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Movements and Home Range Use by Boreal Owls in Central Idaho'

Gregory D. Hayward, Patricia H. Hayward, and Edward O. Garton²

Abstract.--Radio-marked boreal owls moved an average minimum of 1265 m between consecutive day roosts. Winter roosts tended to be further apart than summer roosts. Boreal owls moved greater distances during years of lower prey densities. Males roosted an average distance of 2460 m from their nest. During a high prey year roost to nest distances were shorter than in subsequent years. Radio-marked owls used different home ranges during winter and summer. Summer activity centers shifted an average 2333 m from winter areas and increased in elevation by 230 m. The shift was probably due to the owls' need for cool summer roost sites and higher prey densities in high elevation spruce-fir forests. Yearround home ranges of 12 owls averaged 1528 ha (522-4119 ha), winter areas being larger than summer. Home ranges of adjacent owls overlapped extensively.

INTRODUCTION

Vertebrate movement patterns reveal resource requirements, degree of gene flow between geographic regions, level of population stability and the area necessary to support an individual in a particular environment. Information on movements and home range use by owls, however, is relatively difficult to gather due to their secretive behavior. Little is known about how these birds utilize space.

Although extensively studied in Europe, researchers have paid little attention to space use by the boreal, or Tengmalm's, owl. In North America, Bondrup-Nielsen (1978) followed two boreal owls in Canada and estimated their home ranges. Palmer (1986) intensively radiotracked two male boreal owls in Colorado in 1984 and reported movements and home range data. We are unaware of any other information on movements and use of space by this common forest owl. Yearly movements by boreal owls have received greater attention than daily movements. Studies of yearly movements of boreal owls in the Old World (Lundberg 1979) indicate variation in site tenacity depending on environmental conditions and the sex of the individual. Site tenacity increases from northern to southern regions in Europe in response to snow cover and the amplitude and degree of synchrony of food fluctuations (Korpimaki 1986). In northern Sweden, male boreal owls are site tenacious between and during vole peaks while females are sedentary only during the vole peaks (Lofgren et al. 1986). Comparable information on site tenacity and nomadism is not available for North America, although Palmer's (1986) work also indicated a tendency toward a nomadic life strategy. Catling's (1972) information suggests the species is irruptive in eastern North America.

In this paper, we present preliminary information on the daily, seasonal, and yearly movement patterns in a recently discovered population of boreal owls in the mountains of central Idaho (Hayward and Garton 1983). Our paper is primarily descriptive. We do not intend to draw extensive ecological or life history conclusions from these data but rather present these preliminary results as an example of the movement patterns of a single population of boreal owls in North America.

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^{7, 1987.} Gregory D. Hayward is a Research Associate, Patricia H. Hayward a Research Associate, and Edward O. Garton a Professor of Wildlife Resources at the University of Idaho, Moscow, Id.

STUDY AREA

During the past three years we have studied habitat use by boreal owls (Aegolius funereus) in the mountains of central Idaho, USA. Our primary study area is Chamberlain Basin, located in the 850,000 ha Frank Church-River of No Return Wilderness. The basin, encompassing the headwaters of Chamberlain Creek, occupies about 25,000 ha of rolling mountain ridges rising from 1720 m to 2350 m elevation. The entire basin lies in the Abies life zone, and coniferous forest covers over 95 percent of the area. Lodgepole pine (Pinus contorta) dominates due to past fires (predominantly Abies lasiocarpa / Calamagrostis rubescens habitat type(h.t.)). Generally these stands are over 50 years old, some exceeding 120 years, and the forest structure is relatively open (tree spacing >2m). Large cavities are absent from these forests . At lower elevations, old-growth Douglas-fir (Psuedotsuga menziesii) and ponderosa pine (Pinus ponderosa) stands occupy southern aspects (predominantly Pseudotsuga menziesii / C. rubescens - Pinus ponderosa h.t.) and mature to old-growth Douglas-fir (predominantly A. lasiocarpa / Vaccinium globulare h.t.) grow on more mesic sites which have escaped fire. Forest stands on these sites are multi-layered and often quite open. Cavities excavated primarily by pileated woodpeckers (Dryocopus pileatus) are abundant in stands where ponderosa pine snags are available. stands where ponderosa pine snags are available. At higher elevations mature to old-growth subalpine fir (predominantly A. lasiocarpa / V. globulare and A. lasiocarpa / V. scoparium h.t.) dominates. Wet spruce bottoms (A. lasiocarpa /Streptopus amplexifolius h.t), aspen stands (Picea engelmannii/Equisetum arvense h.t), sagebrush-bunch grass slopes, and willow carrs occupy relatively small areas within the basin.

