individuals were observed at 172 locations. At 142 locations the number of owls observed was not reported. Repeated sampling of 124 locations indicated that resident pairs were present at most sites where single owls responded during a first census. We believe, therefore, that most of the areas where single owls (or unspecified numbers of owls) were reported were occupied by resident pairs. Sightings <1.5 km apart were considered as originating from the same locations (i.e., the same pair of owls), unless it was verified that individuals from adjacent territories were involved. To verify the existence of 2 pairs in close proximity required that the pairs be incited to call simultaneously (or nearly simultaneously) at night, or that they be located during the day.

The range of the species included all of the mountains of western Oregon and the east slope of the Cascade Range (Fig. 7). Only 2 spotted owls were reported from areas east of the Cascades. One was a starving individual observed at Dufur, Wasco County, where it subsequently died (Kirk Horn, pers. commun.). The other was an apparently healthy individual photographed 6 km east of Klamath Lake, Klamath County, in September 1974 (Tex Williams, pers. commun.). We were unable to locate spotted owls in the latter area on subsequent visits.

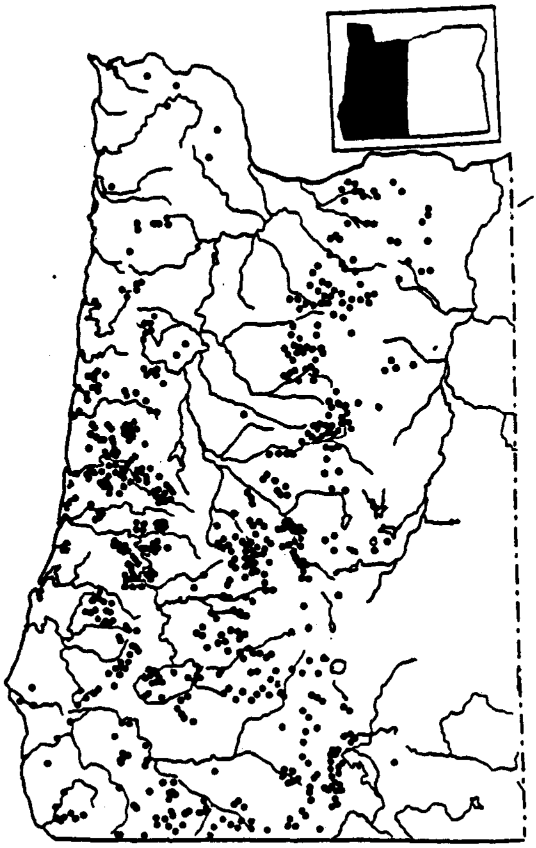

Fig. 7. Western half of Oregon, illustrating 636 locations where spotted owls were located (1969–80).

Elevations at which owls were located ranged from 24 m above sea level near the coast up to 1,340 m in the northern Cascades, 1,524 m in the central Cascades, 2,010 m in the southern Cascades, 1,830 m in the Klamath Mountains, and 1,130 m in the Coast Ranges. The upper limits of the range generally corresponded with the upper edge of the ecotone separating midelevation forests of Douglas-fir, western hemlock, white fir, grand fir, ponderosa pine, or Shasta red fir from subal-

Fig. 8. Old-growth stand of white fir and ponderosa pine in the southern Oregon Cascade Range near Lake of the Woods, Klamath County. A pair of spotted owls nested in the area shown.

pine forests of Pacific silver fir, noble fir, subalpine fir, lodgepole pine, whitebark pine, or mountain hemlock.

Habitats Occupied.—Habitat characteristics were reported for 595 of the 636 sites where spotted owls were located. Spotted owls were found in all of the major coniferous forest associations that occurred in the study area, except for subalpine forests and nearly monospecific forests of ponderosa pine, lodgepole pine, or sitka spruce. Most (98.3%) of the sites where owls were located were forested with old-growth (>200 years old) conifers or mixtures of mature (100–200 years old) and old-growth conifers. Seven pairs (1.2%) occupied second-growth conifer forests in which very small patches of old-growth were present, and 3 (0.5%) occupied second-growth forests in which little or no old-growth was present. No owls were located in forests younger than 36 years old.

The most consistent feature of old-growth forests occupied by spotted owls was the presence of an uneven-aged, multilayered canopy (Figs. 3, 8). Overstory trees in these forests were typically 230–600 years old. Understory layers were generally dominated by younger (30–200 years old) shade-tolerant trees such as western hemlock, western redcedar, Port-Orford cedar, grand fir, white fir, shasta red fir, western yew, vine maple, canyon live oak, California laurel, or tanoak. Although the density and closure of individual canopy layers within these forests varied considerably, composite canopy closure usually averaged moderate to high (65–80%) as a result of the layered structure. Old-growth forests were also characterized by moderate to high numbers of large trees with broken tops, deformed limbs, and heart rot. Spotted owl nests were usually located in such trees (see Reproductive Biology).

Of the pairs found in old-growth or mixed old-growth and mature forests, 4 occupied stands that had been selectively logged prior to the initiation of the study and 9 occupied stands that were selectively logged after we first located them. Selective logging is a harvest method in which canopy density is reduced by removing some of the overstory trees. The understory is either left intact or thinned. Of the 4 pairs occupying previously logged sites, 3 nested in stands that had been logged 30–40 years earlier. The nest of the fourth pair was in an unharvested old-growth stand, 5 m from the edge of an area that had been selectively logged about 10 years earlier. In the former stands, young trees had since filled in many of the openings created by harvest, resulting in multilayered stands that were similar to unlogged old-growth stands except that the density of overstory trees was reduced.

Of the 9 sites that were selectively logged after owls were located, 7 were subjected to relatively light overstory removal, and 2 were heavily thinned. At 6 of the 7 sites subjected to light overstory removal, timber sales were laid out so that a small patch (2.6–10 ha) of unlogged, old-growth was left around the nest tree of the resident owls. On the latter sites, 3 pairs subsequently used their old nest trees in 1 or more years following harvest. The other 3 pairs remained in the same general areas after harvest, but we were unable to document nesting. The nest of the seventh pair was not located prior to harvest, but we suspected it was located in the area harvested (fledglings were observed in the harvest unit prior to harvest). In this case the owls responded to harvest by moving to a new nest tree in an unharvested old-growth stand 1.2 km from the suspected location of the old nest. The new nest was subsequently used for 2 years before the owls disappeared from the area completely.

On the 2 sites where overstory and understory trees were heavily thinned, the spacing between trees in the owl nest areas was increased to 10–20 m as a result of harvest. Canopy closure was reduced to <50%. One of these pairs subsequently disappeared. The other pair shifted their activities to an unlogged old-growth stand bordering the harvested area; a new nest was located in the unlogged area 4 years after harvest of the original nest area.

Of 10 pairs located in predominantly second-growth forests, 7 occupied forests in which 3–20-ha patches of old-growth and scattered individual old-growth trees were intermixed with extensive 40–80-year-old forests. The other 3 pairs occupied relatively uniform 45–60-year-old forests where no old-growth was present. Second-growth forests occupied by spotted owls differed structurally from old-growth in that the trees were smaller and more uniform in age and size. Canopies within these stands were closed (65–80% closure) but were not strongly multilayered. Of the 10 pairs in second-growth forests, we were able to verify nesting by 2, both of which occupied stands in which small patches of old-growth trees were intermixed with the second-growth (second-growth trees at both sites were 70–90 years old). One of the pairs did not nest successfully in the 3 years that we observed nesting attempts. One year the nest failed for unknown reasons, the next year the young were taken from the nest by a predator, and the next year the eggs were somehow destroyed. This pair disappeared in 1980. The other pair nested in 2 consecutive years; we observed young in the nest both years but did not determine if they fledged.

Spacing of Pairs.—Mean nearest neighbor distances were 2.6 km west of the Cascades ($N = 47$, SE = 0.130, range = 1.6–5.2 km) and 3.3 km on the east slope of the Cascades ($N = 18$, SE = 0.266, range = 1.6–6.4 km). The minimum distance between 2 active nests was 1.9 km, but in several instances we suspected that pairs nested even closer together because their principal roost areas were only 1.6–1.8 km apart. We did not locate the nests of the latter pairs. Our observations on the spacing of pairs support Marshall's (1942: 67) observation that where "suitable habitat prevails, pairs [of spotted owls] can be expected at intervals of one to two miles."

In many areas, particularly the Coast Ranges and Klamath Mountains, federal and private lands were distributed in an irregular checkerboard pattern with approximately every other square mile section (259 ha) privately owned (Fig. 5). The distribution and density of spotted owls in such areas was strongly influenced by the distribution of federal lands. Most private lands had been cutover, whereas federal lands often contained residual tracts of old-growth and mature forest that were occupied by spotted owls. Where these tracts of older forest were spaced close together, owl densities were high. In some areas that had been almost entirely logged within the previous century (e.g., the extreme northern end of the Coast Ranges), we had difficulty finding any owls at all (Forsman et al. 1977).

Population Trends.—From 1972 to 1978, 98 sites occupied by pairs of spotted owls were checked at 1–3-year intervals to determine if the sites were still occupied. Sites were considered occupied as

Table 1. Code names, duration of tracking periods, and home range size of radio-tagged adult spotted owls on the H. J. Andrews and BLM study areas, Oregon.

Study area and owl code name	Tracking period	No. of days in tracking period	Home range area (ha)	
			Minimum convex polygon estimate	Ellipse estimate[a]
HJA area				
1A male	4 May 1975–5 May 1976	367	3,254	4,855
1A female	8 June 1975–14 May 1976	332	2,179	3,169
2A male	25 May 1975–3 Apr 1976	314	1,272	1,156
2A female	12 Jul 1975–3 Jun 1976	327	1,220	936
3A female	12 Jul 1975–9 May 1976	302	920	1,002
4A female	26 Jul 1975–1 Jun 1976	311	1,376	1,239
5A male	25 May 1975–11 Jun 1976	383	950	684
5A female	14 Sep 1975–11 Jun 1976	271	1,324	1,173
Mean for all HJA owls[b]			1,177	1,032
Mean for males[b]			1,111	920
Mean for females[b]			1,210	1,087
BLM area				
1C male	2 Apr–22 Jul 1980	111	3,380	3,776
1C female	13 Apr–26 Aug 1980	135	2,140	1,823
2C male	2 Apr–15 Aug 1980	135	549	602
2C female	13 Apr–27 Aug 1980	136	3,376	3,481
3C male	12 Apr–27 Aug 1980	135	997	796
3C female	16 Apr–1 Sep 1980	138	1,038	995
Mean for all BLM owls			1,913	1,912
Mean for males			1,642	1,725
Mean for females			2,185	2,100

[a] For calculation see Jennerich and Turner 1969.

[b] Averages do not include data from 1A male and female because that pair did not occupy the same home range areas for the duration of the study.

long as a pair could be located within a 1.5-km radius of the historical nest or principal roost area. Eight (8%) of the sites were no longer occupied by 1978, indicating an 0.8% rate of population decline per year. In 7 cases, sites were abandoned after nests or major portions of the forest surrounding nests were harvested. One pair disappeared after the female was apparently killed by a predator. She disappeared from the nest overnight and was not seen again. The male eventually left the area. Although we could not discount the possibility that displaced pairs simply relocated elsewhere, this was unlikely, because all of the displaced pairs occupied heavily cutover regions where there was little habitat in which to relocate.

Portions of the forest on at least 54 of the 98 sites monitored from 1972 to 1978 were harvested during the period without completely displacing the resident owls. When part of the forest area occupied by a pair of spotted owls was harvested, the owls usually responded by shifting their area of activity into the remaining uncut forests. When the remaining forests consisted of extensive areas of young second-growth or heavily thinned timber, however, the owls frequently disappeared.

Another indication that the owl population was declining was that owls could not be relocated in 7 (35%) of the 20 areas where they had been observed in Oregon prior to 1970. Because accurate locations of most historical sightings were not available, however, we were unsure in some cases whether we inventoried the exact areas where the historical sightings occurred. For this reason we view the results of this index as being only roughly indicative of population trends. Gould (1974, 1977, 1979) studied occupancy rates of historical sites in California and reported similar trends and problems with analysis.

Land Ownership at Sites Where Owls

Table 2. Percent of locations of radio-tagged owls on the H. J. Andrews and BLM study areas according to activity type.

Study area and owl code name	Number of locations	Activity type						
		Foraging	Roosting	Moving	Calling	Territorial interaction	Incubation or brooding	Unknown
HJA area								
1A male	708	54.0	36.4	5.8	2.4	1.1		0.3
1A female	659	55.2	38.1	2.0	1.7	2.6		0.4
2A male	732	49.7	41.1	3.6	4.2	0.7		0.7
2A female	773	53.8	33.1	5.7	6.8	0.3		0.3
3A female	582	59.3	29.2	1.9	1.7	0.5	6.9	0.5
4A female	669	54.0	25.0	5.5	2.4	0.1	12.0	1.0
5A male	417	51.1	36.7	5.8	3.6	0.2		2.6
5A female	387	41.7	24.8	5.9	1.0		22.5	4.1
BLM area								
1C male	1,986	92.7	4.0	0.2	1.8	0.1		1.2
1C female	1,903	92.7	4.7	0.4	1.4			0.8
2C male	1,754	92.6	5.3		0.7	0.4		0.9
2C female	1,977	92.4	5.0	0.5	0.9	0.1		1.2
3C male	2,042	91.5	4.6	0.6	2.6			0.7
3C female	2,283	93.2	4.2	0.2	1.6	tr[a]		0.8
4C male[b]	7		71.4		28.6			

[a] tr = <0.05%.

[b] The 4C male was an unmarked adult that occasionally roosted with the 2C female. Its sex was determined from vocalizations (see vocal displays).

were Located.—Fifty-three percent (314) of the sites where owls were located were on lands administered by the U.S. Forest Service, 40% (240) were on lands administered by the Bureau of Land Management, 6% (34) were on privately owned lands, 0.3% (2) were in national parks, and 0.8% (5) were on lands owned by the state of Oregon. Land ownership was unknown at 41 sites. The low incidence of occurrence on private and state-owned lands was partly due to the fact that most cooperators were federal employees who searched for spotted owls primarily on federal lands. More important, however, was the fact that the majority of private and state lands in western Oregon had been cutover or burned within the previous 70 years and were no longer occupied by spotted owls (Forsman et al. 1977). Recent inventories in Washington and California indicated that spotted owls also were uncommon on cutover private lands in those states (Gould 1974, 1977; Postovit 1979).

Site Tenacity.—Of 14 radio-tagged adults, 12 remained on the same home range areas for the duration of the tracking period (3–13 months). Two that were identifiable because their transmitters were not removed were still present in the same areas 26 and 37 months after initial capture, respectively. These results indicate that individual adults occupy the same home ranges for long periods of time (probably for life), unless displaced by habitat destruction. Miller (1974) reached a similar conclusion based on observations of a pair of spotted owls during a 7-year period. The continuous occupancy of many sites by pairs of spotted owls during our study was apparently made possible because individuals that died were quickly replaced. This was verified on 5 occasions when marked individuals or individuals with distinctive markings disappeared and were replaced by the next spring (see also Miller 1974).

Home Range Characteristics

On the HJA study area, 261 nights and 268 days were spent tracking owls, and a total of 4,927 owl locations was obtained (Tables 1, 2). The 5 pairs studied on the HJA area were distributed along the 2 major stream drainages (Lookout Creek and Blue River) that crossed the area (Fig.

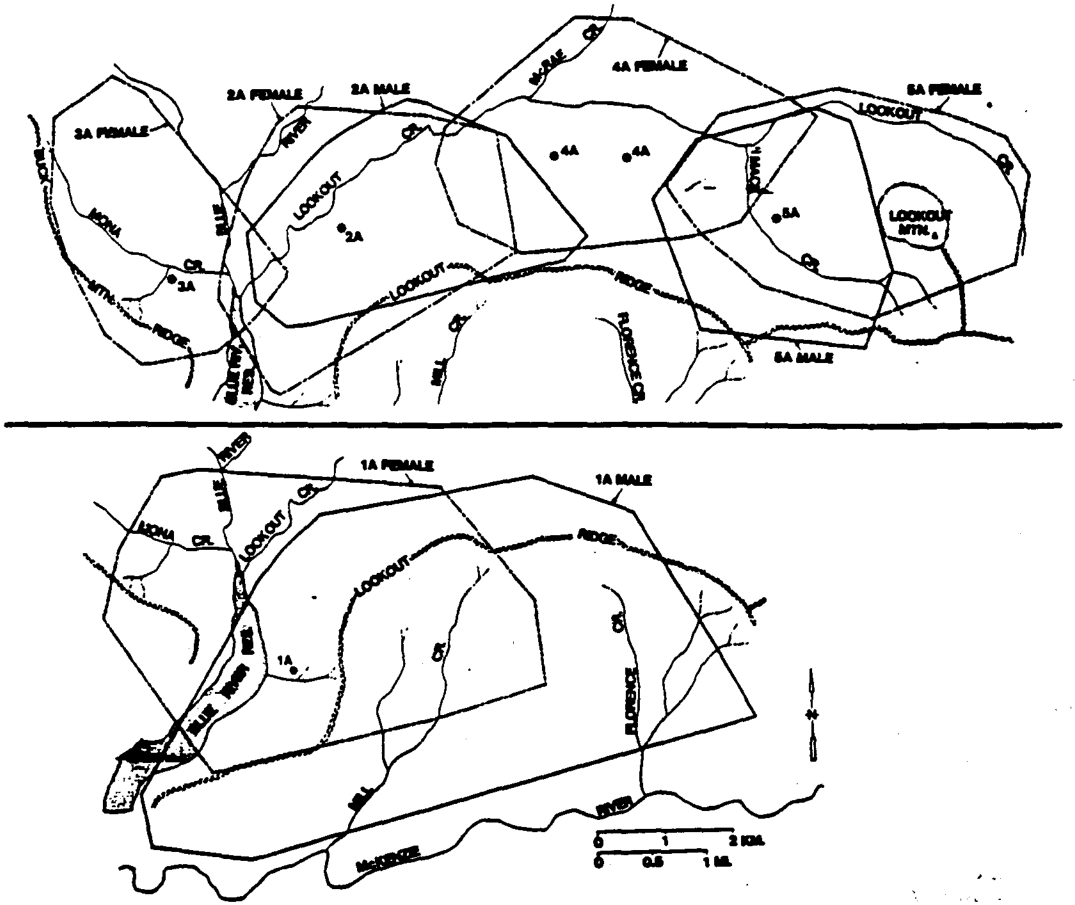

Fig. 9. Outlines of home ranges used by 8 radio-tagged adult spotted owls on the H. J. Andrews study area (May 1975–Jun 1976). Asterisks indicate locations of nests used by each pair.

9). An intensive search indicated that there were no other pairs occupying areas between the radio-tagged pairs. There were, however, at least 4 additional 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 the radio-tagged pairs were collected.

On the BLM study area, 92 nights and 111 days were spent tracking owls, and a total of 11,952 owl locations was obtained (Tables 1, 2). The 3 pairs studied in this area confined most of their activities to the Siuslaw River drainage and its tributaries (Fig. 10). On this study area there were also several pairs of unmarked spotted owls occupying areas adjacent to the home ranges of the marked owls. The unmarked owls were not studied except to note their presence and their main areas of activity.

Total or Cumulative Home Range Size.—Based on the minimum convex polygon method, home ranges averaged 1,177 ha on the HJA study area and 1,913 ha on the BLM study area (Table 1; Figs. 9, 10). The Jennerich and Turner (1969) ellipse method indicated a mean home range of 1,032 ha on the HJA area and 1,912 ha on the BLM area (Table 1). Sizes of male and female home ranges were not

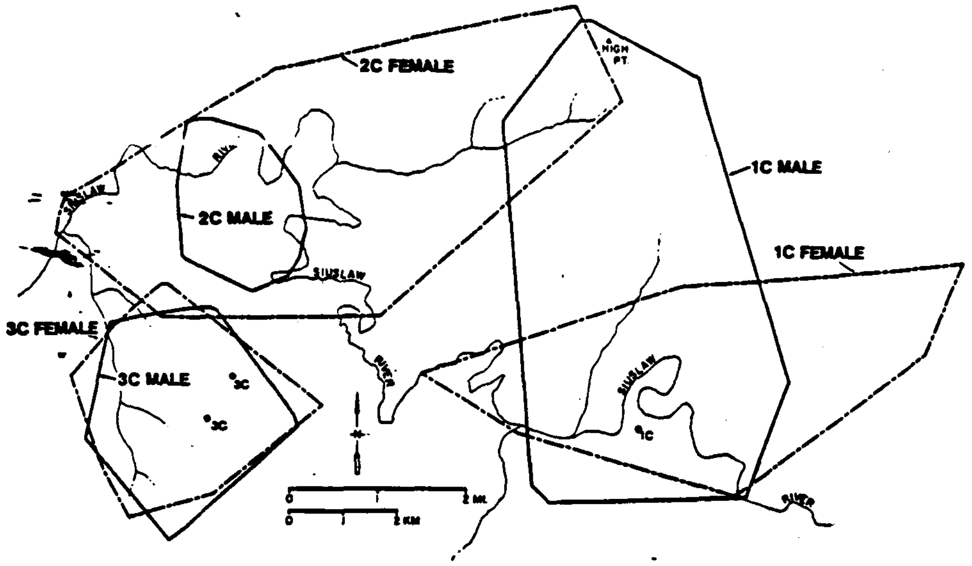

Fig. 10. Outlines of home ranges used by 6 radio-tagged adult spotted owls on the BLM study area (Apr–Aug 1980). Asterisks indicate location of nests used by 2 of the pairs in years preceding the study.

significantly different on either area (HJA area $t = 0.54$, df $= 4$, $P > 0.05$; BLM area $t = 0.49$, df $= 4$, $P > 0.05$) (Table 1). In the following sections, minimum convex polygon estimates of home range size are used for all comparisons.

Home range size was at least partially a function of how long an individual was observed. It was assumed that the total home range had been determined when a plot of home range size as a function of the length of the observation period reached an asymptote (Fig. 11). On the average, 131 days (range = 75–150 days) were required to determine 80% of the total home range used by each owl on the HJA area, and 165 days (range = 105–204 days) were required to determine 90% (Fig. 11). After owls had been observed for 5–6 months, movements outside the home range boundaries already delineated became uncommon. The relatively long period required to determine the total (or near total) home range reflected the fact that owls visited some portions of their home ranges infrequently.

In spite of the fact that owls on the BLM study area were only observed for 4 months, their home ranges averaged larger than the home ranges of owls on the HJA area where owls were observed for 9–13 months (Table 1). Had owls on the 2 areas been tracked for equal periods, the difference in mean home range size would likely have become even larger.

Seasonal Differences in Home Range Use.—Home range data from the BLM area were not subdivided seasonally because data were only collected for part of the year. On the HJA area home range use changed seasonally (Table 3, Fig. 12). The most noticeable differences in home range use on the HJA area occurred between the breeding season (late Feb–Sep) and post breeding season (Oct–Jan). During the breeding season, both nesting and non-nesting individuals confined most of their activities to within 2.6 km of their traditional nests (Fig. 12). During the post breeding season, the owls became solitary and began to wander more extensively, gradually expanding their home ranges in most cases (Table 3, Fig. 12). Apparently, use of areas located far from nest sites was energetically more feasible during winter when the owls did not have to return to

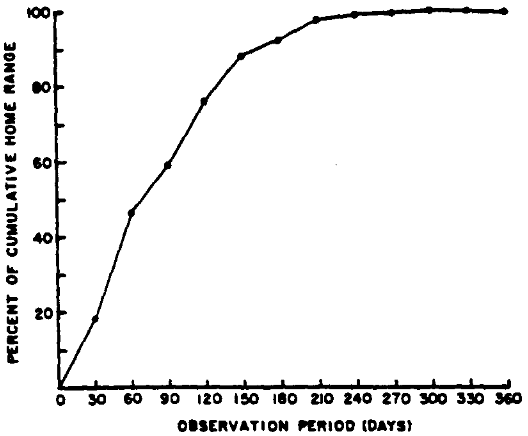

Fig. 11. Size of total home range as a function of the length of the observation period (data averaged for 4 owls on the H. J. Andrews study area). During the observation period the owls were observed approximately 6 days and 5 nights each week.

their nest areas 1 or more times each night. The use of larger home ranges in winter may also have been a response to gradually declining prey populations (Clark 1975).

Influence of Topographic Features on Home Range Shape.—Several home range boundaries on the HJA study area corresponded roughly with high elevation (1,000–1,500 m) ridge crests, suggesting that such ridges formed natural barriers to movement (Fig. 9). It is possible, however, that avoidance of high elevation areas was due to patterns of vegetation distribution rather than physical barriers. Vegetation on the higher ridges on the HJA area was dominated by mature forests and subalpine brushfields of Sitka alder. Owls may have avoided such areas because they preferred to forage in old-growth stands, which were more abundant at lower elevations (see Habitat Selection for Foraging).

Owls occupying home ranges adjacent to Blue River Reservoir on the HJA study area rarely crossed the reservoir except near its upper end where it was <150 m wide. We observed only 1 instance in which an owl made a continuous flight of nearly 400 m across the main body of the reservoir.

Home Range Overlap Between Paired Owls.—Home ranges occupied by paired individuals overlapped by 50–73% on the HJA area and 40–93% on the BLM area ($\bar{x} = 68\%$) (Figs. 9, 10). These estimates did not include 2 pairs (1A and 2C pairs) in which there was some question about whether the owls were established pairs. In all cases, the areas of overlap between paired individuals included the nest area, major roost sites, and the areas that were used most intensively for foraging. The combined home range areas used by paired individuals ranged from 1,149 to 4,225 ha ($\bar{x} = 2,144$ ha).

Although their home ranges overlapped considerably, paired individuals used the same foraging locations (X, Y coordinates) only 4–10% of the time. This suggested that there was little competition for food between pair members.

Home Range Overlap Between Neighbors.—On the average, any 2 owls occupying adjacent territories on the HJA area

Table 3. Home range size (ha) of 6 radio-tagged adult spotted owls during different periods of the year on the H. J. Andrews study area (May 1975–Jun 1976).

		1975			1976	
Owl	6 May–Jul	Aug–Sep	Oct–Nov	Dec–Jan	Feb–Mar	Apr–10 Jun
2A male	661	593	646	824	604	
2A female		336	1,047	1,048	449	335
3A female		332	695	693	224	
4A female		1,062	911	1,154	318	227
5A male	172	262	386		160	834
5A female		596	1,054		227	810
Means	416	530	790	930	330	552

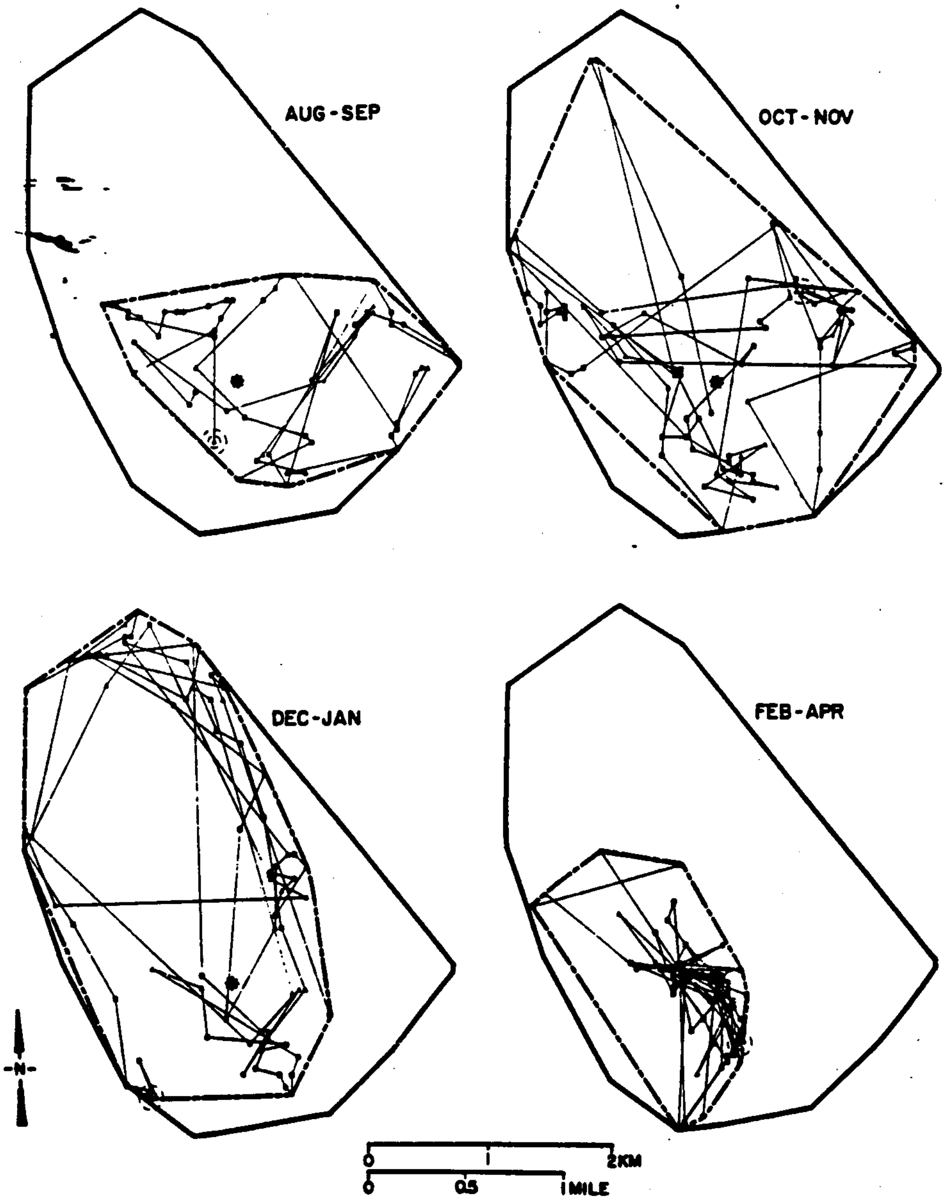

Fig. 12. Computer maps illustrating seasonal changes in home range use by the 3A female on the H. J. Andrews study area (Aug 1975–Apr 1976). Dashed lines indicate boundaries of seasonal areas used and solid lines indicate total home range. Location of nest used in 1976 is indicated by an asterisk.

shared 12% of their home ranges (range = 3–25%, $N = 6$). Shared areas were generally near the periphery of adjacent home ranges where the owls spent a relatively small proportion of their time (Fig. 9). Home range overlap between neighboring individuals did not differ greatly depending upon sex ($\bar{x} = 11\%$ between females, 14% between males and females). Overlap between males could not be calculated because the radio-tagged males on the HJA area did not occupy adjacent

Table 4. Use of cover types for foraging by 8 radio-tagged adult spotted owls on the H. J. Andrews study area (May 1975–Jun 1976).[a]

Cover type	Percent coverage on home ranges[b]	Percent of time spent foraging in type[c]	No. of individuals using cover type: Significantly more than expected	Not significantly different than expected	Significantly less than expected
Old-growth conifer forest	33–66	85–99	8	0	0
Selectively logged old-growth conifer forest	tr–1	0–tr	0	2	4
81–200-year-old conifer forest	3–27	0–16	1	3	3
Mature hardwood forest	0–2	2	0	1	0
61–80-year-old conifer forest	tr–10	0–2	0	3	2
31–60-year-old conifer forest	1–2	0–tr	0	1	2
21–30-year-old conifer forest	3–19	0–tr	0	0	7
5–20-year-old conifer forest	10–31	0–6	0	0	8
Recent clear-cuts covered by brush or grass–forb associations	2–10	0–tr	0	0	6
Rock talus	tr	5	1	0	0
Reservoir	2–6	0	0	0	4
Other[d]	tr–7	0–1	0	3	5

[a] Test used to evaluate habitat use was described by Neu et al. (1974). 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 tests would not have been meaningful.

[b] tr = <0.5%.

[c] As indicated by the percent of owl locations in the cover type.

[d] Other cover types present on the area are listed in Appendix 2.

home ranges. The 1A male and female were not included in home range overlap calculations because it was not clear whether they were an established pair.

Total overlap between the home range of 1 individual and the home ranges of 2 adjacent pairs could only be calculated for the 4A female. She shared a total of 39% of her home range with the 1A and 5A pairs (Fig. 9).

There was little overlap among the home ranges of the 3 pairs on the BLM area. The absence of overlap was not unexpected in the case of the 1C pair, because that pair was located nearly 8 km from the 2C and 3C pairs (Fig. 10). The lack of appreciable overlap between the home ranges of the 2C and 3C pairs may have been due to the fact that there was a wide (0.5–1.6 km) corridor of clear-cut land separating the 2 pairs.

Several unmarked owls on the BLM study area had home ranges that considerably overlapped the home ranges of the marked individuals. These unmarked individuals were heard or seen within the home ranges of the radio-tagged owls on a number of occasions, including 3 instances when unmarked owls called near the center of the area occupied by the 3C pair. The 2C female regularly traveled back and forth between the home ranges of 2 different males, roosting occasionally with each of them.

Habitat Selection for Foraging

Forests.—All of the radio-tagged owls on the HJA and BLM study areas showed a strong preference for foraging in unlogged old-growth forests (Tables 4, 5; Figs. 13–15; Appendix 2). Use of old-growth stands that had been selectively logged was either not significantly different than expected, or significantly less than expected (Table 4), suggesting that selective logging decreased the suitability of old-growth stands for foraging. Use of older second-growth and mature forests (61–200 years old) was variable, ranging from significantly less than expected in most cases, to significantly more than expected in a few cases (Tables 4, 5). Use of young second-growth forests (25–60 years old) was in all cases significantly less than or not significantly different than expect-

Table 5. Use of cover types for foraging by 6 radio-tagged adult spotted owls on the BLM study area (Apr–Aug 1980).[a]

Cover type	Percent coverage on home ranges	Percent of time spent foraging in type[b]	No. of individuals using cover type: Significantly more than expected	Not significantly different than expected	Significantly less than expected
Old-growth conifer forest	20–54	64–98	6	0	0
81–200-year-old conifer forest	0–2	1–2	0	1	1
Mature ash and oak forest	0–tr	tr–1	1	1	0
61–80-year-old conifer forest	1–45	tr–36	1	1	4
36–60-year-old conifer forest	0–2	0–tr	0	0	2
25–35-year-old conifer forest	0–47	0–31	0	1	3
5–24-year-old conifer forest	2–26	0–1	0	0	6
Recent clear-cuts covered by brush or grass–forb associations	9–23	0–tr	0	0	6
Other[c]	0–2	0	0	0	4

[a] Test used to evaluate habitat use was described by Neu et al. (1974). All 6 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 tests would not have been meaningful.

[b] As indicated by the percent of owl locations in the cover type. tr = <0.5%.

[c] Other cover types present on the area are listed in Appendix 2.

ed (Tables 4, 5). Areas that had been clear-cut or burned within the previous 20 years were rarely used for foraging (Tables 4, 5).

Although second-growth forests were not preferred for foraging in most instances, some individuals did spend as much as 36% of their time foraging in such forests (Table 5). This suggested that young forests provided at least marginal foraging habitat after reaching 25–35 years of age. It should be noted, however, that little intensive management had been conducted in any of the young forests on either study area. We do not know if these stands would have been used for foraging had they been intensively managed.

Although recent clear-cuts and burned areas were rarely used for foraging, most owls occasionally made long flights (up to 1.5 km) across such areas en route from one patch of older forest to another. If possible, however, owls usually avoided crossing these open areas by traveling through corridors of uncut timber around cutover areas (Figs. 13–15). This is not entirely obvious from the computer maps of owl movements in Figs. 13–15, because many of the lines across clear-cuts connected sequential locations determined several hours or even days apart (and thus did not necessarily represent the actual flight path).

Talus Outcrops and Rockslides.—Natural talus outcrops and areas of rocky rubble along road cuts were absent on the BLM area and uncommon (<0.3% coverage) on the HJA study area. The only individual that used areas of rocky rubble or rock talus significantly more than expected was the 2A male (Table 4). Between June and September, this male was observed on 8 different nights, perched at points overlooking rockslides. He was apparently hunting for pikas, which were active both day and night in such areas. Foraging in rock talus ceased entirely after about 15 October, probably because pikas curtailed their above-ground activities during winter.

Roads and Miscellaneous Cover Types.—Narrow secondary gravel roads were common on both study areas. All of the radio-tagged owls foraged at least occasionally in forests bordering such roads and appeared undisturbed by the occasional passage of vehicles. However, there was no apparent tendency to concentrate foraging activity near roads or other types of "edge" areas such as boundaries between clear-cuts and old-growth forests (Figs. 13–15).

Miscellaneous cover types on the HJA study area included 7 small rock quarries, Blue River Reservoir, a golf course, a forested public campground, a powerline

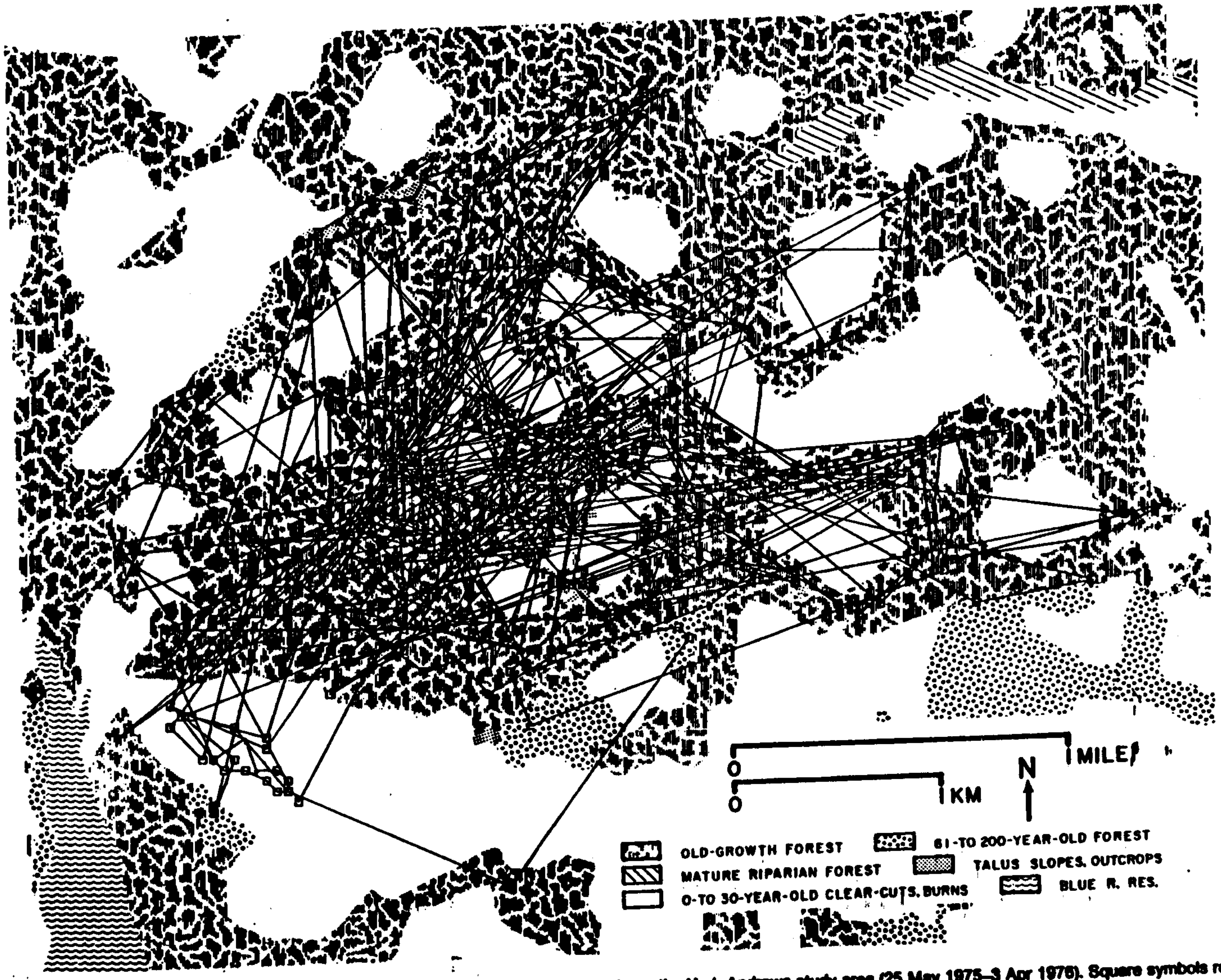

Fig. 13. Computer generated map illustrating home range and habitat use of the 2A male on the H. J. Andrews study area (25 May 1975–3 Apr 1976). Square symbols represent foraging locations and triangles represent roosting locations.