Travel within the study area is restricted to foot, skis, or horseback. An extensive trail system provides access to most of the basin, most areas being no more than 3 km from a trail. The wilderness character of the area provides an opportunity to study the habitat use and movements of the owls in an area free from road building, logging, and other human disturbances, or man-made habitats which might influence movements of the owls.

METHODS

Beginning in February 1984, we captured boreal owls using mist nests and bal-chatri traps. Trapping was restricted to within 4.5 km of our living quarters in the extreme eastern edge of the study area below 1800 m elevation. The owls were marked with 6 g backpack-mounted radio transmitters (Wildlife Materials Inc. model MPB-1220-LD) with an expected battery life of 150 days.

We monitored the movements of radio-marked owls from approximately January through August each of 3 years (1984-1986), recapturing the owls to replace the transmitters periodically. During each field season, we worked at alternate study sites for two, 2-week periods. Therefore, radio-marked owls were not followed continuously.

Using hand held 3-element yagi antennas, the radio signal was audible from 0.5 to 11 km, depending on the topographic position of the owl and receiver. If an owl could not be located by checking from ridgetops within about 8 km of our station, we thoroughly searched the entire area within 14 km radius of the station (the entire upper basin) from fixed-wing aircraft.

We located radio-tagged owls on their daytime roosts and plotted the locations on 1:24,000 topographic maps. These locations were converted a cartesian coordinate system using the UTM system; locations were recorded accurate to 100 m.

In 1984, the marked owls were relocated on an irregular schedule ranging from 1-4 locations every ten days. In 1985 and 1986, we maintained a more regular schedule locating each owl every 2-3 days. Three times in 1986 we located an owl on its daytime roost on at least four consecutive days (different owls in each case). These locations provided some insight into day-to-day movements by the birds.

Each time we located an owl we spent one hour at the roost recording habitat information and observing the bird. On 17 occasions we watched birds on their daytime roosts for over two hours to document movements. In addition, on six days, an, owl found actively hunting during daylight hours was followed to document foraging movements. On six nights we followed boreal owls during the first few hours of foraging activity. Night vision goggles used in conjunction with radio-telemetry aided in nocturnal observations. Three owls were marked with betalights (Hayward, in review) to further facilitate observation of the owls.

Analysis

In the analysis of distances between roost sites used on consecutive days or two days apart, the sampling units were mean distances for individual owls. The measurements of distances between roosts were considered subsamples and the mean distance between consecutive roosts (or roosts used two days apart in the second analysis) was calculated from these values. This procedure avoids problems of psuedoreplication; the distances between several roosts used by an individual owl can not be considered independent (Hurlbert 1984).

The analysis of roost to nest distances was limited to four male owls. The limited sample of owls constrained the analysis such that the sampling unit was each roost to nest distance.

Home range analysis was performed using the computer program HOME RANGE (Samuel et al. 1985) which computes home range estimates using three methods. Home range size was estimated using a modification of Dixon and Chapman's (1980) harmonic mean measure of activity, Jennrich and Turner's (1969) bivariate normal ellipse, and the minimum convex polygon. Because the latter two estimates are not distribution free, as is the harmonic mean, we tested the distribution of owl relocations against the assumed distributions. If over half the owl home ranges differed from the assumed distribution for either the bivariate normal or minimum convex polygon we rejected those methods for a majority of the remaining analysis. Due to the prevalence of polygon home range estimates in the literature, however, we reported these estimates. In addition, our preliminary analysis of home range overlap calculates percent overlap using convex polygon estimates. We prefer to compare utilization distributions, but because our investigation is not complete, we have limited analysis to the current approach.

Prior to home range analysis we screened the input data for outliers, representing distant excursions from the normal activity areas. Extreme observations inevitably plague home range sudies (Schoener 1981). Outliers in a bivariate test, defined as those points with bivariate normal weights lower than 0.6, were considered for removal. If the point represented a movement to an area over two km from the owl's normal use area and was used for less than three days, the point was removed.

Throughout the paper we have divided our field season into two periods, snow free and snow covered, which I will refer to as summer and winter. The period of snow cover each year was defined as the period from January (we entered the field in January each year) until over 50 percent bare ground was exposed on level ground at 1800 m.