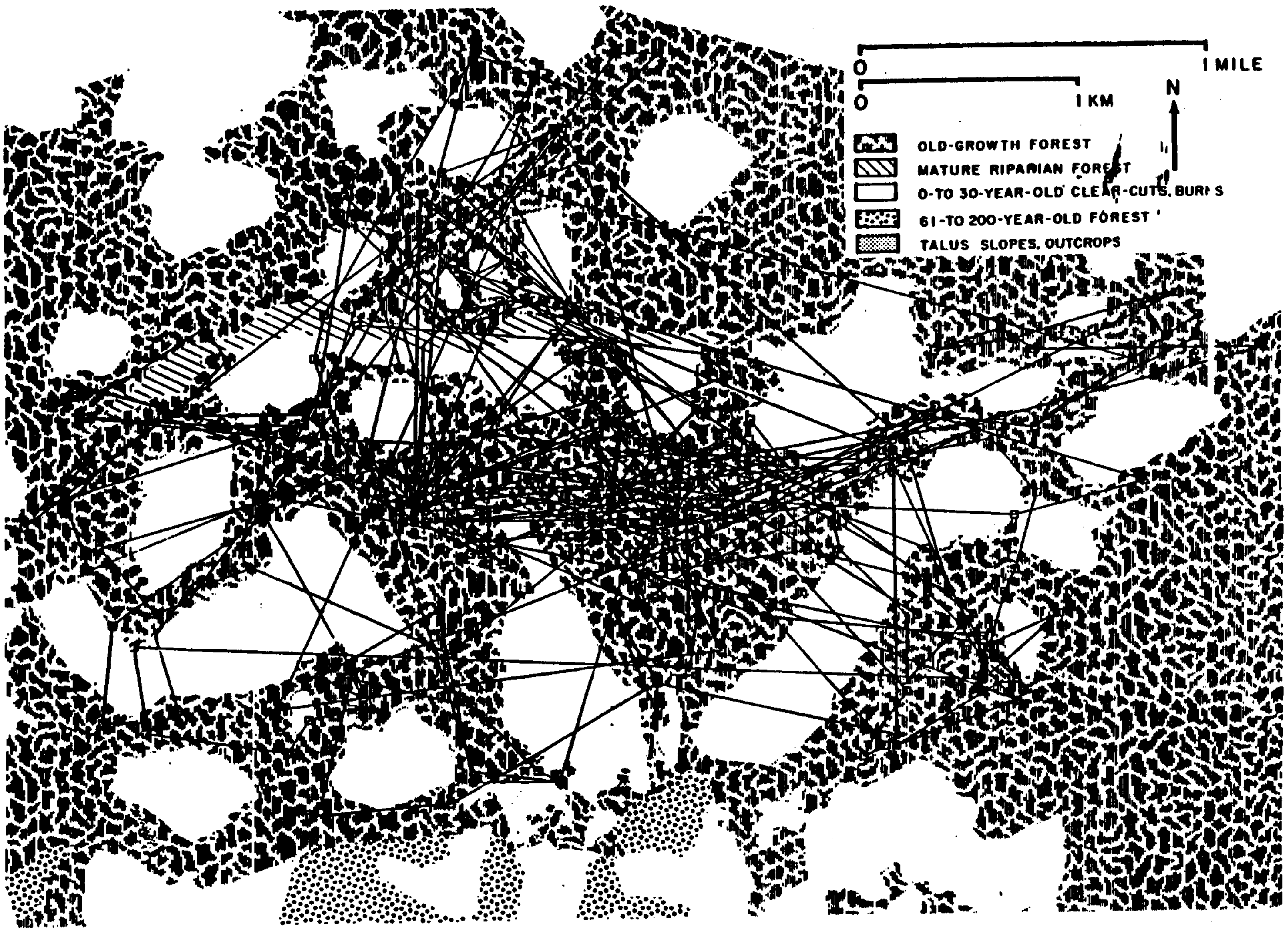

Fig. 14. Computer generated map illustrating home range and habitat use of the 4A female on the H. J. Andrews study area (26 Jul 1975–1 Jun 1976). The 2 concentrations of locations in the center of the home range represent locations of nests used in 1975 and 1976. Square symbols represent foraging locations and triangles represent roosting locations.

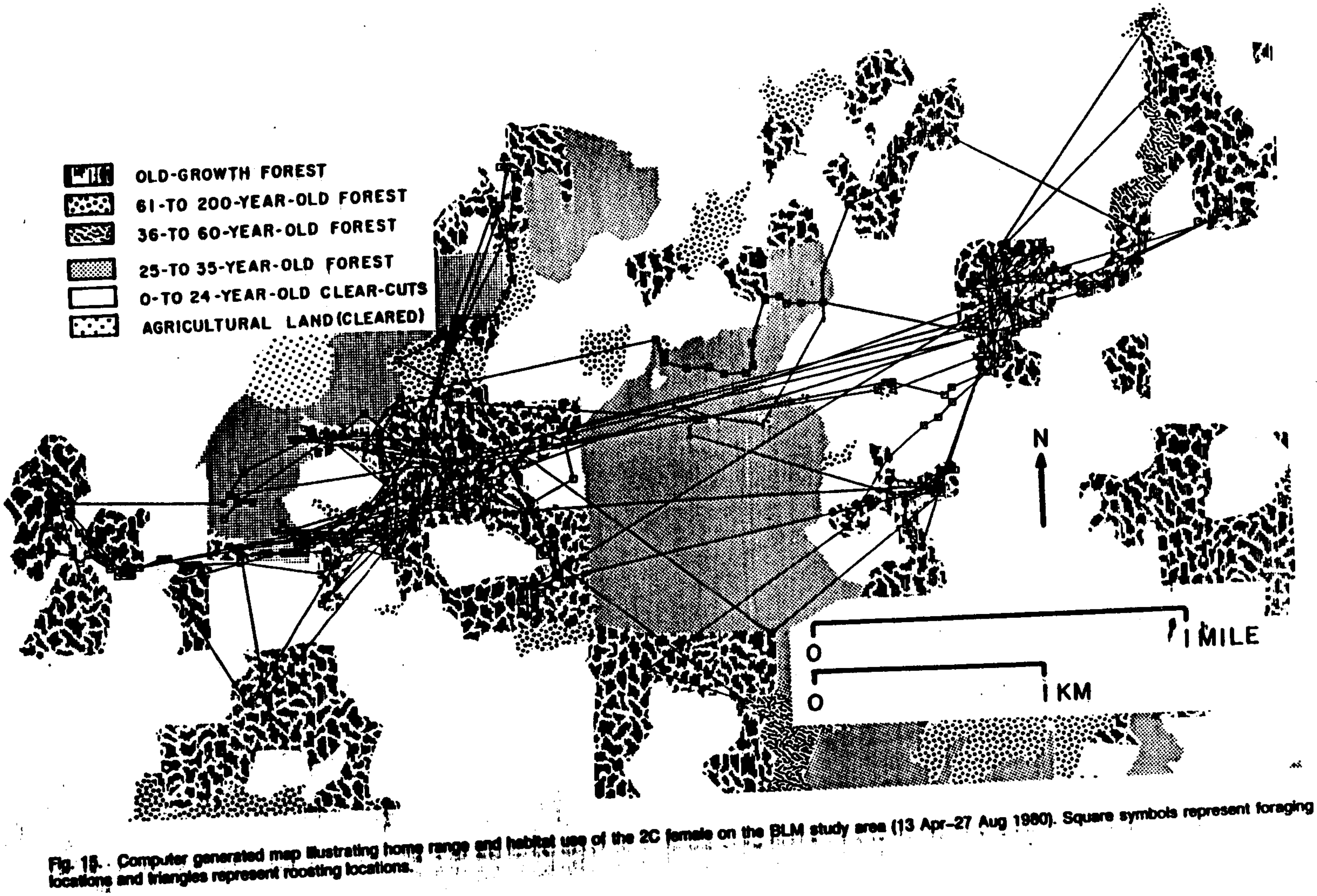

Fig. 15. Computer generated map illustrating home range and habitat use of the 2C female on the BLM study area (13 Apr–27 Aug 1980). Square symbols represent foraging locations and triangles represent roosting locations.

Table 6. Percent occurrence of roosting in different cover types by radio-tagged spotted owls on the H. J. Andrews study area (May 1975–Jun 1976) and BLM study area (Mar–Sep 1980). Number of roosts is in parentheses.

Cover type	HJA (1,098)	BLM (555)
Old-growth conifer forest	97.6	91.0
Mature Oregon white oak and Oregon ash forest		4.0
81–200-year-old conifer forest	1.3	
61–80-year-old conifer forest	0.5	4.0
25–60-year-old conifer forest	0.6	1.0

Table 7. Percent of roosts in different tree or shrub species under different weather conditions on the BLM study area (2 Mar–1 Sep 1980). Roost sample size is in parentheses.

	Weather conditions			
Tree species	Intermittent or steady rain (61)	Overcast, no precipitation (40)	Clear-warm, 10< temp <28 C (160)	Clear and hot, temp ≥28 C (32)
Douglas-fir	57	20	9	
Western hemlock	8	30	26	31
Western red cedar	10	7	11	10
Vine maple	2	10	22	28
Pacific dogwood	5	13	16	28
Incense-cedar			1	
Other broad-leaved trees[a] or shrubs	18	20	14	3
Log or limb on ground			1	

[a] Included Oregon white oak, western hazel, creambush oceanspray, Pacific madrone, bigleaf maple, Oregon ash, red alder, golden chinkapin, and an unidentified willow.

right of way, an agricultural field, and a 9.4-ha area of old-growth Douglas-fir that had been harvested by the shelterwood method (Appendix 2). On the BLM study area, miscellaneous cover types included 2 livestock pastures and a 1-ha-gravel storage area. Foraging was observed in the miscellaneous cover types on only 2 occasions, once when the 2A male foraged in a small rock quarry and once when the 3A female foraged in a public campground.

Seasonal Differences in Habitat Selection for Foraging.—Because owls on the BLM study area were only observed for 4 months, we did not attempt a seasonal comparison of habitat selection. On the HJA study area, seasonal differences in habitat selection for foraging were relatively small. During all seasons, foraging was limited primarily to forested areas, especially old-growth forests. During midwinter (Dec–Feb), when approximately 85% of the diet consisted of arboreal mammals (see Food and Foraging Behavior), the owls foraged almost exclusively in forested areas. During the rest of the year, rock talus and recent clear-cuts were used occasionally, but over 90% of foraging occurred in forests >30 years old.

Habitat Selection for Roosting

On the HJA and BLM study areas, we located 1,098 and 555 owl roosts, respectively. Of these, 645 were visually located by homing in on radio-tagged owls, and 1,008 were located remotely by triangulation. Of the 645 owls observed in day roosts, 640 were perched on limbs in trees or large woody shrubs, and 5 were perched on limbs or logs on the forest floor. All roosts were in forests. Roosting in tree cavities was not observed, except in the case of females about to lay eggs (see Reproductive Biology). Over 90% of all roosts were in old-growth forests, indicating that such forests were strongly preferred for roosting (Table 6).

The type of roost tree used and perch position within the forest canopy were influenced by weather conditions on both study areas. During warm or hot weather, the owls usually roosted low in the forest understory in small trees or shrubs, thereby reducing their exposure to solar radiation and high temperatures (Tables 7, 8). Spotted owl use of cool roosts during hot weather has previously been described by Forsman (1976, 1980, 1981*a*), Barrows and Barrows (1978), and Barrows (1980). When it was cold, raining, or snowing, owls roosted significantly higher in the forest overstory, usually in old-growth or mature conifers (Tables 7, 8) (HJA area $t = 12.75$, df = 191, $P < 0.005$; BLM area $t = 12.22$, df = 251, $P < 0.005$). In addi-

Table 8. Characteristics of roosts used by spotted owls under different weather conditions on the H. J. Andrews study area (May 1975–Jun 1976) and BLM study area (Mar–Sep 1980).

	Weather conditions and area									
	Intermittent or steady rain		Overcast, no precipitation		Clear and cold, temp ≤10 C		Clear–warm, 10< temp <28 C		Clear–hot, temp ≥28 C	
	HJA	BLM	HJA	BLM	HJA	BLM	HJA	BLM	HJA	BLM
No. of roosts measured	103	61	69	40	60	0	78	160	12	32
Mean perch height (m)	23.5	14.9	18.7	7.3	20.4		10.1	5.2	3.6	4.3
Mean dbh of roost trees (cm)	115	84	85	33	88		45	25	18	15
Roosts protected from rain (%)[a]	58.3	51	23.2	5	7.2		1.3	3.0	0	0
Roosts in trees >80-years-old (%)	81.6	62	56.5	10	59.4		16.7	6.0	0	0

[a] A roost was protected from rain (and snow) if the owl was perched close against the trunk of a large tree, either on the underside of a leaning trunk or under a series of large overhanging limbs.

tion, they tended to roost close against tree trunks, under some sort of overhead protection, such as a leaning trunk or a clump of overhanging limbs, where they were sheltered from rain and snow (Table 8). One result of this study that seemed to contradict the hypothesis that spotted owls selected the coolest possible roosts during hot weather was that the majority of roosts on the BLM study area were on south aspects, ragardless of weather conditions (Table 9). We could not explain this result.

Habitat Selection for Nesting

Forty-seven nests were located during the study, all in trees. Forty-two (90%) were in multilayered old-growth forests, 2 (4%) were in a stand dominated by 100–140-year-old Douglas-fir, with a few old-growth Douglas-fir trees interspersed, and 3 (6%) were in 70–80-year-old forests dominated by Douglas-fir, with residual old-growth trees scattered among the younger trees (0–5 old-growth trees/ha). In most cases, nest sites on the HJA and BLM study areas were centrally located within home ranges (Figs. 13–15).

Canopy closure was measured at 26 nests and averaged 69% (range = 35–91, SE = 2.65). Only 2 nests were located in stands with canopy closure less than 55%. Both were located at the edge of small dirt logging roads, such that the canopy on 1 side of the nests was entirely open. The effect of the logging roads was the same as if the nests had been located at the edge of small clearings in the forest.

There was no significant preference for any particular exposure for nesting (Fig. 16) ($\chi^2 = 5.66$, df = 4, $P > 0.05$) (to conduct a χ^2 test we assumed that slopes on north, east, south, and west aspects were equally available). It was our impression that aspect was of minor importance in nest site selection as long as a suitable nest tree and a closed canopy forest were present.

Nest trees were found on slopes ranging from 0 to 85%. Most were located on slopes under 75% (Fig. 16). The majority (57%) of nests were located on the lower half of hillsides. Thirteen (28%) were on the upper half of hillsides, 2 (4%) were on ridgetops, and 5 (11%) were on relatively flat ground in areas of moderate topographic relief.

The majority (84%) of nests located during the study were within 250 m of a stream or spring (range = 15–1,417 m) (Fig. 16). We could not determine whether there was a significant preference for nest sites close to water, however, because we did not determine mean distances between randomly selected points and the nearest source of water in each nest area. We suspect, however, that the presence of water is an important factor in habitat selection by spotted owls because we frequently observed both captive and wild spotted owls drinking and bathing.

Table 9. Percent of spotted owl roosts on different aspects under different weather conditions on the BLM study area (2 Mar–1 Sep 1980). Roost sample size is in parentheses.

	Weather conditions			
Aspect	Intermittent or steady rain (68)	Overcast, no precipitation (42)	Clear–warm, 10< temp <28 C (171)	Clear–hot, temp ≥28 C (34)
Flat	31	21	9	6
North (315–44°)	9	10	22	15
East (45–134°)	5	17	13	20
South (135–224°)	36	33	40	41
West (225–314°)	19	19	16	18

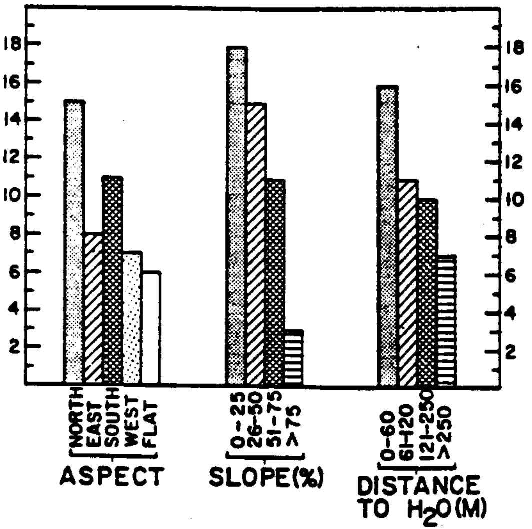

Fig. 16. Placement of 47 spotted owl nests located in Oregon from 1970 through 1980, with respect to aspect, slope, and distance to water. North = 315–44°, East = 45–134°, South = 135–224°, West = 225–314°. Distance to water was unknown at 3 nests.

Reproductive Biology

Nests.—Of 47 nests, 30 (64%) were in cavities and 17 (36%) were on platforms of sticks or other debris on limbs. Forty-one (26 cavities, 15 platforms) were in Douglas-fir trees, 4 (3 cavities, 1 platform) were in white fir, 1 (cavity) was in a ponderosa pine, and 1 (platform) was in a sugar pine. All 30 cavity nests were in old-growth trees. Nine of the platform nests were in old-growth trees, 7 were in 100–200-year-old trees, and 1 was in an 80-year-old tree. Forty-five nests were in living trees, and 2 were in dead trees. Nest height above the ground ranged from 10.0–55.3 m ($\bar{x} = 27.3$, SE = 1.67) (Table 10).

Of the 30 cavity nests, 26 were in cavities that formed when tops of old-growth trees broke off, exposing the hollow interior of the tree (Fig. 17). Four were in cavities that formed when large limbs ripped loose from tree trunks (Fig. 18). Cavities in treetops were typically shaped like a stovepipe, open at the top, with the walls formed by the hardened shell of the broken trunk. All but 2 trees in which treetop nests were located had live secondary crowns that overtopped the broken trunks and shielded nest cavities from rain and direct sunlight (Fig. 17). The 2 exceptions were dead trees.

Of 17 platform nests, 9 were in abnormally dense clusters of limbs ("brooms") caused by dwarf mistletoe (*Arceuthobium* spp.) infections. Eight were on relatively healthy limbs. At least 9 were constructed by other species, including goshawks (1), Cooper's hawks (1), red-tailed hawks (1), woodrats or squirrels (3), and unknown (3). The other platforms consisted of natural accumulations of debris (twigs, conifer needles, cones, lichens, etc.) that had become entrapped by limbs. Nests in trees infected by dwarf mistletoe were frequently situated in such dense tangles of limbs that it was difficult to see into the nests. Although most (65%) platform nests were located against tree trunks, some were located as far as 2.8 m out on limbs.

The nesting substrate in all cavity nests consisted of natural accumulations of rotted wood and, frequently, many old conifer needles, cones, and small twigs. Platform nests were generally lined with a compacted mass of old conifer needles and small twigs. Nests that were reused several times also had a powdery mixture of bones and old pellets intermixed with the substrate. None of the owls that we observed attempted to build or repair nests. Each female simply scraped out a shallow depression in the existing debris. The depression eventually became lined with a small amount of down from the brood patch. In addition, 1 nest contained a few

Table 10. Characteristics of 47 spotted owl nests and nest trees located in Oregon (1970–79).

Measurement	Nests in cavities				Nests in platforms[a]			
	N[b]	Mean	SE	Range	N	Mean	SE	Range
Nest height (m)	30	30.1	1.78	11.7–55.3	17	22.0	1.58	10.0–37.5
Tree height (m)	28	38.1	2.37	18.6–64.0	16	42.0	3.42	23.5–68.6
Bole height (m)[c]	20	15.7	1.14	7.3–24.4	14	13.6	1.48	6.7–28.6
Dbh (cm)	28	135	6.03	74–205	16	106	11.93	36–179
Tree diam. at nest height (cm)	22	78	4.83	51–105	8	75	11.99	23–126
No. of secondary tops in nest tree	23	3	0.50	0–8				
Avg. nest diam. (cm)[d]	20	50	0.93	30–112	8	62	1.32	41–76
Cavity depth (cm)	22	26	7.39	0–123				
Width of cavity entrance (cm)	18	30	4.11	10–77				

[a] Included stick platforms constructed by other birds or mammals as well as platforms that formed naturally when accumulations of sticks, moss, and other debris collected on top of dense tangles of limbs.

[b] All variables were not measured at each nest because all nest trees were not climbed and because some measurements did not apply to all nests. Also, some nest trees were cut or fell down before we obtained a full set of measurements.

[c] Bole height is height above ground of first live limb.

[d] Average diameter of cavities or platforms was determined by measuring at right angles across the widest and narrowest axes of the nest, summing the 2 values, and dividing by 2.

green sprigs of Douglas-fir needles lining the nest scrape. It appeared that the female had added these to the nest. Bent (1938:185) reported that female barred owls sometimes lined their nests with lichens or "fresh, green sprays of white pine." Based on our observations, we believe that reports of nest building by spotted owls (Bendire 1882, Heller 1893) were erroneous. Both Bendire and Heller saw spotted owls using platform nests and *assumed* that the owls had built the platforms.

Eighty-one percent of all nests in northwestern Oregon were in cavities, compared to only 50% in the Klamath Mountains and on the east slope of the Cascades. These differences appeared to reflect regional differences in availability of the different nest types. Dwarf mistletoe infections in Douglas-fir (and the numerous debris platforms that were associated with dwarf mistletoe infections) were common in the mixed conifer forests of the Klamath Mountains and the east slope of the Cascades, but did not occur in western Oregon.

Of 25 nests that were checked in 2 or more years, 17 were used more than once. The longest period of occupancy was a nest that was used 6 times in an 8-year period (in 2 years owls were present but did not nest). The maximum number of nests used by a single pair was 5 during a 6-year period. In the latter case, 2 nests were in the same tree and all 5 were within 50 m of each other. One of the 5 nests was used twice. Distances between alternate nest sites used by individual pairs ranged from the minimum just described up to 1.2 km.

The attrition rate of nest trees was high. Eight (17%) of the nests examined from 1970 through 1978 were no longer usable by the end of 1978. Three were cut down, 4 fell down, and the bottom of 1 rotted through. In addition, 2 nest trees died but remained standing. One was not subsequently reused. The other was reused at least twice after it died.

Timing of Nesting.—The mean date of clutch initiation (calculated by backdating from the date when owlets left the nest) was 2 April ($N = 21$, range = 9 Mar–19 Apr). Owls at lower elevations in southwestern Oregon generally nested 1–2 weeks earlier than owls in the Coast Range and Western Cascades and 2–4 weeks earlier than owls on the east slope of the Cascades.

Clutch Size and Rate of Egg Production.—Clutch size was 2 at each of 4 nests examined during the incubation period. In lieu of information on clutch size at most nests, we used the number of young leaving the nest as an index of minimum

Fig. 17. A typical spotted owl nest cavity in the broken top of an old-growth Douglas-fir. Note large limbs that have grown upward, forming a secondary crown.

Fig. 18. A spotted owl nest in a large cavity that formed when a limb ripped loose from the trunk of an old-growth Douglas-fir.

clutch size. Broods of 2 were most common, but broods of 1 were also common (Table 11). Broods of 3 were uncommon. The mean number of young produced per successful nest during all years combined was 2.0, again suggesting a modal clutch of 2. Bent (1938:204) reported that "The spotted owl lays two or three eggs, usually only two, and very rarely four . . . ." We observed no broods of 4. Bendire (1892) described a nest containing 4 young, and Dunn (1901) reported a nest with 4 eggs.

One of our captive owls laid clutches of 2–3 eggs every year from 1975 through 1980. In 2 years she laid a second clutch after the first was removed from her nest box. Regardless of clutch size, the interval between laying of successive eggs was always 72 ± 6 hours. We were unable to obtain comparable data from wild birds but suspected that the rate at which eggs were laid was similar in both wild and captive individuals.

Incubation Period.—In 1976, one of our radio-tagged females abandoned her 2 eggs after incubating for approximately 28 days. Assuming that 1 of the eggs was laid 72 hours after the other, then the 2 eggs had been incubated for 28 and 25 days, respectively. We recovered the eggs and found that both contained healthy embryos that were nearly full term. Based on the development of these embryos we estimated that the eggs would have hatched in another 2–5 days. This would indicate an incubation period of 30 ± 2 days.

Percent of Population Attempting to Nest.—On the average, only 62% of the pairs checked each year attempted to nest (range = 16–89%) (Table 11). Why some pairs did not nest in some years was unknown. Local or regional fluctuations in prey abundance may have influenced breeding, a phenomenon that has been observed in other owls (Pitelka et al. 1955, Southern 1970, Rusch et al. 1972).

Nest Success.—Eighty-one percent of all nesting attempts were successful (Table 11). Nest failures were attributable to a variety of causes. Some pairs acted as if they were going to nest (displaying at the nest) but then apparently never laid eggs. Known causes of failure after eggs were laid included abandonment of eggs containing healthy embryos (3 nests), destruc-

Table 11. Summary of nesting data for spotted owls in Oregon.

	Year				
	1972	1973	1974	1975	1976
No. pairs checked	28	31	37	14	20
Percent nesting	89	16	46	57	75
Percent of nesting pairs fledging young	92	40	72	75	87
No. of broods observed (by size class)					
1 young	8	1	7	0	0
2 young	12	1	6	1	6
3 young	3	0	0	0	1
Undetermined	0	0	0	5	6
Mean no. young fledged/successful nest	1.87	1.50	1.46	2.00	2.14
Mean no. young fledged/nesting attempt	1.72	0.60	1.11		

tion of eggs or nestlings by predators (2 nests), death of nestlings from disease or exposure (1 nest), destruction of eggs when a platform nest collapsed (1 nest), and premature departure of owlets from the nest (3 nests). Of the 3 cases where females abandoned eggs, it appeared that the female was killed at 1 nest (she disappeared overnight) and that incubation was disrupted at another nest when a large overhanging piece of rotten wood fell into the nest cavity. In the third case the female (a radio-tagged individual) simply stopped incubating.

Copulation and Nest Selection.—Between October and January, adult spotted owls lived a largely solitary existence, roosting together and calling infrequently. In February or early March, 33–68 days before the eggs were laid, the resident male and female on each territory began to roost together near the eventual nest site (usually the same nest used in previous years). They also began to call almost every night, especially at dusk just before they began to forage and again at dawn when they rejoined near the nest. We did not determine when males began to feed females, but both pair members continued to forage until about 12 days before eggs were laid. Thereafter, females became increasingly sedentary, seldom moving more than a few hundred meters from the nest. During the last 5–7 days before the eggs were laid, females spent most of their time at night perched in the vicinity of the nest tree, waiting for males to arrive with food.

Visual observations of pair behavior during the prenesting period were made at 2 nests, beginning 13 and 17 days, respectively, before the first eggs were laid. At both nests, observations were conducted each evening from about 1 hour before sunset to 2 hours after sunset. Both pairs copulated on the first evening they were observed, indicating that copulation began at least 2–3 weeks before the eggs were laid. Copulation and the behavior associated with it were relatively stereotyped. Each night the first copulation usually occurred at dusk just after the owls left their roosts. Before copulation occurred, the male usually perched near the female and gave the 4-Note Location Call or Agitated Location Call at irregular intervals (see Vocal Displays). The female responded with the Contact Call at intervals of 5 seconds to several minutes. These preliminary vocalizations continued for several minutes or more, after which the male flew to the female and they copulated. During copulation the female perched crosswise on a limb and gave the Female Copulatory Call. The male arched his wings over his back and fluttered them rapidly until copulation was completed. In addition, the male gave either the Male Copulatory Call or the Agitated Location Call during copulation. Occasionally, before copulation occurred, the male flew into the nest tree and perched near the nest while giving the Nest Call.

After copulation occurred the male usually flew to a perch near the nest and gave the Nest Call for several minutes before flying off to hunt. The female either watched this performance from a nearby tree or followed the male into the nest tree. During this display, females sometimes entered the nest and gave the Nest Call for several minutes.

The above sequence of events, with only minor variations, was repeated on most evenings during the last 13 days before eggs were laid. The maximum number of copulations observed in 1 evening was 2. The minimum time between consecutive copulations was 35 minutes. Both pairs ceased copulation within 4 days after completing their clutches.

Adult Behavior During Incubation and Brooding.—Several days before the first egg was laid, females began to roost in the nest or on limbs near the nest during the day. A female observed in 1974 was typical. On 4 April, at least 2 days before she laid the first egg, she began roosting in her nest cavity. During the first 2 days that she roosted in the cavity we always found her perched upright looking out of the cavity. On the evening of 6 April she was lying flat in typical incubation posture and we suspected she was about to lay or had already laid the first egg.

Incubation was performed entirely by females and was initiated soon after the first egg was laid. During the first 48 hours of incubation females occasionally left the nest for up to 2 hours at night, possibly to forage near the nest. By the time the second egg was laid, however, females incubated continuously except for occasional 10–20-minute periods during the night when they left their nests to regurgitate pellets, defecate, preen, or receive food from the male. During incubation, all foraging was done by the male. Males typically roosted within 200 m of their nest trees during the day and began to forage shortly after sunset. Occasionally, however, radio-tagged males roosted up to 1.1 km from their nests.

When arriving at the nest with food, males usually announced their arrival by calling quietly (Contact Call or 4-Note Location Call) from a tree near the nest. Females usually responded by leaving the nest to accept the food. Food transfer was from beak to beak. If the female did not leave the nest, the male would usually carry the food directly to the nest.

At most nests, eggs hatched between 8 April and 20 May. For 8–10 days thereafter, females brooded their young almost constantly, leaving their nests for only brief periods during the night. When the young were 2–3 weeks old, females began foraging for progressively longer periods each night. Two radio-tagged females were first observed foraging considerable distances (up to 2.6 km) from their nests when their young were approximately 16 and 13 days old, respectively. Up to that time the foraging activities of both females had been restricted to within a few hundred meters of the nest. After they began to forage farther from their nests both females regularly left their young unattended for periods of 1–4 hours and occasionally up to 6 hours on clear warm nights.

Male behavior during the nestling period was essentially the same as during the incubation period except that males carried food directly to the nest and left it there when females were away from the nest. It appeared that the food was simply left in the nest for the female to feed to the young. Males were not observed feeding nestlings.

During the day, females continued to roost in their nests until 3–6 days before the young left the nest. Thereafter, females were often found roosting in a tree near the nest, maintaining vocal contact with their young by giving the Contact Call at irregular intervals during the day.

Defense of the Nest and Young.—Adult spotted owls behaved aggressively towards us only if we climbed nest trees or approached owlets that had left the nest

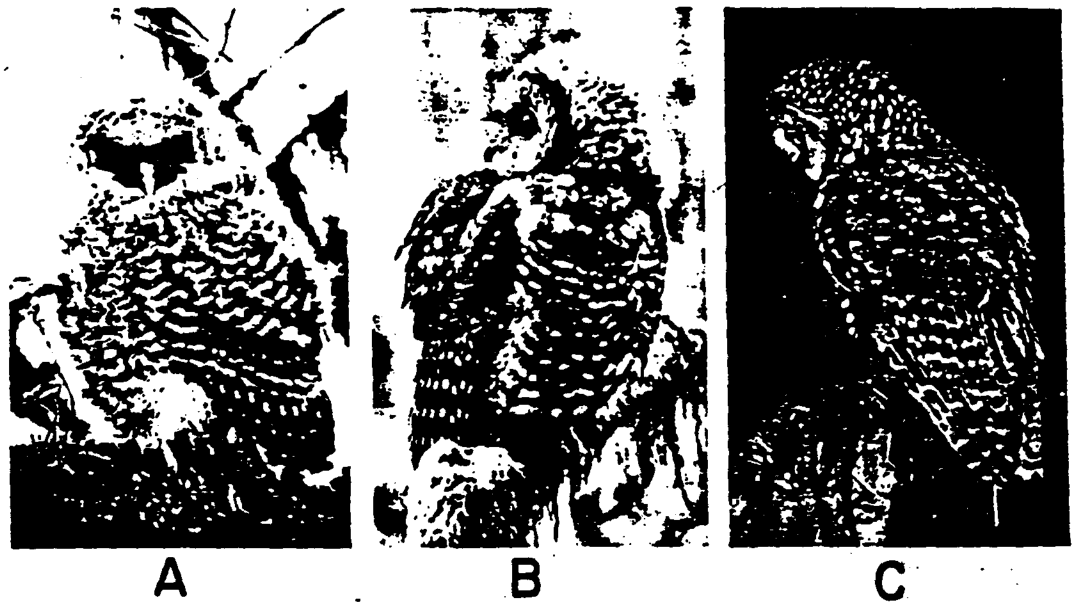

Fig. 19. Juvenile spotted owls, illustrating development during the first summer. (A) 42–46 days old, 10 days after leaving the nest; (B) ca. 110 days old in August; (C) ca. 150 days old in late September.

but could not fly. Some individuals were extremely pugnacious, striking repeatedly with their talons when their nest trees were climbed or their young were approached on the ground. Others flew around us as we climbed their nest trees, but never actually hit us. At most nests both males and females participated in nest defense.

Two instances were observed in which spotted owls defended their young from predators other than man. In 1 encounter, a female spotted owl dived repeatedly at 2 ravens that were hopping around on limbs just outside her nest cavity. This incident was instigated when we called the female out of her nest during the day. Although the owl seemed to be holding her own against the ravens, we frightened the ravens away rather than risk losing a clutch because of human disturbance. On another occasion a male spotted owl attacked and drove off an adult female Cooper's hawk that was in the process of attacking a recently fledged owlet.

Development and Behavior of Nestlings.—When they hatched, owlets were covered by pure white natal down, and their eyelids were closed. Until their eyelids opened 5–9 days later, the owlets were relatively inactive. When owlets were 10–20 days old, the juvenile (mesoptile) plumage, which was pale brown and barred, began to replace the natal down on the wings, back, and top of the head (Forsman 1981*b*). At this age owlets began to sit upright in the nest and became more active. At night they could sometimes be heard begging in the nest, especially when adults called or entered the nest area.

Most owlets left the nest when they were 34–36 days old, between 15 May and 24 June. Several days before fledging, some owlets began to perch on limbs adjacent to the nest. Others peered from nest entrances, but did not venture out until they fledged. Nine owlets that were raised in platform nests fell or jumped from the nest prematurely when they were 15–25 days old. Of these, 7 were killed by the fall or disappeared before reaching the flying stage. No owlets were lost in this manner from cavity nests, suggesting that cavity nests provided a more secure environment for the young. Zarn (1974) was misinformed when he stated that spotted owls leave the nest when only 1 week old.

Fig. 20. Contrast between juvenile rectrices (A) and rectrices acquired in subsequent molts (B). Juvenile rectrices were sharp-pointed and had a clear white terminal band. Rectrices acquired in later molts were more rounded and had the terminal band mottled with brown.

When owlets left the nest at the normal 34–36 days of age, replacement of the natal down by the juvenile plumage was nearly complete, but the remiges were only one-half to two-thirds developed (Fig. 19). As a result, fledglings were weak fliers and often fell to the ground when they left the nest. Some managed to flutter downward into trees below the nest.

Within 3 days after leaving the nest most owlets were able to fly or climb into elevated perches. However, individuals that left the nest prematurely (15–25 days old) sometimes spent as long as 10 days on the ground. Juvenile spotted owls were clumsy but persistent climbers and could climb almost any tree trunk to reach an elevated perch. To climb trees, owlets grasped the rough bark with their talons and then walked upward while flapping their wings. When they became tired they stopped moving and draped their outspread wings against the trunk to hold themselves in place. Occasionally, the beak was also used to grasp limbs or flakes of bark. Once strong enough to get off the ground, owlets usually roosted on limbs in trees, or occasionally, on logs or other debris on the ground.

Development and Care of Fledglings.—After leaving the nest, siblings stayed together for the rest of the summer, usually remaining near the nest. Of 17 broods that were checked at regular intervals during summer, 13 were still within 250 m of the nest in late August, and 2 were 490 and 670 m from the nest, respectively. Two broods could not be relocated in August. When last observed in July they were 365 and 1,050 m from the nest, respectively. Of the 15 broods located in August, at least 7 were still within 200 m of the nest in early September.

The mobility and foraging skills of owlets improved gradually during summer. Within a week after leaving the nest, most owlets were able to make short, clumsy flights between trees and began to exhibit incipient foraging behavior, pouncing on leaves, pieces of moss, or small twigs and tearing at them with the beak or talons. Three weeks after leaving the nest owlets were able to hold and tear up prey on their own, and by late July they became proficient at pouncing on relatively immobile objects such as crawling insects. By mid-August they were able to capture live mice that we tethered in roost areas.

As the owlets matured, the adults roosted with them less frequently. On 49 occasions when we located owlets during the day in August or September, adults were present only 23% of the time. By comparison, owlets observed in May and June were attended by 1 or both adults 81% of the time.

Although adults infrequently roosted with their young in late summer, they continued to feed them at night until late August or early September. Whenever they were hungry, owlets gave the Begging Call loudly and persistently, especially so if an adult appeared with food or called nearby. Begging behavior declined in late August and ceased by late September or early October. By this time owlets were apparently self-sufficient, although they had not yet begun to disperse.

Replacement of the juvenile plumage by the Basic I plumage began at age 47–56 days and was complete by the end of September or early October (Fig. 19). During this molt all juvenile feathers except the remiges, rectrices, and greater primary coverts were replaced. Owlets in the Basic I plumage were indistinguishable from adults except that their rectrices had clear white, sharp-pointed tips. These distinctive rectrices were retained for the first 26 months of life (Forsman 1981*b*). Tips of rectrices acquired in later molts were more rounded and were mottled with brown (Fig. 20).

Juvenile Mortality and Natural Enemies.—In 1972, we observed 29 owlets at weekly or biweekly intervals from the time they left the nest until late August. Only 19 (65%) were still alive at the end of August. The cause of mortality was determined in only 1 case when an owlet was killed by a great horned owl. In all other instances, owlets simply disappeared and were presumed dead. Predation was the suspected cause of mortality in most instances because owlets appeared healthy shortly before they disappeared.

One other case of juvenile mortality observed during the study was attributable to a great horned owl (see Dispersal of Juveniles). The fact that great horned owls were the cause of mortality in both cases in which the predator could be identified, suggested that great horned owls were an important source of juvenile mortality. Great horned owls were heard or seen in most areas occupied by spotted owls.

Because they were so secretive during the day, spotted owls suffered little mortality from diurnal raptors. This was indicated by the fact that there were at least 10 occasions during the study when spotted owls nested successfully within 400 m of active goshawk nests. In 1 instance, nests of the 2 species were only 125 m apart. As mentioned earlier, we did see 1 instance in which a female Cooper's hawk attempted to capture a recently fledged owlet.

Dispersal of Juveniles.—In August 1975 we radio-tagged 2 owlets each on the HJA study area and on the east slope of the Cascades near Abbot Butte, Deschutes County. Before the radio-tagged owlets left their parental nest areas, 1 of the transmitters at Abbot Butte stopped transmitting, and 1 of the owlets on the HJA study area died. Movements of the other 2 owlets are described below.

After leaving the nest in June the owlet on the HJA area spent the entire summer within a 35 ha area around the nest (Fig. 21). The owlet at Abbot Butte was only checked at 2–3-week intervals during the summer, so the full scope of its movements was unknown. Each time it was located during the summer, however, it was within 300 m of the nest tree, so we assumed that it did not travel far from the nest area.

On 12 October the owlet on the HJA area suddenly left the parental nest area and within 2 days moved 4.4 km to the southeast. For the next 45 days it wandered about over an area of approximately 2,900 ha, just east of the parental home range (Fig. 21). The farthest straight-line distance traveled from the parental nest during this period was 10.1 km. On 26 November the owlet was killed, apparently by a great horned owl. A large owl pellet containing remains of the owlet was found near the discarded transmitter.