All confidence intervals are calculated for a=0.05, as are statistical tests. The information below summarizes the movement patterns of 12 boreal owls. Our sample of movements varied widely among owls (Table 1).

RESULTS

Daily Movements

We located consecutive daytime roost sites of 12 owls (4 females, 8 males) on 94 occasions. We feel these observations give an index of the minimum distance which the owl foraged during the previous night. Our evidence indicates that the daytime roost is likely near the end of the final foraging bout. Boreal owls observed foraging during daylight chose roosts within 50 m of their final foraging perch.

Distances between roosts on consecutive days ranged from 0 to 6816 m; mean distance being 1265±374 m (Table 2). During winter consecutive roosts tended to be further apart than during summer. Mean distance, however, did not differ Table 1. Monitoring period and number of relocations for radio-marked bornal owls at Chamberlain Basin. Only owls relocated on at least 10 occasions are included. The distribution of relocations for owls highlighted by * was significantly different from bivariate normal (p > 0.10) and those marked by twere significantly different from bivariate uniform (p > 0.10).

Boreal Owl	Sex	Monitoring Period	Number of Relocations Winter Summer		
8033*	H	16 Mar - 22 Sep 1984		9	
8034 ^t	F	31 Jan - 22 Sep 1984	10	9	
8037*t	F	5 Feb - 22 Sep 1984	16	8	
B042		15 Feb - 22 Sep 1984	8	16	
8043*t		15 Feb - 5 Jul 1984 17 Mar - 21 Aug 1985 15 Jan - 29 Jan 1986	5 19 3	2 14	
8055*t	F	19 Mar - 7 Jul 1984 23 May - 20 Oct 1986	9	2 41	
8076*t		18 Feb - 22 Aug 1985	24	19	
8077*		18 Feb - 20 Aug 1985	31	14	
B084*	H	31 Mar - 30 Aug 1985 14 Jan - 29 Jan 1986	12 2	17	
8095t	F	11 Mar - 7 May 1986	12		
8096*t		26 Apr - 20 Oct 1986	5	53	
8097*t	H	25 Mar - 7 Jul 1986	13	27	

significantly (winter: n=11 owls, $\bar{x}=1460\pm433m$; summer: n=7 owls, $\bar{x}=868\pm483m$). Three boreal owls in Colorado, averaged 708 m between consecutive day roosts (Palmer 1986).

Because we rarely located owls on consecutive days, we used distances between roosts located two days apart as a second index of the distance traveled by owls during their daily activities. This index provided a second sample with which to test differences in movement patterns between seasons and years.

Owls moved further between roosts in winter than summer but again, the differences were not significant (pooled data from the three years: winter n=9 owls, $\bar{x}=2204\pm1071m$; summer n=7 owls, $\bar{x}=1069\pm427m$). Considering winter and summer movements within any one year, differences were not significant. Point estimates of the mean, however, are all larger for winter than summer (Table 3). From 1984 through 1986, our indices of small mammal abundance declined (authors' unpublished data). Through this period of declining food supply, both winter and summer movements showed a trend toward longer movements between roosts (Tables 2 and 3). Although means are not significantly different, point estimates of the means consistently increased over the three years.

Another index of the minimum distance traveled by boreal owls during daily activity is provided by the distance between roost and nest sites of male owls during the nesting seasons. The mean distance between daytime roosts and the nest sites of four

Table	2. Ninety-five percent confidence
	intervals on the mean distances, in
	meters, between roosts used on consecutiv
	days. Sample size in parentheses.

Year	Winter	Summer		
1984	973±317(4)	502±5734(2)		
1985	1638±897(4)	277±1993(2)		
1986	1585±1399(4)	1157±1243(3)		
Pooled	(1984-1986):	1.5.5.4		
	1460+433(11)	869+483(7)		

owls was 2460 m (\pm 473m). Male owls rarely roosted within 500 m of the nest sites and on only one occasion (*n*=43) did a male boreal owl roost within 100 m of the nest site. Over 75 percent of roosts were located over 1000 m from the nest and up to 5600 m from it. The distance between roosts and nest sites showed no significant tendency to increase or decrease during the course of nesting (incubation through fledging). In 1984, when our index of prey availability was higher than the following years, roost to nest distances were significantly less than those measured for an owl in 1986 (Table 4).