We were unable to determine exactly when the owlet at Abbot Butte left the parental nest area, but on 18 October it was located 16.4 km southeast, in an old-

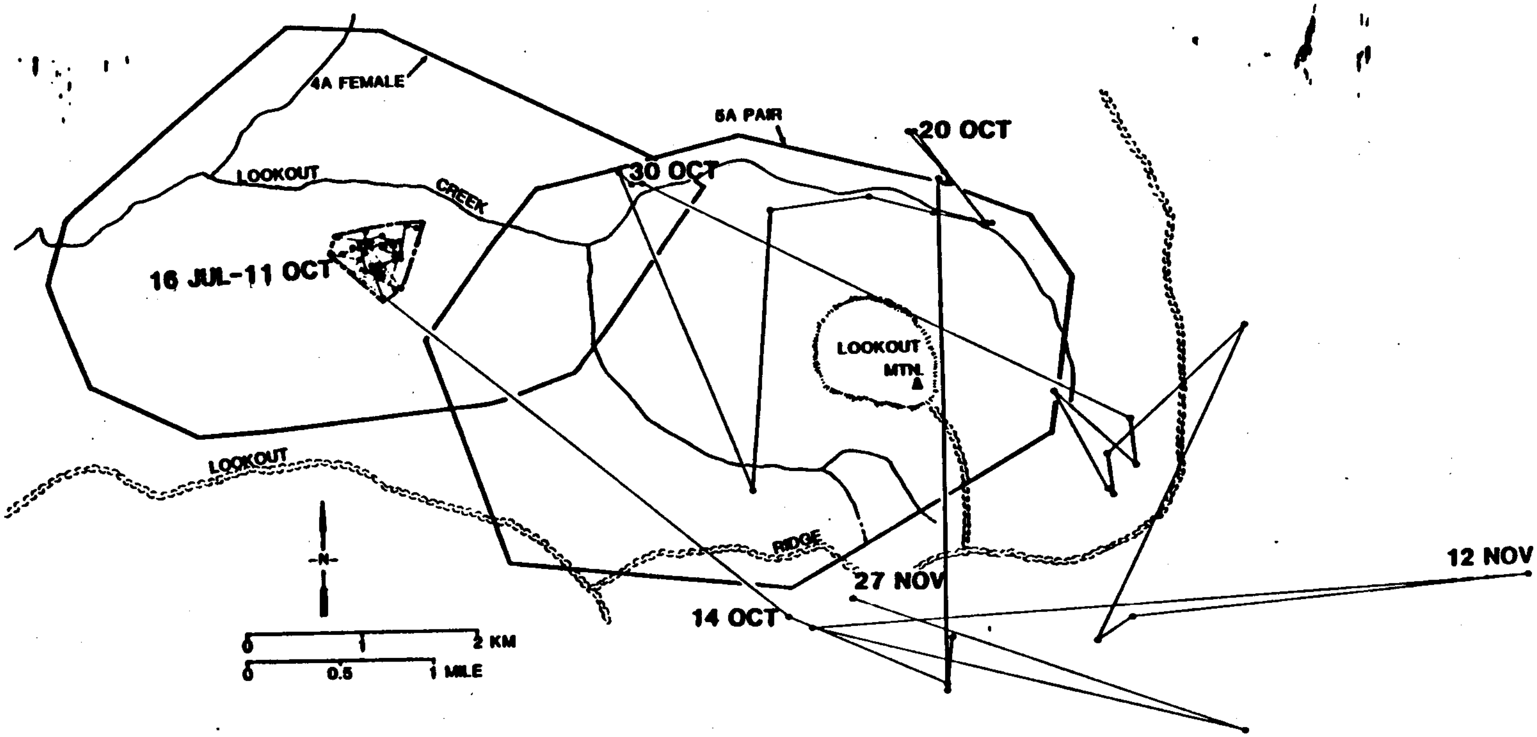

Fig. 21. Movements of the 4A owlet on the H. J. Andrews study area (16 Jul–26 Nov 1975). Before it became independent from its parents the owlet confined its activities to a 35-ha area around the parental nest (are inside dashed line). Thereafter, it wandered over a large area. The home ranges of the 4A female (the owlet's mother) and 5A pair are indicated by solid lines.

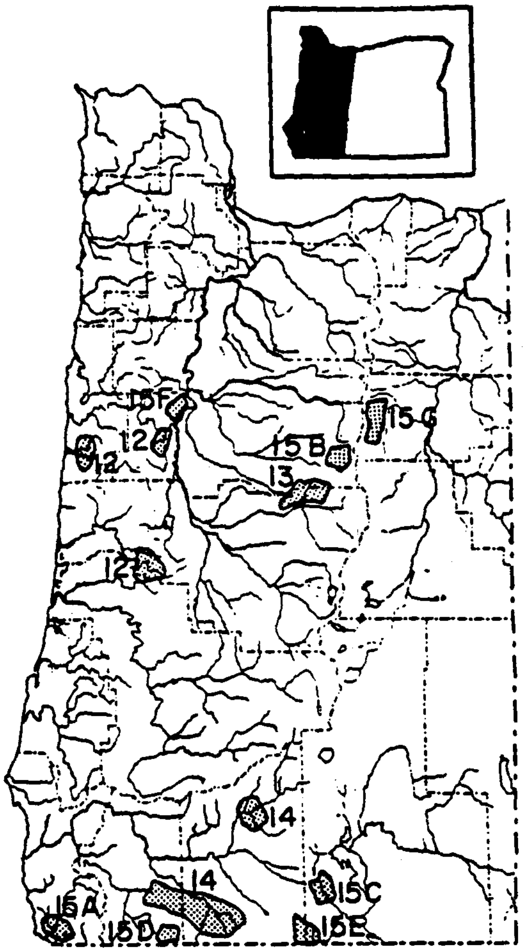

Fig. 22. Areas where data on food habits of spotted owls were collected in Oregon from 1970 through 1980. Numbers indicate which tables in text should be consulted for each area.

growth forest of Douglas-fir, white fir, and ponderosa pine. It had apparently traveled across extensive areas of open ponderosa pine forest to arrive at this location. When we checked this owlet again on 6 December, it had been killed and eaten by an unknown predator. Its remains were found 12 km southeast of the parental nest site.

Food and Foraging Behavior

Composition of the Diet.—From April 1970 to September 1980, 4,527 prey items were identified from pellets or kills of 62 pairs of spotted owls, including 19 pairs in the Coast Ranges, 23 pairs in the Klamath Mountains, and 20 pairs in the Cascade Range (Fig. 22). The diet included 31 species of mammals, 23 species of birds, 2 species of reptiles, a crayfish, a terrestrial snail, 29 genera of insects, and several unidentified spiders (Appendix 3). Ninety-two percent of all prey and 98% of total prey biomass was comprised of vertebrates. Mammals comprised over 90% of the biomass consumed in all areas (Tables 12–15). Mean prey weights calculated for 10 different areas ranged from 54 to 150 g (Tables 12–15).

The composition of the diet varied among regions and forest types. In general, the diet was dominated by flying squirrels and red tree voles in forests of Douglas-fir and western hemlock, and by dusky-footed woodrats in mixed conifer forests in the Klamath Mountains (Tables 12–15). Other prey that were important in terms of numbers or biomass were deer mice, western red-backed voles, snowshoe hares, bushy-tailed woodrats, and pocket gophers. Pocket gophers and western red-backed voles were most common in the diet at higher elevations in the Cascade Range and Klamath Mountains (Areas B, C, D, E, G in Table 15). Birds comprised 5.3% of the diet on the average (range = 2.6–9.3%). Insects were uncommon in the diet except in a few areas, and in all areas comprised only a small fraction of the total prey biomass (Tables 12–15).

Seasonal Variation in the Diet.—On the HJA study area, flying squirrels comprised over 60% of all prey taken during fall and winter (Table 16). The proportion of flying squirrels in the diet began to decline in late March and April, and by midsummer flying squirrels comprised only 27% of the diet. As the proportion of flying squirrels in the diet declined during spring and summer, snowshoe hares, shrews, pocket gophers, western red-backed voles, small birds, and insects became increasingly common in the diet (Table 16). Although the percentages differed somewhat, seasonal changes in the diet on the

Table 12. Diet of spotted owls occupying forests of Douglas-fir and western hemlock in the Oregon Coast Ranges. Prey item sample size is in parentheses.[a]

	Percent of total prey							Percent of biomass
	1970 (45)	1972 (694)	1973 (126)	1974 (33)	1975 (60)	1980 (256)	All years combined (1,214)	All years combined (103,961 g)
Mammals								
N. flying squirrel	51.1	31.6	37.1	45.5	58.3	34.4	35.2	47.2
Red tree vole	20.0	21.0	34.7	6.1	11.7	9.4	19.1	6.0
Deer mouse	4.5	15.6	10.5	30.3	5.0	2.3	11.7	3.0
W. red-backed vole		6.3	4.9		8.3	4.7	5.5	1.5
Woodrat spp.[b]	6.7	5.2	2.4	6.1		6.3	4.9	15.3
Snowshoe hare or brush rabbit	2.2	2.7	2.4	3.0	8.3	9.0	4.3	16.5
Microtus spp.		1.2			1.7		0.7	0.3
Sorex spp.		1.4	1.6		1.7	0.4	1.2	0.1
Other mammals	2.2	3.3		3.0		6.2	3.3	4.2
Unidentified mammals		4.2	0.8	3.0	1.7	1.6	3.0	3.1
Birds		2.7	3.2		3.3	4.7	3.0	2.5
Reptiles	2.2			0.8			0.3	0.1
Insects and arachnids	11.1	4.8	1.6	3.0		21.1	7.8	0.2

[a] No. of pairs from which pellets were collected each year ranged from 4–8. χ^2 for differences in diet among years = 151.66, df = 10, $P < 0.005$ (test based on numbers of prey). Only years in which $N > 50$ were compared.

[b] Prey species not specifically identified in the table are listed in Appendix 3, along with scientific names of all prey.

BLM study area closely paralleled the changes observed on the HJA study area (Table 17).

On all study areas, predation on brush rabbits and snowshoe hares was restricted primarily to small juveniles captured between May and August. Seventy-four percent of the individuals captured

Table 13. Diet of spotted owls in forests of Douglas-fir and western hemlock on the H. J. Andrews study area, Oregon. Prey item sample size is in parentheses.[a]

	Percent of total prey						Percent of biomass
	1972 (182)	1975 (99)	1976 (472)	1977 (38)	1978 (26)	All years combined (817)	All years combined (69,246 g)
Mammals							
N. flying squirrel	27.5	32.3	50.0	50.0	34.7	42.4	57.5
Red tree vole	12.1	12.1	13.3	21.1	15.4	13.3	4.2
W. red-backed vole	1.7	7.1	11.9	7.9	23.1	9.2	2.5
Deer mouse	17.0	10.1	5.7	7.9		8.7	2.3
Snowshoe hare	4.9	6.1	0.9		3.8	2.5	15.0
Bushy-tailed woodrat	2.2	2.0	2.1	2.6	3.8	2.2	6.9
Sorex spp.[b]	6.0	1.0	2.1			2.7	0.3
W. pocket gopher	6.0	10.1	1.7			3.6	3.6
Microtus spp.	3.3	1.0	1.7	5.3		2.0	0.5
Townsend's chipmunk	0.6	4.0	1.1			1.2	1.1
Other mammals	3.3	5.1	1.1	2.6	7.7	2.3	2.6
Unidentified mammals	2.8	5.1	3.6			3.3	1.5
Birds	5.0	1.0	2.5	2.6	7.7	3.1	1.9
Reptiles	0.5					0.1	0.1
Insects and arachnids	7.1	3.0	2.3		3.8	3.4	tr[c]

[a] No. of pairs from which pellets were collected each year ranged from 2 to 7. χ^2 for differences in diet among years = 91.57, df = 10, $P < 0.005$ (test based on numbers of prey). Only years in which $N > 50$ were compared.

[b] Prey species not specifically identified in the table are listed in Appendix 3, along with scientific names of all prey.

[c] tr = <0.05%.

Table 14. Diet of spotted owls occupying mixed conifer and mixed evergreen forests in the Klamath Mountains, Oregon. Prey item sample size is in parentheses.[a]

	Percent of total prey							Percent of biomass
	1972 (30)	1973 (155)	1974 (97)	1976 (97)	1977 (175)	1978 (100)	All years combined (651)	All years combined (98,187 g)
Mammals								
Dusky-footed woodrat	43.3	40.7	39.2	46.5	33.7	37.0	39.0	69.9
N. flying squirrel	6.7	18.7	17.5	26.8	14.9	16.0	17.7	13.6
W. red-backed vole	3.3	7.8	7.2	4.1	10.9	19.0	9.5	1.4
Deer mouse	20.0	5.2	4.1	7.2	3.4	2.0	5.0	0.7
Microtus spp.[b]		1.9	4.1	6.2	12.6	5.0	6.1	1.5
Red tree vole		10.3	5.2	1.0	3.4	4.0	4.9	0.9
Brush rabbit		3.2	1.0	1.0	3.4	4.0	2.6	6.2
Other mammals	10.0	3.2	9.3	1.0	4.0	3.0	4.3	1.5
Unidentified mammals	6.7	3.2		2.1	4.6	1.0	2.8	1.5
Birds	3.3	5.2	10.3	4.1	6.3	8.0	6.4	2.8
Insects	6.7	0.6	2.1		2.8	1.0	1.7	tr[c]

[a] No. of pairs from which pellets were collected each year ranged from 2 to 11. χ^2 for differences in diet among years = 32.38, df = 8, $P < 0.005$ (test based on numbers of prey). Only years in which $N > 50$ were compared.

[b] Prey species not specifically identified in the table are listed in Appendix 3, along with scientific names of all prey.

[c] tr = <0.05%.

weighed <400 g and 92% weighed <700 g. The largest lagomorph captured was a snowshoe hare weighing approximately 1,500 g.

Pocket gophers were commonly taken by owls on the HJA study area during May and June when the ground was clear of snow, but were uncommon in the diet at other times of the year (Table 16). Similarly, predation on coast moles on the east slope of the Cascade Range was limited to mid-April–early July, with a peak about 20 June. Giger (1965) suggested that coast moles were most vulnerable to predation by owls between April and June when juvenile moles were dispersing aboveground. On both the HJA and BLM study areas, predation on western red-backed voles peaked in April (Tables 16, 17).

The few mountain beavers taken by spotted owls were small juveniles (150–300 g) captured from 1 to 25 June (Table 17). Apparently, young mountain beavers were susceptible to predation by spotted owls for only a few weeks after leaving their natal burrows in June.

Predation on insects was restricted primarily to summer and early fall on all areas. Two insects that were especially common in the summer diet in some areas were *Ergates spiculatus* (a large flying beetle) and *Cyphoderris monstrosa* (a large arboreal cricket) (Areas B, E, G in Table 15, 17). Marshall (1942) also reported predation on *Cyphoderris* by spotted owls.

Annual Variation in the Diet.—Annual variation in the diet was examined in 3 areas where the largest samples of data were collected (Tables 12–14). Dietary composition differed significantly among years in all 3 areas. It was not clear, however, whether the year to year variation in the diet was due to changes in prey populations or to sampling bias (pellets were not always collected at the same time or from the same pairs each year).

Although statistically significant, dietary changes among years did not involve a complete restructuring of the diet. In all areas the numerical ranking of the major prey in the diet (from most to least common) changed only slightly or not at all from year to year (Tables 12–14). Some prey comprised a remarkably stable proportion of the diet, e.g., the dusky-footed woodrat in the Klamath Mountains (Table 14) and the red tree vole on the HJA study area (Table 13).

Foraging Behavior.—Nine predation

Table 15. Diet of spotted owls in 7 areas in Oregon in which data were not subdivided annually because of small sample size in some years. Total number and biomass (g) of prey in each sample are in parentheses.[a]

	Area A		Area B		Area C		Area D	
	Percent of total prey (118)	Percent of total biomass (9,641 g)	Percent of total prey (191)	Percent of total biomass (9,654 g)	Percent of total prey (173)	Percent of total biomass (17,398 g)	Percent of total prey (87)	Percent of total biomass (6,292 g)
Mammals								
N. flying squirrel	17.8	25.1	12.0	27.4	46.8	53.5	26.4	42.0
Red tree vole	49.1	16.2	3.7	2.0			14.9	5.6
Woodrat spp.[b]	10.2	33.0	1.6	8.2	8.1	29.3	3.4	12.6
W. red-backed vole	0.9	0.2	14.7	6.7	20.8	4.8	31.0	9.9
Deer mouse	6.8	1.8	2.6	1.1	3.5	0.8	3.5	1.0
W. pocket gopher			9.4	16.2	0.6	0.5	8.0	9.7
Snowshoe hare or brush rabbit	2.5	10.4	2.1	10.9	1.7	4.9	2.3	9.5
Townsend's chipmunk			1.6	2.5	0.6	0.5	2.3	2.5
Other mammals	3.4	6.6	11.0	15.3	2.8	0.4	1.2	0.4
Unidentified mammals			5.2	5.6	2.9	0.7	1.2	4.0
Birds	9.3	6.7	3.1	2.4	5.8	4.5	3.5	2.7
Reptiles			0.5	0.5				
Insects			32.5	1.2	6.4	0.1	2.3	0.1

	Area E		Area F		Area G	
	Percent of total prey (152)	Percent of total biomass (19,102 g)	Percent of total prey (566)	Percent of total biomass (30,514 g)	Percent of total prey (555)	Percent of total biomass (50,310 g)
Mammals						
N. flying squirrel	19.7	18.1	13.8	29.4	25.1	31.8
Red tree vole			38.2	19.1		
Woodrat spp.	26.3	56.3	4.9	24.3	7.0	20.6
W. red-backed vole	5.3	1.0	1.1	0.4	5.4	1.4
Deer mouse	13.1	2.3	22.1	9.0	8.5	2.0
W. pocket gopher	5.3	3.6			5.0	4.8
Snowshoe hare or brush rabbit	4.6	9.4	0.7	3.3	5.4	24.9
Townsend's chipmunk	2.0	1.3			0.1	1.4
Coast mole			0.5	0.5	3.2	1.9
Other mammals	1.4	0.2	5.7	4.0	6.8	5.5
Unidentified mammals	2.0	2.4	1.2	1.1	1.5	2.2
Birds	8.5	5.3	7.9	8.6	5.8	4.0
Reptiles			0.5	0.2		
Crayfish			0.2	0.1		
Insects	11.8	0.1	3.2	tr[c]	25.9	0.5

[a] Location of areas is shown in Fig. 18. Years of data collection, number of pairs examined, and dominant vegetation in the different areas were:

Area A:	Pellets collected in 1972 and 1974 from 2 pairs occupying old-growth forests of Douglas-fir, tanoak, California laurel, western hemlock, and coast redwood, 10 km east of Brookings on the southern Oregon coast.
Area B:	Pellets collected in 1970 and 1972 from 3 pairs occupying old-growth forests of Douglas-fir, Pacific silver fir, and western hemlock on the west slope of the Cascade Range near Tombstone Summit, Linn County, elevation = 975–1,400 m.
Area C:	Pellets collected in 1972, 1973, and 1974 from 5 pairs occupying high elevation (1,460–1,700 m) mixed forests of white fir, shasta red fir, Douglas-fir, and ponderosa pine in the southern Cascade Range near Lake of the Woods, Klamath County.
Area D:	Pellets collected in 1972 and 1974 from 2 pairs occupying high elevation forests of white fir, Douglas-fir, and shasta red fir in the Klamath Mountains near Oregon Caves National Monument, Josephine County.
Area E:	Pellets collected in 1972 and 1973 from 3 pairs occupying mixed associations of Douglas-fir, white fir, ponderosa pine, and incense-cedar in the southern Cascade Range near Parker Mountain, Klamath County.
Area F:	Pellets collected in 1970, 1972, 1973, and 1974 from 2 pairs occupying mixed forests of Douglas-fir, grand fir, and Oregon white oak at the edge of the Willamette Valley, 4 km northwest of Corvallis, Benton County.
Area G:	Pellets collected in 1972, 1973, 1975, 1976, 1977, and 1978 from 3 pairs occupying mixed forests of Douglas-fir, white fir, ponderosa pine, and incense-cedar on the east slope of the Cascade Range near Abbot Butte, Jefferson County.

[b] Prey species not specifically identified in the table are listed in Appendix 3, along with scientific names of all prey.

[c] tr = <0.05%.