Although radio-telemetry (triangulation) indicated male owls did some foraging near the nest site, we feel the birds frequently foraged at the distances indicated by the roost to nest distances. Following prey deliveries at the nest on three nights, one owl returned to the area of its daytime roost several km from the nest. During the incubation period, male owls generally visited the

Table 3. Ninety-five percent confidence intervals on the mean distance, in meters, between roosts located over a three-day period (one day separating each roost location). Subsamples are unequal among owls and reported sample sizes indicate the number of owls. Data include 130 distances.

Year	Winter	Summer		
1984	1335±1390(3)			
1985	1753±430(5)	802 <u>+</u> 1192(3)		
1986	4551±10,323(2)	1380±751(3)		
Pooled	(1984-1986): 2205±1071(9)	1069 <u>+</u> 427(7)		

Table	4. D	istance	in me	ters t	betwee	en da	ytime	100 -
	roosts	and an	owl's	nest	site	for	male	boreal
	owls du	uring i	ncubat	ion a	nd nes	tlin		shoi

A.D.L.		and the second		
Year	Ow1	n	Mean ± 95% Bound	Range
1984	B033	6	1676(±383)	1334-2062
	B042	9	1333(±865)	100-3220
1985	B077	3	4096(±2825)	2802-5166
1986	B097	25	2886(±667)	583-5608

nest 1-3 times each night. Later in the breeding season the male may visit the nest as many as 10 times in a night.

Foraging

Observation of hunting owls on ten occasions, totaling 18.6 hrs, provided some indication of travel rate, distances between hunting perches, and duration of perches--measures of hunting behavior. During these observations, the owl was not always visible, so some hunting perches used very briefly were overlooked.

We measured the total distance covered by the foraging owl during the observation session by plotting its path on 1:24,000 topographic maps. Although these measurements are not particularly precise, they can be used to calculate a minimum travel rate while foraging (by dividing by the observation period). Foraging owls traveled from 1 to 36 m per minute with a median rate of 10 m /min for the 10 observation sessions. The owls remained on each hunting perch from a matter of seconds to over 1/2 hr (n=94, \bar{x} =6.35±1.6 min). Prior to locating prey, the owls tended to move more rapidly, remaining on each perch 2-4 minutes. After detecting prey, however, an owl often remained on a perch for over 10 minutes before pouncing on the prey.

The distance traveled between perches was not always estimated, but for sixty estimated distances, the mean flight distance was 33 m (\pm 8.3 m). This estimate is negatively biased as flights longer than 50 m often could not be estimated because the owl moved again before the perch was located.

While foraging, the owls concentrated their activity in a relatively small area compared to the total length of the foraging flights. The owls we followed doubled back frequently, and thus covered a relatively small rectangular area rather than a long narrow path.

Diurnal Movements

Owls were generally sedentary during daylight, rarely moving more than 50 m. Frequently, however, the roosting birds became active during mid-day and moved 5-20 m to a new roost or to cached prey. In 1986, movements from roosts were often associated with retrieval of cached prey, avoidance of sun, or disturbance due to high winds. On 17 occasions when roosting owls were observed more than two hours, the owl changed roosts 71 percent of the days. The new roost was an average of 27 m from the first roost. Palmer (1986) noted roost changes during 56 percent of observations.

Although not quantified, we noted an increase in diurnal foraging over the three year period. In 1984, we rarely observed our radio-marked owls foraging during daylight. In 1985, four marked owls occasionally hunted during the day. During the autumn of 1986, however, we observed two marked owls hunting nearly one third of the days radiotracked. This frequency was higher than at any other observed period. Palmer (1986) observed hunting on 15 percent of summer locations.

Seasonal Movements

Radio-marked owls consistently used different home ranges during winter and summer. Harmonic mean center of activity (defined by the minimum harmonic value in an analysis of roost locations (Samuel et al. 1985)), shifted a mean of 2333 m (±1518) between winter and summer for seven owls (limited to birds with 8 or more locations each season). Six of these owls used summer home ranges to the west of winter areas. The smallest shift between winter and summer activity centers was made by the only owl whose activity center moved eastward. Our study area generally rises in elevation from east to west indicating that roost locations shifted to higher elevations in summer. In fact, the elevation of winter (n=10, $\bar{x}=1807\pm71$ m) and summer (n=11, $\bar{x}=2038\pm121$ m) activity centers was significantly different. Considering only owls with over eight observations in each season, the difference in elevation was also significant (p=0.008, Wilcoxon matched pairs sign rank).