Table 16. Seasonal comparison of the diet of radio-tagged spotted owls in the H. J. Andrews study area, (May 1975–Jun 1976). Number of prey in each sample is in parentheses.

	Percent of total prey					
	May (82)	Jun–Jul[a] (56)	Sep–Dec (28)	Jan–Feb (46)	Mar (73)	Apr (104)
Mammals						
N. flying squirrel	39.0	26.7	57.2	71.7	67.0	44.2
Red tree vole	12.2	12.5	7.1	15.2	13.7	15.4
W. red-backed vole	9.8	7.1		8.7	11.0	16.3
Deer mouse	12.2	17.8	3.6			5.8
Snowshoe hare		7.1				0.9
Townsend's chipmunk	1.2		7.1		1.4	0.9
W. pocket gopher	2.4	5.4				
Bush-tailed woodrat	4.9	1.8	7.1			4.0
Shrews	4.9	3.6			1.4	0.9
Other mammals[b]	4.9	5.4		4.4	2.7	3.6
Unidentified mammals	2.4	5.4	17.9	2.2	1.4	4.0
Birds	1.2	3.6		2.2	1.4	4.0
Insects and arachnids	4.9	3.6				

[a] Some months were combined because of small sample size. Also, data from the same months in different years were combined. No data were available for August.

[b] Included chickaree, creeping vole, pika, shrew mole, coast mole, Pacific jumping mouse, water vole. Scientific names of all prey are given in Appendix 3.

attempts by spotted owls were observed, including 7 attempts (1 successful) to capture squirrels or birds in trees, and 2 attacks (1 successful) on mice or squirrels on the ground. Whether the intended prey was on the ground or in a tree the usual method of attack was to dive upon the prey from an elevated perch. When attacks on squirrels in trees were unsuccessful, owls often hopped or flew from limb to limb after the fleeing animal. On 1 occasion, when 2 chipmunks retreated into a woodpecker cavity in a rotten snag, a female spotted owl flew to the cavity and clung to the lip of the cavity with her feet while attempting to reach inside with her beak. As she did so, the chipmunks escaped through a hole on the opposite side of the snag.

Insects were captured either on the ground or on limbs in trees. The usual method of attack on insects was to pounce on them with the feet or to land beside them and pick them up with the beak. We saw no evidence of aerial pursuit of insects.

Upon capture, vertebrate prey were killed by seizing and immobilizing them with the feet and then tearing at the base of the cranium with the beak, crushing the posterior cranium or breaking the neck, or both. The heads of vertebrate prey were usually eaten first, a typical behavior in hawks and owls (Mumford and Zusi 1958, Collins 1963, Mikkola 1970, Catling 1972, Balgooyen 1976). Small prey were sometimes swallowed whole, but animals larger than deer mice were usually at least partially dismembered. Adult spotted owls usually removed and discarded the stomachs of mammals larger than deer mice. Tails of squirrels and woodrats were also discarded, presumably because they had little food value. Owlets were considerably less selective with respect to what they ate, often swallowing squirrel and woodrat tails.

Food Caching.—Spotted owls regularly cached excess food, retrieving it later. We observed 24 instances of this behavior in wild owls and many instances in captive owls. Prey remains were cached on top of limbs in trees or on the ground beside logs, trees, or large rocks. Caching behavior was observed during all seasons, whenever owls caught more than they could eat. On 1 occasion when we tethered 5 live mice in front of a roosting adult male, he killed

Table 17. Seasonal comparison of the diet of radio-tagged spotted owls on the BLM study area (Apr–Aug 1980). Number of prey in each sample is in parentheses.

	Percent of total prey				
	Apr (43)	May (56)	Jun (45)	Jul (47)	Aug (61)
Mammals					
N. flying squirrel	60.5	50.0	42.3	12.8	14.8
Red tree vole	4.7	12.5	8.9	10.6	8.2
W. red-backed vole	23.2			4.3	
Deer mouse	4.7	3.6	4.4		
Snowshoe hare or brush rabbit		7.1	20.1	17.1	3.3
Bush-tailed or dusky-footed woodrat	2.3	8.9	4.4	4.3	3.3
Mountain beaver			8.9		
Townsend's chipmunk		3.6	2.2	4.3	1.6
W. pocket gopher		1.8	2.2		
Other mammals[a]			4.4	4.3	1.6
Unidentified mammals	2.3	5.4			1.6
Birds	2.3	5.3	2.2	10.6	3.3
Insects[b]		1.8		31.9	62.3

[a] Included ermine, chickaree, big brown bat, shrews. Scientific names of all prey are given in Appendix 3.

[b] *Ergates spiculatus* comprised 93% of all insects taken.

and ate the first 2, then killed the others and cached them on a nearby limb. This was the only instance in which small prey were cached and in which stored prey were not decapitated and partially eaten. Other prey cached by free ranging owls included 13 flying squirrels, 4 woodrats, 5 snowshoe hares, 1 chipmunk, and 1 screech owl. When caching prey, owls pushed and pulled the prey into position with the beak, wedging it securely in place.

A Comparison of Prey Selection by Males and Females.—In most hawks and owls, including the spotted owl, males are smaller than females, a condition referred to as reversed sexual size dimorphism. A popular theory concerning the evolution of reversed sexual size dimorphism is that divergence in body size permits males and females to partition the prey resource, collectively feeding upon a wider range of prey (Selander 1966, Storer 1966, Reynolds 1972, Snyder and Wiley 1976). Theoretically, the smaller male should feed on smaller prey than the female.

To compare prey selection by male and female spotted owls, we used data from the HJA and BLM study areas where we were able to mark roost trees occupied by individual owls of known sex and then return to the same roosts the next day to collect pellets that had been regurgitated. For χ^2 comparisons of dietary composition, uncommon prey were lumped into groups (Table 18). On the HJA area we lumped all mammals listed below deer mice in Table 18 into 1 group and birds and insects into another. On the BLM area we lumped deer mice and red-backed mice into 1 group and all mammals listed below woodrats in Table 18 into another. On both areas, there was no significant difference in the composition of the diet of males and females (HJA area $\chi^2 = 7.9$, df = 5, $P > 0.05$; BLM area $\chi^2 = 11.13$, df = 7, $P > 0.05$) (Table 18) or the mean weight of prey taken by males and females (Table 19). We concluded that males and females did not partition the food resource on the basis of size or species on either study area.

Vocal Displays

Calls given by spotted owls included a variety of hooting and loud barking calls as well as clear whistling calls. The hooting calls of females were consistently higher pitched than those of males, mak-

Table 18. Diet (% composition) of male and female spotted owls on the H. J. Andrews study area (May 1975–Jun 1976) and BLM study area (Apr–Aug 1980). Number of prey in each sample is in parentheses.

	HJA study area		BLM study area	
	Males (125)	Females (88)	Males (84)	Females (76)
Mammals				
N. flying squirrel[a]	56.0	54.5	28.5	27.7
Red tree vole	11.2	12.5	11.9	11.8
W. red-backed vole	4.0	9.1	3.6	
Deer mouse	8.8	9.1	3.6	2.6
Snowshoe hare or brush rabbit[b]	1.6	1.1	14.3	9.2
Dusky-footed or bushy-tailed woodrat	1.6	1.1	2.4	14.5
W. pocket gopher	3.2			1.3
Chickaree	0.8		1.2	
Townsend's chipmunk	0.8	2.3	4.8	
Pika	2.4			
Shrew-mole	0.8			
Creeping vole	3.2			
Water vole	0.8			
Pacific jumping mouse		1.1		
Sorex spp.			1.2	
Long-tailed weasel			1.2	
Mountain beaver				5.3
Big brown bat				1.3
Birds	1.6	4.6	8.3	3.9
Insects	3.2	4.6	19.0	22.4

[a] Scientific names are in Appendix 3.

[b] Included mostly snowshoe hares on the HJA study area and a mixture of snowshoe hares and brush rabbits on the BLM study areas. All rabbits, hares, and mountain beavers captured were juveniles.

ing sex identification by call relatively easy. With the exception of copulatory calls, all types of calls were given by both sexes. However, some call types were given more frequently by 1 sex than the other. In the descriptions that follow, calls are divided into 13 different types. Some calls, particularly the hooting and barking calls, were characterized by considerable variation in cadence and number of notes. The following descriptions include only the more common patterns, but calls that were particularly variable will be so indicated.

Four-note Location Call: This is the hooting call most frequently mentioned in the literature (Ligon 1926, Bent 1938). It

Table 19. Mean weights of prey captured by male and female spotted owls on the H. J. Andrews study area (May 1975–Jun 1976) and BLM study area (Apr–Aug 1980).

	Males			Females			
Study area and seasonal period	No. prey	Mean weight (g)	SE	No. prey	Mean weight (g)	SE	Significance of difference between means[a]
HJA Area							
Sep–Feb (fall–winter)	18	108.4	12.2	52	86.8	6.9	$P > 0.05$
Mar–Apr (spring)	58	99.7	5.6	21	84.5	9.1	$P > 0.05$
May–Jul (summer)	52	75.6	12.2	20	74.6	39.0	$P > 0.05$
Overall average	128	91.1	5.9	93	84.7	10.2	$P > 0.05$
BLM Area							
Apr–Aug (late spring–summer)	85	90.5	10.2	76	114.7	12.9	$P > 0.05$

[a] *t*-test.

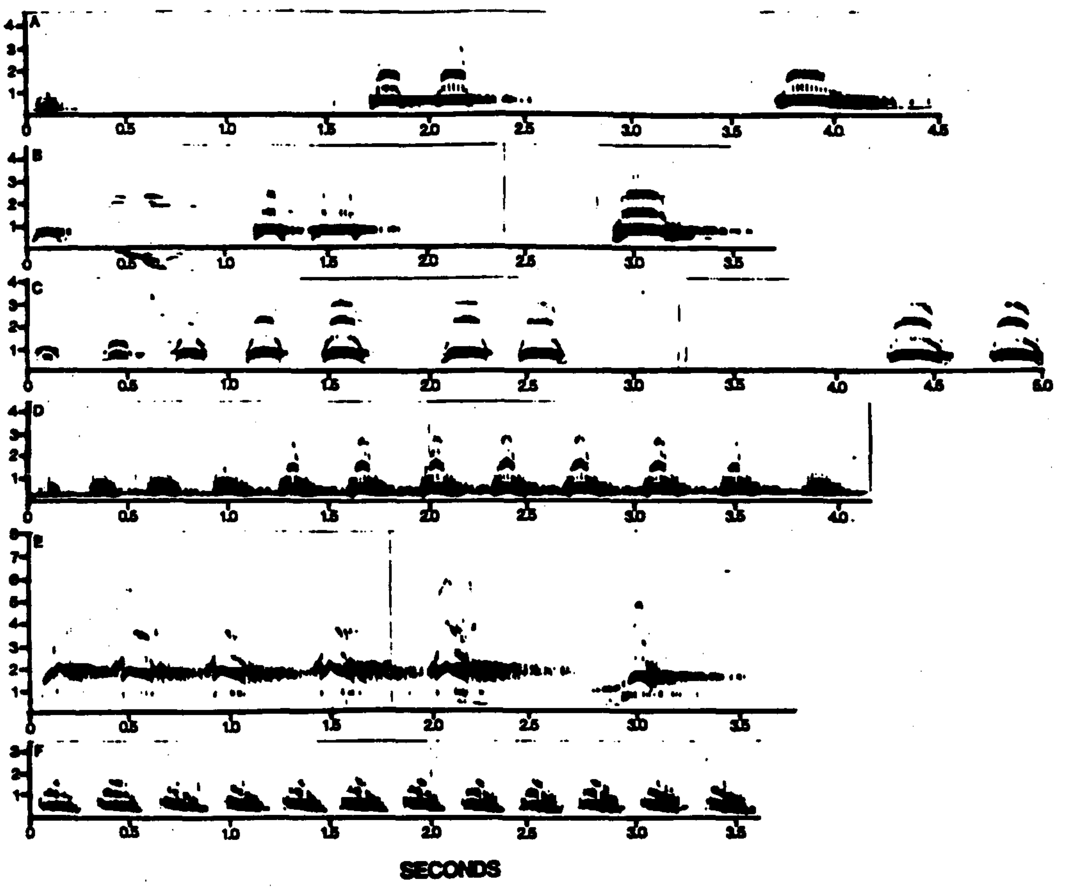

Fig. 23. Sonograms of hooting and barking vocalizations commonly given by spotted owls. (A) Male 4-Note Location Call; (B) Female 4-Note Location Call; (C) Series Location Call—unevenly spaced series; (D) Series Location Call—evenly spaced series; (E) Bark Series; (F) Nest Call.

most commonly had 4 notes in a series: a single introductory hoot followed by a short pause, 2 closely spaced hoots, another pause, and then a final hooting note trailing off at the end (Fig. 23A,B). A phonetic rendition was *hoo* - - - *hoo-hoo* - - - - *hooo*. The introductory note was sometimes omitted. Ligon (1926:423) described this call as *coo* - - - *coo-coo* - - - - *coo-o-o*. This call was given by both sexes in a variety of situations and seemed to function as a general location call between paired birds and as a territorial challenge. It was given commonly when paired birds called back and forth on their territories and during territorial disputes. Males often gave a very subdued version of this call when they arrived near the nest with food. During territorial disputes or before and after copulation, the 4-Note Location Call was frequently alternated with other types of calls described below. The 4-Note Location Call was the principal call used for locating and censusing spotted owls. Under good conditions this call could be heard over 1 km away.

Agitated Location Call: This call was given in situations of apparent sexual or aggressive excitement. It usually began like the 4-Note Location Call but was more intense and ended in a loud *owl* note. A phonetic rendition of the most common version was *hoo* - - - *hoo-hoo* - - - *owl* Frequently, this call was given several times in a rapid series, with the introductory note left out after the first 4-note phrase. Both sexes gave this call during territorial disputes and males sometimes gave it immediately before, after, or during copulation. Females did not usually give this call in association with copulation.

Series Location Calls: This category included a variety of calls characterized by 7–15 hooting notes in series. The arrangement of notes was extremely variable both within and among individuals. A common pattern was an introductory series of 5–7 evenly spaced notes, followed by several notes or pairs of notes at longer intervals (Fig. 23C). Sometimes all notes in a series were evenly spaced (Fig. 23D). These calls were commonly given during territorial disputes. Series Location Calls were also given occasionally by paired individuals as they called back and forth within their territories.

Bark Series: This call was a rapid series of 3–7 loud barking notes given at the rate of 2–3 notes/second (Fig. 23E). We phoneticized it as *ow!-ow!-ow!-ow!-ow!*, or sometimes *yenk!-yenk!-yenk!-yenk!*. This call was given by females (less frequently by males) during territorial disputes. It also appeared to function as a long-distance contact call between paired birds.

Nest Call: This call was given by both sexes when they called from the nest tree during prenesting displays. It was heard infrequently in other situations. The call was a steady series of evenly-spaced, subdued hoots, sometimes given for several minutes or more with only minor breaks (Fig. 23F). The individual notes were given at the rate of about 3/second. Males usually gave this call while perched on limbs just outside their nests whereas females usually gave it from within the nest.

Contact Call: This call was a hollow whistled note ending in an upward inflection (Fig. 24A). We phoneticized it as *cooo-weep!*. Females gave this call when they were roosting near their mates or young during the day and when the male delivered food to the nest area. Each evening during the 2–3 weeks before eggs were laid, nesting females usually gave the Contact Call repeatedly (at 15–45-second intervals) from their day roosts until the male flew to them and copulated. In all of the above situations, the call apparently served to inform the male or young of the female's location, thereby facilitating food exchanges, copulation, and general coordination of activities. Males sometimes gave the Contact Call when they arrived near the nest with food. The Contact Call might also have been termed the "Adult Begging Call" because in the course of development it evolved directly from the Juvenile Begging Call (see below). Because the adult version played a more general role in communication than simply "begging," we chose the more general term of Contact Call. Southern (1970) used the term "Contact Call" in reference to a very similar call given by the tawny owl.

Agitated Contact Call: The Agitated Contact Call was a high intensity version of the Contact Call. Instead of the mellow whistled quality of the Contact Call, the *cooo-weep!* notes were given loudly and shrilly, often with a raspy or grating quality (Fig. 24B). This call was given by females during territorial disputes and, infrequently, in other situations. Males gave this call infrequently.

Wraaak! Call: This call consisted of a loud, grating, 2-syllabled note that was sometimes given during territorial interactions. We phoneticized it as *wraaak!* or *raaak!* (Fig. 24C). On 1 occasion during a territorial interaction, a female began giving this call at 2–5-second intervals, then gradually changed to the Agitated Contact Call as the interaction proceeded.

Chitter: This call consisted of a rapid series of low chittering notes (Fig. 24D). It was given by adults and owlets when they were handled, apparently indicating fear or irritation. It was also given by females during copulation and occasionally by males or females when they were engaged in allopreening (Forsman and Wight 1979). Clark (1975) described a similar call in the short-eared owl.

Female Copulatory Call: This call was slightly variable but the basic pattern con-

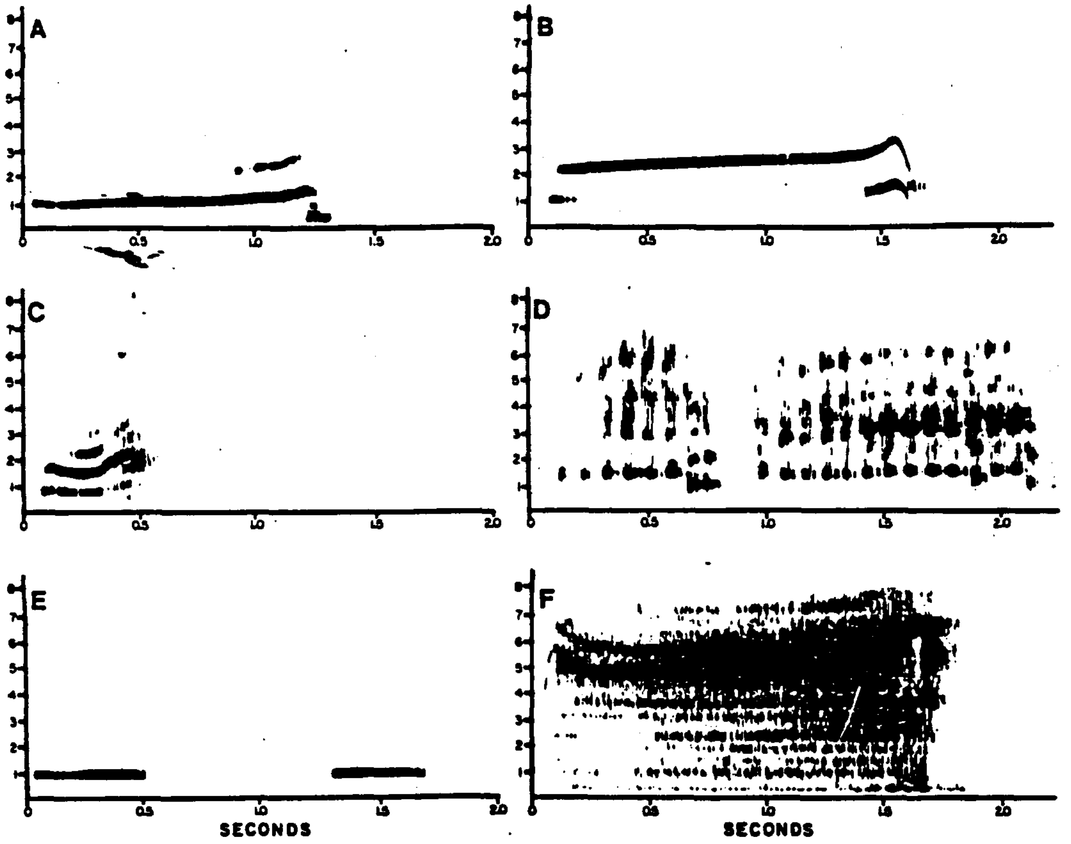

Fig. 24. Sonograms of spotted owl vocalizations characterized by whistling, chittering, grating, or sibilant sounds. (A) Contact Call; (B) Agitated Contact Call; (C) Wraaak! Call; (D) Chitter; (E) Cooing Calls; (F) Juvenile Begging Call.

sisted of a rapid series of chittering notes as the female was mounted that graded into a high pitched, wheezy, prolonged whistled note as copulation occurred. The call ceased as the male dismounted.

Male Copulatory Call: Immediately before copulating, males usually flew towards the female giving a mixture of 4-Note Location Calls and Agitated Location Calls. After they mounted, however, some males switched to a series of emphatic single hoots during copulation. We phoneticized the latter call as *hoo!-hoo!-hoo!hoo!-hoo!*. This call was usually followed by Agitated Location Calls as the male dismounted and flew away.

Alarm Call: This call was a terse, single-syllabled warning given in response to approaching predators. It was given very quietly and was audible only at close range. This call defied phonetic representation but resembled a nasal grunt or groan. We heard the Alarm Call given in response to the presence of red-tailed hawks, Cooper's hawks, and goshawks. In addition, 1 of our captive owls frequently gave the Alarm Call when dogs or unfamiliar humans walked by her cage.

Cooing Calls: This category included a variety of subdued whistles and cooing sounds given at close range between adults (Fig. 24E). These calls were given in many contexts, most commonly when paired adults were roosting together or allopreening.

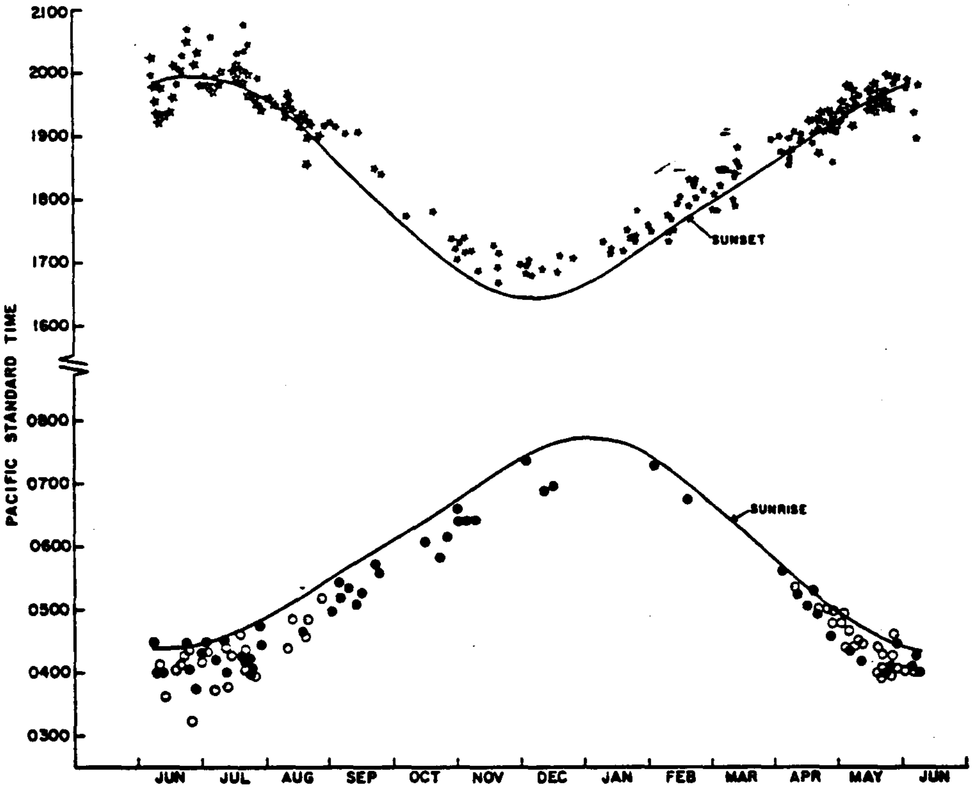

Fig. 25. Activity periods of spotted owls on the H. J. Andrews and BLM study areas. Stars indicate when activity began with respect to sunset, and circles indicate when activity ceased with respect to sunrise. Solid and open symbols represent the H. J. Andrews and BLM areas, respectively. Each point represents 1 observation.

Juvenile Begging Call: Owlets under 6 months of age gave only 3 different calls, 2 of which were uncommon. The uncommon calls included a low chittering sound (similar to the adult Chitter) uttered when owlets were handled or otherwise distressed, and a barely audible grunting sound (similar to the adult Warning Call) that was given when owlets were startled. The only call that was commonly given by all owlets was the Begging Call, a raspy, high-pitched whistle that was given persistently when they were hungry (Fig. 24F). This call was similar in duration and inflection to the adult Contact Call (Fig. 24A) but was much higher pitched and entirely lacked the clear whistled quality of the adult call. We phoneticized it as *sweeeeet!*. Owlets were easily induced to beg if the call of an adult was imitated near them. The begging call was not loud, carrying <200 m under most conditions.

One of the owlets raised in captivity gave only typical Begging Calls until 27 September, when it was approximately 6 months old. After that date a gradual change in the quality of the Begging Call was noted. The raspy quality of the call began to diminish gradually, and the call began to assume the clear whistled quality of the adult Contact Call. By 7 October the transition was complete. Thereafter, the owlet gave the typical adult Contact Call with only an occasional hint of raspiness. This same owlet was first heard giving the typical 4-Note Location Call on 7 February and the Bark Series on 13 February. Both of the latter calls were given clearly but at reduced volume.

In the wild the earliest date that we

Table 20. Average horizontal distance moved (m/hour) by spotted owls while foraging under different weather conditions and during different seasons on the H. J. Andrews study area (May 1975–Jun 1976).[a]

Weather conditions	Period				Means
	Mar–Apr	May–Jun	Jul–Sep	Oct–Feb	
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

[a] Data compiled from 8 adults.

heard a young of the year attempt to give adult vocalizations was 18 October when a radio-tagged juvenile gave the 4-Note Location Call in response to our imitation of adult calls. The quality of this juvenile's call was very poor. Although the cadence was normal, the volume was so low and the notes were so raspy that the call could barely be heard 75 m away. These observations indicate that juvenile spotted owls develop most of the adult vocal repertoire during fall and winter of their first year.

Activity Patterns

Timing of Activity.—On the average on the HJA study area, owls left their day roosts to begin foraging 14 minutes after sunset (range = −54 to +60 min) and stopped foraging 21 minutes before sunrise (range = −45 to +6 min) (Fig. 25). Activity generally began earlier (in relation to sunset) during spring and early summer than during fall and winter. Activity periods on the BLM study area were practically identical (Fig. 25).

During the day the owls spent most of their time roosting in trees, occasionally moving in place, but generally remaining inactive. On 9 occasions, however, we saw spotted owls attempt to capture diurnal or crepuscular mammals that wandered into roost areas (2 attempts successful). We also found that spotted owls would readily leave their day roosts to capture live mice that we tethered on the ground beneath roost trees. They also made occasional short flights during the day to retrieve cached prey, change roost trees, or drink or bathe at streams near their roosts. The relative infrequency of diurnal activity was indicated by the low proportion of diurnal animals in the diet (4.5% on HJA area, 7.4% on BLM area).

Rate of Movement While Foraging.—Spotted owls foraged at night by moving from perch to perch, watching and listening for prey. Time spent at individual perches ranged from only a few seconds to several hours. The average rate of movement (in terms of horizontal distance) while foraging in this manner was 247 m/hour on the HJA study area and 323 m/hour on the BLM study area (range = 0–3,371 m/hour). Our estimates of distance moved were undoubtedly conservative, because it was impossible to detect all of the short flights that radio-tagged owls made while foraging.

On the HJA area, the rate of movement while foraging was highest during spring and summer and lowest during fall and winter (Table 20). This difference was most pronounced in nesting individuals, but was characteristic of non-nesting individuals as well. The increased rate of movement of nesting individuals during spring and summer was undoubtedly related to increased energy demands. Regardless of their nesting status, however, spotted owls had less time to forage during the short spring and summer nights than during winter and may have compensated by spending less time resting at night during spring and summer.

On the average, owls moved less when

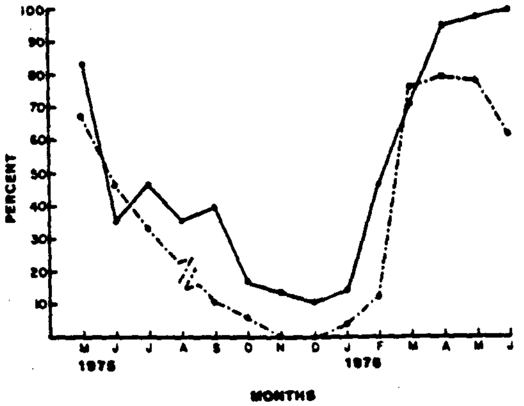

Fig. 26. Percent of days on which adult spotted owls on the H. J. Andrews study area roosted together as pairs (dashed line) or near (within 400 m) their traditional nest sites (solid line). Percentages were calculated on a monthly basis from May 1975–Jun 1976. Data for August 1975 were inadequate to calculate pair association.

it rained or snowed (Table 20). However, when the data were examined on a seasonal basis the only consistent relationship between weather conditions and rate of movement was that movement ceased almost altogether when heavy rains were accompanied by strong winds (Table 20). It appeared, therefore, that seasonal weather patterns were responsible for little if any of the seasonal differences 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 at the same location for up to several hours. These quiescent periods did not seem to fit any recurring pattern, probably because 2 of the major variables affecting movement at night (prey encounters and prey capture) did not occur on a predictable schedule. When owls captured large prey (e.g., squirrels, woodrats, or hares), they commonly cached what they could not eat and then roosted in the vicinity until the prey was consumed. This response to prey capture was verified on a number of occasions when owls stopped moving during the night and were found roosting the next morning near a cached, partially eaten prey animal.

Social Behavior

During midwinter (Nov–Jan) when the owls were largely solitary, they called infrequently, and only 1 territorial interaction was observed. After the resident male and female on each territory began to roost together in late February or March (Fig. 26), they became more vocal and began to interact more frequently with neighboring pairs. The increased level of social activity continued through summer, and then declined in October.

During 353 nights of observation on the HJA and BLM study areas, we witnessed only 17 territorial interactions (defined as any instance in which at least 2 individuals from different areas called within hearing distance of each other). The relative infrequency of interactions precluded the identification of distinct territorial boundaries. In fact, we concluded that such boundaries probably did not exist. The owls appeared to space themselves far enough apart to avoid frequent contact with each other. Instead of distinct boundaries between territories, there were broad areas of home range overlap that were contested occasionally by the adjacent parties, but defended consistently by none.

In the few instances in which resident individuals detected intruders, they usually responded with the 4-Note Location Call or with a mixture of hooting, barking, and whistling calls. 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 both individuals were of the same sex and if one was well inside the home range of the other, the intruder would stop calling and retreat. If the interaction occurred in an area of home range overlap and both birds were of the same sex, they sometimes approached each other and then pursued each other from tree to tree, calling in an agitated manner. Eventually 1 or both birds would leave the area. One interaction of this type between 2 males lasted over 2 hours. Territorial interactions between birds of the same sex did not always escalate into encounters at close range; on at least 1 occasion, the 3A pair and the 1A female called from opposite sides of Blue River Reservoir without ever approaching closer than 300 m to each other.

Resident individuals did not appear nearly as aggressive in rebuffing members of the opposite sex encountered within the home range. Five interactions were observed involving a male and female from adjacent home ranges. In all 5 cases the owls called excitedly but did not retreat from each other, even when 1 individual had wandered well inside the home range of the other. Another indicator that males and females did not behave aggressively towards each other was that 3 radio-tagged owls (2 females, 1 male) occasionally roosted with individuals of the opposite sex other than their regular mates.

Because interactions between male and female spotted owls from adjacent home ranges did not 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. It was also 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 (as much as possible) other males from the home range and females excluded other females. This pattern of home range defense, combined with the tendency of residents to remain within traditional home ranges, made it virtually certain that the same individuals re-paired each spring, as long as each individual was able to exclude others 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.

DISCUSSION

The spotted owl population in Oregon is undoubtedly larger than indicated by our sample because we did not inventory all areas of suitable habitat in the state. We estimate that only 50–60% of the potential spotted owl habitat was searched for owls. If we assume that population densities were similar in the searched and unsearched areas, then the statewide population was roughly 1,000–1,200 pairs of owls.

Studies of spotted owls in California and Washington suggest that populations are declining there also. Gould (1974, 1977) checked numerous historical sites where spotted owls had been reported in California and was able to relocate owls at only 72% of the sites. Because many of the historical sightings were poorly documented, however, Gould considered his results as being only suggestive of a decline, rather than an accurate indicator of total decline. Data on population trends in Washington are limited, but Postovit (1979) found few owls in second-growth forests in western Washington. The paucity of spotted owls on private lands in our study was also noted in California and Washington (Gould 1974, 1977; Postovit 1979). The majority of owls found by Gould and Postovit were in old-growth forests or mixed forests of old-growth and mature trees.

Most home ranges of spotted owls on the HJA and BLM study areas were larger than home ranges reported for barred and great horned owls (Nicholls 1970, Nicholls and Warner 1972, Fuller 1979). These results do not support the theory that raptor body size and home range size are positively correlated (Schoener 1968). We suspect that the relationship between raptor body size and home range size is not consistent because it is confounded by factors such as habitat quality and regional and local differences in the types of prey utilized.

Why spotted owls in Oregon consistently preferred old-growth forests for foraging was unknown. It is possible that the principal prey utilized by the owls (flying squirrels) were most numerous in older stands. No data were available on the abundance of flying squirrels on the study area, but studies by Gashwiler (1959) and Hooven (1972) indicated that flying squirrels were eliminated from recently clear-cut areas. Flying squirrels probably do not begin to repopulate clear-cut areas until at least 20–30 years after harvest, when trees become large enough to support arboreal nests.

It was also possible that the owls foraged selectively in older forests because the biomass of nocturnal prey within the size range preferred by the owls (20–300 g) was greater in older forests than in recent clear-cuts and young second-growth. Although populations of some nocturnal mammals (notably deer mice and some voles) increase after clear-cutting (Gashwiler 1959, Hooven 1972), it is not clear if such increases compensate for the reduction in biomass associated with the elimination or reduction of populations of flying squirrels, red tree voles, western red-backed voles, and snowshoe hares.

Recent clear-cuts and young second-growth forests also may have been avoided because foraging perches were absent there. In addition, the dense brush and herb layers that developed on many clear-cut areas may have made it difficult for owls to attack prey on the ground. Foraging in open areas also could have increased the risk of predation by larger predators such as the great horned owl.

Because as much as 77% of the forests within the home ranges of some individuals had been clear-cut within the previous 40 years, it was obvious that the owls were able to tolerate considerable reductions in the amount of older forests within their home ranges. There were indications, however, that they were able to do so only by increasing the size of their home range areas, thereby encompassing additional areas of older forest. This was suggested by the fact that owls in more heavily cutover areas (BLM study area) had larger home ranges on the average than owls in less heavily cutover areas (HJA study area) (Table 1). Similar relationships between home range size (or territory size) and habitat quality have been reported in other birds (Stenger 1958, Seastedt and MacLean 1979).

We believe that older forests were preferred for roosting because they provided the most protective environment for roosting under most weather conditions. Old-growth forests had deep, multilayered canopies that produced numerous patches of shade during warm weather and also had numerous large trees suitable for roosting in cold, wet weather. By comparison, young stands had relatively shallow canopies (measured from top to bottom) and few large trees of the type preferred for wet weather roosts.

One factor that undoubtedly caused spotted owls to select old-growth forests for nesting was that suitable nests were most common in older forests. Large cavities and heavy dwarf mistletoe infestations were generally uncommon or absent in young forests, but were common in old forests. The fact that the owls showed a strong preference for roosting in old-growth stands also suggested that such stands provided an optimal environment in which to raise the young after they left the nest.

In contrast to spotted owls in Oregon, which nest almost exclusively in trees, spotted owls in the mountains and canyonlands of southern California and the southwestern U.S. frequently nest in caves or potholes in cliffs (Peyton 1910, Dickey 1914, Ligon 1926). These regional differences in nest types are undoubtedly due to differences in the types of habitat occupied. There are few cliffs or caves suitable for nesting in the humid forests of Oregon and Washington, whereas cliffs and caves are abundant in the mountains and canyonlands of southern California, Arizona, and New Mexico.

The tendency of spotted owls to use a traditional nest area or nest tree for many years has been reported by other observers. Miller (1974) observed a pair of spotted owls that remained in the same area for at least 7 years, nesting in 5 years. Peyton (1910) located a nest in 1908 that was still being used by spotted owls 21 years later in 1929 (Bent 1938).

Timing of nesting in Oregon did not differ appreciably from dates given by

Bent (1938) for southern California. He listed 15 records of eggs observed or collected between 1 March and 10 May. Eight of the records fell within the period 27 March–1 April, "indicating the height of the season" (Bent 1938:207).

The display sequence in which male spotted owls called from a perch near the nest just before or after copulation is common in owls (Haverschmidt 1946, Jansson 1964, Konig 1965, Ligon 1968). Ligon (1968) found that male elf owls called from inside the nest cavity and that females followed them inside. He interpreted this behavior as an attempt by the male to entice the female into the nest.

Except for females that were about to lay eggs, spotted owls were never observed roosting in cavities. Ligon (1968) found that female elf owls began to roost in their nest cavities 1–2 weeks before laying eggs. He suggested that this behavior may have been adaptive because it insured that other birds or mammals did not usurp the nest and because it preconditioned males to feed females at the nest.

Apparently, most young strigids leave the nest before they are fully capable of flight (Dement'ev et al. 1966, Hoglund and Lansgren 1968, Southern 1970, Dunstan and Sample 1972). Dunstan and Sample (1972) suggested that this might occur because nestlings were unable to exercise their wings within cramped nest cavities. The fact that young great gray owls and spotted owls (which frequently occupy open platforms) also leave their nests before they can fly well seems to contradict this explanation. Hoglund and Lansgren (1968) suggested that young great gray owls left the nest before they could fly because they became increasingly uncomfortable as the season advanced and the sun began to shine more directly into nests. This explanation hardly seemed to apply to spotted owls because they were usually protected from direct sunlight by nest cavities or dense foliage.

A more likely reason for leaving the nest as early as possible is to escape increasing parasite numbers in the nest. As pellets, fecal matter, and prey remains accumulated in nests, and as warm temperatures began to predominate in late May and June, spotted owl nests began to attract increasing numbers of flies. Three nestlings in 2 nests during this period were bitten repeatedly around the eyes by bloodsucking flies (family Hipoboscidae), causing enough hemorrhaging to glue the eyelids shut with dried blood and debris. Similarly, Fitch et al. (1946) and Fitch (1947) reported that *Eusimlium clarum*, a bloodsucking fly, caused heavy mortality among nestling red-tailed hawks and caused scabs to form on the eyelids of nestling great horned owls. Bohm (1978) and Tirrell (1978) indicated that parasites may cause a significant reduction in nestling vigor and growth rate in some raptors. If the reduction in fitness associated with parasitism is greater than that associated with leaving the nest at an early age, then selection should favor leaving the nest as early as possible.

The climbing ability of young spotted owls is typical of many species of owls, including great horned, barred, screech, great gray, tawny, and hawk owls (Smith 1963, Hoglund and Lansgren 1968, Dunstan and Sample 1972, Scherzinger 1980, R. Palmer, pers. commun.). The tendency of young spotted owls to leave the nest before they can fly well and to climb into elevated perches has led some authors (e.g., Dickey 1914, Karalus and Eckert 1974) to mistakenly suggest that adult spotted owls physically transport their young from the nest.

Our observations on 2 dispersing owlets were too limited to determine much about dispersal. The relatively short distances traveled 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).

The mixture of arboreal and terrestrial species in the diet of spotted owls in Oregon indicated that the owls foraged at all levels in the forest, from the ground to the upper canopy. The preponderance of flying squirrels and woodrats in the diet suggested either that the owls searched selectively for squirrel or rat-sized mammals or were most adept at capturing such mammals, or both. The preponderance of forest-dwelling mammals in the diet reflected the strong preference of the owls for foraging in forest areas as opposed to clear-cuts and other large openings. Small amounts of information on the diet of the spotted owl in other parts of its range indicate that spotted owls depend on woodrats or northern flying squirrels for the bulk of their food in most areas, but also forage opportunistically on a variety of small mammals, birds, and insects (Dickey 1914; Ligon 1926; Marshall 1942, 1957; Smith 1963; Beebe and Schonewald 1977; Kertell 1978; Barrows 1980).