Nest sites of radio marked owls (5 nests), were all located in the lower 1/3 of the study area. During the winter prior to nesting, the home range activity center for five marked owls (3 females, 2 males) could not be shown to differ from the nest location (mean distance of activity center to nest, 1364±1927m; not significantly different from zero). Summer home ranges defined by roost locations, however, were not centered on nest sites but averaged 2126 m (±1967m) away (2 females, 5 males). Nest sites were generally on the periphery of summer home ranges.

During nesting, female activity was restricted to the immediate vicinity of the nest. During incubation the female left the cavity once or twice during the night for about 15 minutes, flying 30-60 m (observations at three nest sites ond camera records at another). After the eggs hatched, she left more frequently but only for brief periods (10-20 min) and one female was observed (through night vision goggles) carrying debris from the nest.

Female behavior following the brooding period (generally to nestling age of 20-25 days) was variable. Considering radio-marked females at four nests which produced fledglings, on only one occasion did a female consistently participate in feeding the young. One female moved out of the study area when she left the nest (young 21 and 23 days old) and another female who nested in 1984 and 1986 was only known to have delivered prey to the young on two nights in 1986 after leaving the nest three days earlier. She remained in the basin following nesting but concentrated activity about 5 km from the nest. In this case the male owl had abandoned the nest six days before she left and the young ultimately perished.

Home Range

In this section, we would like to summarize preliminary information related to how the owls utilize space. How did the owls ditribute their use of space throughout their home range? What differences, if any, exist in utilization distributions between winter and summer? How large are intensively used areas (i.e. core areas)? And how broadly do seasonal home ranges overlap among owls? These results, however, must be considered preliminary as we have not completed fieldwork and, due to time constraints, the analysis has not included some sophisticated techniques for dissecting the internal anatomy of home range (Samuel and Garton 1985).

Here we define the home range as that area traversed by the individual in its normal activities of food gathering, mating and caring for young (Burt 1943). The utilization distribution (UD) describes the proportion of total activity that takes place in a given area. The UD, then, is useful in describing how an individual uses space within its home range in relation to environmental features. Core areas are those portions of the utilization area used more frequently than others.

We analyzed the home ranges of twelve radiotagged owls monitored for various periods from 1984-1986. We compared the distribution of relocations for seasonal and overall home ranges to a bivariate normal and bivariate uniform distribution to test the underlying distributions required for the Jennrich and Turner (1969) and minimum convex polygon methods (Samuel and Garton 1985). Samuel and Garton (1985) suggested a minimum of 30 relocations and a=0.10 for sufficient power to test the assumed distributions. Considering seasonal and overall samples with over 30 relocations, we rejected the assumption of bivariate uniformity in 8 of 10 cases and rejected the assumption of bivariate normality in 9 of 10 cases. Due to this high rejection rate we preferred a distribution free analysis utilizing the modified harmonic mean UD (Dixon and Chapman 1980) in the program HOME RANGE (Samuel et al. 1985). Home ranges of boreal owls in Chamberlain Basin were quite large. Considering our locations of twelve owls (each with 10 or more relocations) 85 percent UD's covered an average of 1528 ha (\pm 687) (Table 5). The large overall utilization distributions (range of 85 percent contours 522-4119 ha) reflect the shift in areas used in winter and summer.

Mean seasonal home ranges were substantially smaller than the respective overall home range (Tables 5,6). This difference could be due to a smaller sample of locations for seasonal home ranges or simply show that smaller areas are used in any one season than the year round home range. Our simulations (unpublished data) indicate that harmonic mean measures of home range are slightly influenced by sample size but not to the extent seen in Tables 5 and 6. Furthermore, correlations between sample size and home range size from the owl data were low. In seven of nine tests, correlations were below 0.3. We conclude that the area required to support an owl during a given season appears to be less than the area required to meet the birds' needs for an entire year. No difference can be shown for mean area of UD's between seasons (t-test, Table 6). A Wilcoxon matched pairs, sign rank test (*n*=5,p=0.125), considering only owls with at least eight locations for each season, also showed no seasonal differences.

Table 5. Home range size of boreal owls at Chamberlain Basin. Percent utilization distributions (UD's) were calculated using the program HOMERANGE (Samuel et al 1985). Minimum convex polygon estimates are reported only for comparison with literature as few distributions corresponded to the assumed bivariate uniform for this estimate.

		п	A	Minimum Convex		
Year	Ow1		35%	55%	85%	Polygon (ha)
1984	B033	13	158	311	639	557
	B034	19	72	168	522	627
	B037	24	335	931	2723	2688
	B042	24	102	343	602	776
1985	B043	35	332	812	1813	2789
	B076	43	269	623	1992	1052
	B077	46	308	922	1937	1736
	B084	29	291	681	1490	1555
1986	8055	40	83	445	886	2293
	8095	12	77	278	534	3496
	8096	57	187	478	1076	1098
	8097	40	709	1357	4119	2507
Mean 95%	+ Bound	2	44±114	612±220	1528±6	87

Table 6. Seasonal home range size (ha) of boreal owls in Chamberlain Basin with 10 or more relocations. See text and Table 5 for details on calculating the estimates.

				Area of Utilization Distribution		
Season	Year	0w1	n	35%	55%	85%
Winter	1984	9034 9037	10 16	26 87	113 303	311 970
	1985	8043 8076 8077 8084	19 24 31 12	159 121 283 152	429 313 669 357	1170 1057 1714 807
	1986	B095 B097	12 13	77 121	277 351	534 1962
Mean ±	95% Bou	nd		128±62	352±130	1070±464
Summer	1984 1985	8042 8043 8076 8077	16 14 19 14	113 2 8 124	168 197 56 427 135	523 446 158 924
	1986	8096 8097 8055	53 27 40	148 236 190	361 739 423	820 1837 1023
Mean ± 95% Bound				111±69	338±173	845±421

The owls concentrated their activity in a small portion of their seasonal home ranges. general, this is demonstrated by comparing the areas encompassed by the average 55 percent and 95 percent harmonic contours for winter and summer which indicates the owls concentrated over half of their activity in one quarter of the home range. In winter the mean 55 percent harmonic contour for 8 owls encompassed 24 percent of the area circumscribed by the mean 95 percent contour. Likewise, the ratio for summer was 30 percent of the area. During any one season, most owls concentrated their activity in two or three areas. within the home range and explored other areas infrequently. The owls rarely stayed in a particular area for more than two to three weeks; rather, they moved among two or three core areas. Relocations of two owls demonstrate the pattern of use confined to particular core areas (Figs. 1,2). The summer home range of a male boreal owl (B096) shows three areas of relatively high use separated by unused forest (Fig. 1). The winter home range of another male (B077) exhibits this same pattern of non-uniform use of space (Fig. 2).

Home Range Overlap

Seasonal home ranges of radio-marked owls overlapped extensively each year of the study. Because of the low number of relocations for each owl in 1984, we restricted analysis of overlap to the last two years. In the winter 1985, the home range of B077 (estimated by minimum convex polygon) encompassed 82 percent of the area used by B084. The complementary overlap (B084-B077) was 43 percent (Fig. 3). Measurements and behavior indicated both owls were males. During summer 1985 these same owls overlapped 51 percent (B084-B077) and 80 percent (B077-B084). In the summer and autumn 1986, three adjacent owls, including a mated pair and another male from a failed nest used much



Figure 1.--Summer home range of a nesting male boreal owl. Concentric lines represent 95 percent and 55 percent utilization distribution contours. A "+" indicates individual locations; "•" represents the activity center.

of the same area (Fig. 4). Overlap values among these three owls ranged from 21 to 80 percent and averaged 51 percent. The two males' home (B096, B097) ranges overlapped 39 and 63 percent.

The degree of overlap in use of space among unmated boreal owls was further demonstrated in daily radiotracking records. On 1 May 1986 two males, each known to be singing nightly at nest sites separated by 2.4 km were found roosting within 200 m of one another. On the night of 14 February 1984, three boreals, two known to be males, were caught in the same mist net. Likewise,



Figure 2.--Winter home range of a male boreal owl who nested the following May. See Figure 1 for details.



Figure 3.--Home range overlap among four male boreal owls during the winter 1985.

on 18 February 1985, two males were caught in a mist net. Two owls which ultimately mated were located roosting within 10 m of one another on 23 March 1984, 0.9 km from the nest of that year. On five other occasions prior to nesting, however, the members of the pair were never less than 1 km apart.