The absence of significant differences in prey selection by male and female spotted owls was not surprising considering that female spotted owls are only about 10% larger than males (Earhart and Johnson 1970). Nevertheless, if owls that are only slightly dimorphic do not partition their prey on the basis of size, then there must be some more fundamental reason for the evolution of reversed sexual size dimorphism.

The prey caching behavior of spotted owls is typical of many owls, hawks, and falcons (Pitelka et al. 1955, Mumford and Zusi 1958, Schnell 1958, Collins 1963, Mueller 1974, Balgooyen 1976, Collopy 1977, Phelan 1977). As discussed by Balgooyen (1976), Callopy (1977), and Phelan (1977) prey caching is adaptive for several reasons, the most obvious being that by storing and returning to excess prey, a predator reduces the amount of energy it would expend if it did not completely use all prey captured.

Radiotelemetry studies of other supposedly nocturnal owls have indicated activity patterns both similar to and noticeably different than observed 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 and BLM study areas. Great horned owls studied by Fuller (1979) usually began activity within 30 minutes of sunset and ended activity within 30 minutes of sunrise. Barred owls studied by Nicholls (1970) and Fuller (1979) were most active during the night but were also frequently active during the day; diurnal activity increased considerably when the owls were feeding young. Like spotted owls, great horned and barred owls were active for longer periods during winter than summer (Fuller 1979).

In contrast to our findings, Miller (1974: 115) reported that a female spotted owl "foraged at all hours of the day or night" when feeding young. However, Miller did not differentiate between opportunistic attempts to capture prey in roost areas and long distance foraging flights away from roost areas. If the foraging behavior Miller referred to was of the former type, then differences between her observations and ours may have been more semantic than real.

MANAGEMENT IMPLICATIONS

The most serious threat to the spotted owl in Oregon is the gradual elimination of its preferred habitat (old-growth and mature forests). To alleviate this threat we recommend that a system of old-growth management areas be established on federal forest lands throughout the range of the spotted owl in Oregon. When possible, such areas should be selected on the basis of occupancy by spotted owls. Old-growth management areas should be spaced at intervals of 2–10 km so that pairs of owls or segments of the population do not become reproductively isolated. To achieve a spacing of 2–10 km between old-growth management areas throughout the range of the spotted owl in Oregon would require that approximately 400 areas be established, assuming that the areas are irregularly spaced at 2–10-km intervals.

Within each old-growth management area, 400 ha of old-growth forest should be maintained in a relatively natural (i.e., unlogged) condition within a 2.5-km radius of the nest of the resident pair of owls. The 400 ha figure is based on the fact that all of the radio-tagged pairs we studied had more than 396 ha of old-growth within their home ranges (the home range of a pair included the combined home ranges of the male and female). We believe that 400 ha of old-growth will provide adequate habitat for individual pairs, assuming the most extreme scenario in which all surrounding areas are covered by intensively managed second-growth forests <80 years old (a likely situation in the future). It is possible that less extensive areas of old-growth may be needed if extensive areas of mature forest or older (>80 years old) second-growth forest are available as alternative (albeit less optimal) foraging habitat. However, until this has been documented, adherence to the 400-ha old-growth minimum should be maintained.

Old-growth forests within each management area should include some patches that are at least 40–100 ha in area and should be connected by travel corridors of mature or old-growth forest if possible. Old-growth habitat in management areas should not be harvested until replacement old-growth stands are regenerated on adjacent areas (this includes salvage logging of logs and dead or damaged trees). The above recommendations closely parallel recommendations made by the Oregon–Washington Interagency Wildlife Committee, a group of biologists representing the U.S. Forest Service, Bureau of Land Management, U.S. Fish and Wildlife Service, Oregon Department of Fish and Wildlife, and Washington Department of Game (Oregon–Washington Interagency Wildlife Committee 1980).

Assuming that a management plan similar to the above is implemented, there remains the problem of how to manage pairs outside the old-growth management areas. We assume that most of these pairs will disappear in the long term, as their habitat is eliminated. To slow the rate at which such pairs are eliminated, however, we recommend that harvest of known nest sites or principal roost areas be avoided. We also recommend that forest managers enhance the suitability of selectively logged stands by leaving 2–5-ha patches of old-growth trees scattered within logged stands.

The most important factor to consider in the establishment of a spotted owl management plan in Oregon is the rate at which the remaining old-growth forests are being harvested. In the Coast Ranges in particular, most old-growth forests have already been cut, and only isolated islands of old-growth will remain by the year 2000 (Beuter et al. 1976). As a result, options for management are rapidly being lost, particularly options for maintaining the desired distribution of old-growth management areas. It is imperative, therefore, that management be initiated as soon as possible. If future studies demonstrate that the proposed management plan is unnecessarily conservative (i.e., retains more old-growth than is necessary), then the excess old-growth can always be harvested at some future date. In contrast, it will be virtually impossible to adjust management in the opposite direction if the decision to manage the owl is delayed, and it eventually becomes apparent that not enough old-growth has been retained. Once harvested, it is extremely unlikely that old-growth forests will ever be regenerated.

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APPENDIXES

Appendix 1. Vernacular and scientific names of plants mentioned in this report. Nomenclature follows Franklin and Dyrness (1973).

Bigleaf maple	*Acer macrophyllum*
California-laurel	*Umbellularia californica*
Canyon live oak	*Quercus chrysolepis*
Coast redwood	*Sequoia sempervirens*
Creambush oceanspray (Roch spiraea)	*Holodiscus discolor*
Douglas-fir	*Pseudotsuga menziesii*
Dwarf mistletoe	*Arceuthobium* spp.
Golden chinkapin	*Castanopsis chrysophylla*
Grand fir	*Abies grandis*
Incense-cedar	*Libocedrus decurrens*
Lodgepole pine	*Pinus contorta*
Mountain hemlock	*Tsuga mertensiana*
Noble fir	*Abies procera*
Oregon ash	*Fraxinus latifolia*
Oregon white oak	*Quercus garryana*
Pacific dogwood	*Cornus nuttallii*
Pacific madrone	*Arbutus menziesii*
Pacific silver fir	*Abies amabilis*
Ponderosa pine	*Pinus ponderosa*
Port-Orford-cedar	*Chamaecyparis lawsoniana*
Red alder	*Alnus rubra*
Shasta red fir	*Abies magnifica* var. *shastensis*
Sitka alder	*Alnus sinuata*
Sitka spruce	*Picea sitchensis*
Subalpine fir	*Abies lasiocarpa*
Sugar pine	*Pinus lambertiana*
Tanoak	*Lithocarpus densiflorus*
Vine maple	*Acer circinatum*
Western (California) hazel	*Corylus cornuta*
Western hemlock	*Tsuga heterophylla*
Western redcedar	*Thuja plicata*
Western white pine	*Pinus monticola*
Western (Pacific) yew	*Taxus brevifolia*
White fir	*Abies concolor*

Appendix 2. Cover types used for habitat selection analyses on the H. J. Andrews and BLM study areas.

Cover type	Area in which cover type occurred	Description
Old-growth conifer forest	HJA, BLM	Multilayered old-growth associations of Douglas-fir, western hemlock, and western redcedar with understories dominated by western hemlock, vine maple, Pacific dogwood, bigleaf maple, and western yew. Also included mixed associations of old-growth Pacific silver fir, Douglas-fir, and western hemlock on the HJA study area. On the HJA study area, old-growth overstory trees were typically 275–450 years old, 50–70 m tall, and 100–150 cm dbh. On the BLM study area, old-growth overstory trees were typically 220–350 years old, 50–65 m tall, and 100–170 cm dbh. Canopy closure in most stands averaged between 70 and 80%.
Selectively logged old-growth conifer forest	HJA	Same as above except that some removal of logs and dead or damaged trees had occurred, resulting in a slight reduction in canopy closure. On the BLM study area this cover type was uncommon and was lumped with unlogged old-growth conifer forest.
81–200-year-old conifer forest	HJA, BLM	Unlogged mature forests of Douglas-fir with variable amounts of western hemlock, vine maple, and Pacific dogwood in the understory. Also included small areas of mixed associations of Pacific silver fir, Douglas-fir, and western hemlock on the HJA study area. Trees typically 40–65 m tall and 40–130 cm dbh.
Mature hardwoods	HJA, BLM	This type included a 4-ha mixed stand of large Oregon ash and Oregon white oak on the BLM study area. On the HJA study area it included riparian mixtures of bigleaf maple, red alder, western redcedar, western hemlock and Douglas-fir.

Appendix 2. Continued.

Cover type	Area in which cover type occurred	Description
61–80-year-old conifer forest	HJA, BLM	Unlogged older second-growth forests dominated by Douglas-fir. Trees typically 20–40 m tall and 25–75 cm dbh. Understory development in these stands was variable, ranging from few understory trees and little ground cover to a well-developed layer of vine maple, Douglas-fir, Pacific dogwood, and western hemlock. In most stands overstory trees were relatively uniform in size.
31–60-year-old conifer forest	HJA, BLM	Included 31–60-year-old forests of Douglas-fir on the HJA study area and 36–60-year-old forests of Douglas-fir on the BLM study area (unlogged stands). Overstory trees typically 18–40 m tall and 20–60 cm dbh.
21–35-year-old conifer forest	HJA, BLM	Included 21–30-year-old stands of Douglas-fir on the HJA study area and 25–35-year-old stands of Douglas-fir on the BLM study area. These sites had been clear-cut between the late 1930's and early 1950's. Trees typically 10–20 cm dbh and 15–46 m tall. Along streams on the BLM area these stands often consisted of mixtures of red alder and Douglas-fir.
5–20-year-old conifer forest	HJA, BLM	Stands of Douglas-fir that were 5–20 years old on the HJA study area and 5–24 years old on the BLM study area. Growing on sites clear-cut or burned between 1950 and 1973.
Recent clear-cuts or burns	HJA, BLM	Clear-cut or burned areas overgrown by mixtures of woody shrubs such as vine maple, Pacific dogwood, and salal, or by grass-forb associations.
Rock talus outcrops and rockslides	HJA	Areas of coarse rocky rubble.
Rock quarries or gravel storage areas	HJA, BLM	Small (0.2–1 ha) areas where rock was quarried or stored.
Shelterwood harvest unit	HJA	A mixed stand of old-growth Douglas-fir and western hemlock in which all trees had been harvested except for individual old-growth trees that were spaced 20–30 m apart.
Blue River Reservoir	HJA	This type included the reservoir and grassy slopes forming a narrow border around the reservoir. Reservoir was drained during winter months.
Blue River Reservoir campground	HJA	A public campground characterized by a mixed stand of mature and old-growth Douglas-fir, bigleaf maple, western redcedar, and western hemlock that had been selectively thinned to open up campsites and parking areas.
Golf course	HJA	The Tokatee golf course bordered the southern edge of the study area and fell within the home range area used by the 1A male.
Powerline right of way	HJA	Cleared area beneath a high voltage powerline near the southern boundary of the study area.
Pastureland	BLM	Areas cleared for grazing by domestic livestock.

Appendix 3. Vernacular and scientific names of animals mentioned in this report. If a species occurred in the diet its mean weight or range of weights is also given.

Vernacular[a]	Scientific name	Mean weight (g) or range of weights used for biomass calculations	Source for weight estimate[b]	Table numbers (from text) in which species occurred in diet[c]
Mammals				
Big brown bat	*Eptesicus fuscus*	16	3	13
Brush rabbit	*Sylvilagus bachmani*	150–900	1	12; 14; 15F
Bushy-tailed woodrat	*Neotoma cinerea*	265	2	12; 13; 14; 15B, C, D, E, F, G
California vole	*Microtus californicus*	39	3	14; 15C, E
Chickaree	*Tamiasciurus douglasii*	208	2	12; 13; 15A, B, D, F, G
Coast mole	*Scapanus orarius*	53	2	12; 13; 14; 15F, G
Creeping vole	*Microtus oregoni*	19	2	12; 13; 14; 15A, B, C, E, F
Deer mouse	*Peromyocus maniculatus*	22	2	all areas
Dusky-footed woodrat	*Neotoma fuscipes*	269	2	12; 14; 15A, E, F
Dusky shrew	*Sorex obscurus*	9	2	15B
Ermine	*Mustela erminea*	41	3	12; 13
Heather vole	*Phenacomys intermedius*	27	2	15G
Long-tailed weasel	*Mustela frenata*	200	2	14; 15F
Marsh shrew	*Sorex bendirii*	18	2	13
Mazama pocket gopher	*Thomomys mazama*	87	2	13; 14; 15B, C, D, E, G
Mountain beaver	*Aplodontia rufa*	120–400	1	12; 15A
Northern flying squirrel	*Glaucomys sabrinus*	115	2	all areas
Pacific shrew	*Sorex pacificus*	12	2	12; 13; 15F
Pika	*Ochotona princeps*	158	2	13; 15B, G
Red tree vole	*Phenacomys longicaudus*	27	2	12; 14; 15A, B, D, F
Shrew mole	*Neurotrichus gibbsii*	9	2	12; 13; 14; 15C, G
Silver-haired bat	*Lasionycteris noctivagans*	10	2	12
Snowshoe hare	*Lepus americanus*	150–1,500	1	12; 13; 15A, B, C, D, E, F, G
Townsend's chipmunk	*Eutamias townsendii*	80	2	12; 13; 14; 15B, C, D, E, F, G
Townsend's vole	*Microtus townsendii*	54	3	12
Trowbridge shrew	*Sorex trobridgii*	5	2	12; 13; 15B, E, G
Vagrant shrew	*Sorex vagrans*	5	2	12
Water shrew	*Sorex palustris*	11	2	15B
Water vole	*Arvicola richardsoni*	70	2	13; 15B, G
Western jumping mouse	*Zapus trinotatus*	24	3	12; 13; 15B, F
Western red-backed vole	*Clethrionomys occidentalis*	23	2	all areas
Unidentified shrew		10	4	12; 13; 14; 15A, C, D, F, G
Unidentified squirrel		265	4	12; 13; 14; 15B, D, E, F, G
Unidentified woodrat		100	4	12; 13; 14; 15G
Unidentified vole/mouse		25	4	12; 13; 14; 15B, C, D, E, F, G
Birds				
Barred owl	*Strix varia*			
Black-backed three-toed woodpecker	*Picoides arcticus*	69	10	15G
Blue grouse	*Dendragapus obscurus*	500	1	12; 15C, F
Brown creeper	*Certhia familiaris*	8	6	12; 14

Appendix 3. Continued.

Vernacular[a]	Scientific name	Mean weight (g) or range of weights used for biomass calculations	Source for weight estimate[b]	Table numbers (from text) in which species occurred in diet[c]
Chestnut-backed chickadee	*Parus rufescens*	10	4	12; 13
Cooper's hawk	*Accipiter cooperii*			
Dark-eyed junco	*Junco oreganus*	18	6	12; 15F
Elf owl	*Micrathene whitneyi*			
Evening grosbeak	*Hesperiphona vespertina*	64	6	12; 13; 15F
Golden-crowned kinglet	*Regulus satrapa*	6	6	12
Goshawk	*Accipiter gentilis*			
Gray jay	*Perisoreus canadensis*			
Great gray owl	*Strix nebulosa*			
Great horned owl	*Bubo virginianus*			
Hairy woodpecker	*Dendrocopus villosus*	70	6	15E
Hawk owl	*Surnia ulula*			
Kestrel	*Falco sparverius*			
Long-eared owl	*Asio otus*	262	5	15G
Mountain quail	*Oreortyx pictus*	244	6	12; 15E
Olive-sided flycatcher	*Nuttallornis borealis*	34	6	13; 15A
Pygmy owl	*Glaucidius gnoma*	67	5	12; 13; 14; 15F
Raven	*Corvus corax*			
Red-shafted flicker	*Colaptes cafer*	146	6	12; 14; 15C, G
Red-tailed hawk	*Buteo jamaicensis*			
Robin	*Turdus migratorius*	81	6	12; 14; 15F
Saw-whet owl	*Aegolius acadicus*	83	5	12; 13; 15E, F, G
Screech owl	*Otus asio*	140	4	12; 13; 14; 15E
Steller's jay	*Cyanocitta stelleri*	107	6	12; 13; 14; 15C, D, E, F, G
Tawny owl	*Strix aluco*			
Thrush spp.	*Hylocichla* spp.	26	6	13
Varied thrush	*Ixoreus naevius*	79	7	12; 14; 15A, B, E
Western tanager	*Piranga ludoviciana*	31	6	15C, E
White-headed woodpecker	*Dendrocopus albolarvatus*	58	9	15C
Winter wren	*Troglodytes troglodytes*	9	6	13
Yellow-bellied sapsucker	*Sphyrapicus varius*	46	6	12; 13; 15A, F, G
Unidentified medium-sized bird		70	4	12; 13; 14; 15A, F, G
Unidentified small bird		30	4	all areas
Unidentified small owl		90	4	12; 13; 15F, G
Reptiles				
Garter snake	*Thamnophis* spp.	50	8	12; 13
Western fence lizard	*Sceloporus occidentalis*	10	8	12
Crustaceans				
Crayfish	*Pasifastacus* spp.	20	4	15F
Insects				
	Prophalangopsidae			
	Cyphoderris monstrosa	2	4	13; 15B, C, E, G
	Blattidae			
	Cryptocercus punctulatus	1	4	15D, E
	Pentatomidae			
	Chlorochroa spp.	0.5	4	12
	Cicadidae			
	Okanagana spp.	0.5	4	14; 15E
	Corydalidae			
	Dysmicohermes disjunctus	2	4	15B
	Raphidiidae			
	Genus unknown	0.5	4	15G

Appendix 3. Continued.

Vernacular[a]	Scientific name	Mean weight (g) or range of weights used for biomass calculations	Source for weight estimate[b]	Table numbers (from text) in which species occurred in diet[c]
Insects (cont.)	Cerambycidae			
	Ergates spiculatus	2	4	12; 13; 14; 15C, D, E, G
	Prionus californicus	2	4	13; 15B
	Ortholeptura valida	0.5	4	15B
	Cerambicidae			
	Ortholeptura spp.	0.5	4	15C
	Centrodera spurca	0.5	4	12; 15G
	Monochmus oregonensis	0.5	4	15C
	Arhopalus productus	0.5	4	13
	Acmaeops spp.	0.5	4	15G
	Plectrura spinicauda	0.5	4	13
	Carabidae			
	Scaphinotus marginatus	0.5	4	12
	Pterostichus lama	0.5	4	13; 15F
	Pterostichus herculaneus	0.5	4	12
	Pterostichus neobrunneus	0.5	4	15G
	Pterostichus amethystinus	0.5	4	13
	Cupedidae			
	Priacma serrata	0.5	4	15G
	Scarabacidae			
	Pleocoma dubitalis	0.5	4	15F
	Bolboceras obesus	0.5	4	15G
	Polyphylla decemlineata	0.5	4	13
	Tenebrionidae			
	Unidentified spp.	0.5	4	12
	Elateridae			
	Ctenicera spp.	0.5	4	15B
	Cicindelidae			
	Omus californicus	0.5	4	12
	Lucanidae			
	Ceruchus striatus	0.5	4	15B
	Sinodendron rugosum	0.5	4	12
	Curculionidae			
	Panscopus spp.	0.5	4	14
	Unidentified spp.	0.5	4	13
	Dyslobus lecontei	0.5	4	13
	Dyslobus spp.	0.5	4	13; 15G
	Formicidae			
	Formica fusca	0.2	4	15G
	Camponotus spp.	0.3	4	12; 13; 15B, C, E, G
	Unidentified ant	0.2	4	13; 14
	Unidentified insects	0.5	4	12; 13; 14; 15C
Spiders				
	Unidentified spider	0.5	4	12; 13
Gastropods				
	Unidentified snail	2.0	4	12

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[a] Vernacular and scientific names of mammals follow Jones et al. 1973.

[b] Sources were (1) weights estimated based on size of skeletal fragments in individual pellets, (2) Chris Maser (unpubl. data), (3) specimens in Oregon State University collections, (4) estimated average not substantiated by specimens, (5) Earhart and Johnson (1970), (6) Kilgore (1971), (7) unpublished data from records at Point Reyes Bird Observatory, California, (8) Ron Nussbaum (unpubl. data), (9) Bock and Lynch (1970), and (10) Grinnell et al. (1930).

[c] Areas are described in each table.