Year to Year Movements

Movements of radio-marked owls provide some indication of the degree of site tenacity in the Chamberlain Basin population. Four owls, one



Figure 4.--Home range overlap among three boreal owls during summer 1986. Boreals 97 and 98 were a mated pair, 97 being the male. Boreal 96, a male, attracted a mate who abandoned prior to laying. female and three males, were found in the Basin in more than one year. The female nested with a different mate in 1984 and 1986 in cavities 1.4 km apart. A male captured 14 February 1984 was recaptured 17 March 1985, 0.5 km away from his first capture site. This owl (B043) wore an active transmitter from March 1985 through January 1986 when it moved out of the basin with a fresh (11 day old) transmitter. A second male (B085), captured at its nest in 1985, was using a home range within several km of the nest Febrary 1986 when it died (cause thought to be starvation). The third male, first captured in March 1985 (B084) was using a similar home range in February 1986 when it left the basin (same two week period as B085 died and B043 left). This owls' radio signal was relocated on 7 May 1986 80 km to the west near Upper Payette Lake, Valley Co., Idaho.

One female was thought to have left the basin within 8 days after she first left her nest. On 5 July, when her young were 20 and 22 days old, the owl was roosting near the cavity at 2100 h, the first day she was found off the nest. By 2207 h she was moving from the nest and could not be located until 13 July when a faint signal was heard about 7 km from the nest. The radio signal was never heard again.

A male also appeared to have left the Basin when he abandoned his nest 17 days into the nestling period. A camera at the nest failed to register any nest visits the night after we first failed to locate his radio signal. Whether the owl was killed by a predator, which also destroyed the radio, or the bird left the region is unknown.

DISCUSSION

Our results reveal six important features about boreal owls at Chamberlain.

- Boreals used large seasonal areas for birds of their size.
- Differences in seasonal home range and movements indicate that resource requirements likely differ substantially between seasons, and at Chamberlain all those requirements are not met within one forest type.
- Use of space within seasonal home ranges was not uniform but concentrated in particular core areas.
- The owls did not maintain exclusive territories but overlapped broadly in seasonal home ranges.
- seasonal home ranges.
 5) During the period of declining prey resources (1984-1986), the distances moved between roosts tended to increase.
- The pattern ofyear to year occupancy indicated a mixture of nomadic and sedentary behavior.

Boreal owls used extremely large areas at Chamberlain. Despite our relatively small sample of relocations, estimated home ranges were larger than the 1-5 km² reported by Bondrup-Nielsen (1978) for boreal owls in Canada. Home range sizes for three males in Norway ranged between 94 and 226 ha (Jacobsen and Sonerud, these proceedings). Breeding season minimum convex polygon home range estimates for two Colorado male boreal owls (240 and 352 ha, minimum convex polygon) (Palmer 1986) were similar to summer home ranges calculated for two males nesting in our study area the same year (317 and 335 ha).

Home ranges reported for other species are also substantially smaller than Chamberlain boreal owls. Forsman et al. (1984) cited home ranges less than 2000 ha for spotted owls (*Strix occidentalis*), while Forbs and Warner (1974) reported 113 ha home ranges for Michigan saw-whet owls (*Aegolius acadicus*). Smith and Gilbert (1984) calculated 103 and 130 ha home ranges for Connecticut screech owls (*Otus asio*) radiotracked for five months (January -May). Boreal owl home ranges fell within the range reported for the large eagle owl (*Bubo bubo*) of Europe (1400-15,000 ha) (Mikkola 1983). The use of such a large area by a relatively small owl indicates either low resource abundance or that areas of resource concentration are widely dispersed.

In the heterogeneous habitat at Chamberlain, all resource requirements were not met by contiguous forest stands. Thus, seasonal requirements were satisfied in different areas. This feature is reflected in changes in location of home ranges from winter to summer accomplished by a shift to higher elevations in summer, and by the consistent trend for winter movements to be longer than summer. Also, the nest site was never centered in home ranges, rather, roosting and foraging habitat was chosen distant from the nest site. In Colorado, the home ranges of boreal owls shifted after the breeding season (Palmer 1986). Such a shift might also indicate changing resource needs and availability.

In winter, movements are likely primarily directed toward securing sufficient prey to meet daily maintainance costs. Specific areas may be used because they provide higher than average prey availability or lower the owls' average energy costs. Our observations indicate that daytime roost requirements play little role in dictating winter movements and home range. In summer, however, roost site requirements may be partly responsible for the shift to high elevations away from the nest site. Boreal owls are easily heat stressed; gullar fluttering by inactive roosting owls occurred at temperatures as low as 75° F. Prey availability might also play a role in choice of space during summer since the same cool, mature forests which provide optimum summer roosts also have the most abundant small mammal populations (unpublished data). Areas of abundant cavities were distant from the high elevation forests so that nest sites were usually distant from roosting and foraging areas.

The concentration of activity in small portions of seasonal home ranges in Chamberlain and

suggestion that forest stands varied in their value to boreal owls. Future analysis comparing the habitat within core areas to less used portions of the home range may indicate what features of forest structures and compositon are important in boreal owl habitat.

Territories of boreal owls in Europe (Solheim 1983) and Canada (Bondrup-Nielson 1978) have been characterized as simple breeding territories with no defense of foraging areas. Only a small region around the nest is defended as an exclusive area. Our information shows that boreal owl movements are not influenced by conspecifics and overlap among owls is substantial. In Norway, male boreal owls averaged 56% overlap (Jacobsen and Sonerud, these proceedings). Palmer (1986) also found two male boreal owls overlapping as much as 98 percent in early summer. Defense of the large foraging areas used by the owls would be difficult if not impossible.

From 1984-1986, during a period of declining small mammal abundance, home range size tended to increase as well as the length of day to day movements. Faced with lower prey availability, two basic strategies may be employed. First, the owls may conserve energy through reduced foraging activity and/or reproductive expenditure. An alternative strategy is to increase foraging effort at the expense of other activities. Increased activity may make the owls more vulnerable to predation. During winter, a majority of the energy expenditure is for self maintainance. Because boreal owls are relatively small birds, they cannot rely on accumulated reserves for extended periods. A strategy of energy conservation, therefore, is not feasible. Instead, the owls appeared to search over progressively larger areas as prey resources declined.

During summer, energy expenditure may be directed toward reproduction as well as self maintainance. The range of strategies to cope with reduced prey is, therefore, increased. Breeding efforts may range from failure to initiate nesting through raising a large brood, with corresponding variation in energy expenditure. At Chamberlain, the number of calling owls decreased and frequency of nest abandonment increased as prey resources declined indicating a reduction in reproductive expenditure. In addition, summer home ranges and daily movements increased from 1984-1986.

Populations of boreal owls vary in the degree of site tenacity or nomadism which they exhibit. In Europe, there is a general trend for increased nomadism in more northern populations (Korpimaki 1986). Korpimaki (1986) found that within Finland the degree of nomadism was positively correlated with winter snow depth. Lundberg (1979) hypothesized that due to the conflicting pressures of food stress favoring nomadism and nest site scarcity favoring site tenacity, the movement pattern of male and female boreal owls differ. He hypothesized that males would exhibit site tenacity and females nomadism. Lundberg's reasoning finds support from theory and empirical evidence. The large potential clutch size of boreal owls and cyclic pattern of food production fit Anderssons's (1980) model for a species likely to exhibit nomadism. On the other hand, von Haartman (1968) showed that residency was favored by the increased reproductive output afforded by early nesting in cavity nesters. Wallin and Andersson (1981), Solheim (1983), Lofgren et al. (1986) and Korpimaki (1986) have demonstrated that boreal owls exhibit both site tenacity and nomadic tendencies. In the most intensive investigation, Lofgren et al. (1986) showed that males were site tenacious throughout a prey cycle whereas females were tenacious only during prey peaks.

Our owls also showed a mixed strategy of site tenacity and nomadism, but differences between sexes were not clear. Some males and females remained in the study area during a period of declining prey. Both sexes also exhibited nomadism during the same period. The only individual located far from the study area was a male, but several others disappeared from the area and were never relocated. In Colorado, Palmer (1986) also observed a tendency toward nomadism in both male and female owls.

Deep snow (0.5-2.0 m) which remains in our study area for five months each year and relatively low prey populations likely contribute to the nomadic character of the boreal owl population at Chamberlain. Winter prey scarcity may frequently force many owls to search elsewhere for food. Conversely, if prey populations fluctuate but do not exhibit a cyclic pattern, the tendency for nomadism should be reduced (Andersson 1980). Small mammals in the Rockies have not been shown to be cyclic. The conflicting forces of severe winter food scarcity but lack of a consistent cycle may be responsible for the mixed pattern of site tenacity and nomadism.

SUMMARY

The boreal owls we studied moved over large home ranges throughout the year. Within seasonal home ranges, the owls concentrated their activity in several core areas, frequently moving back and forth among preferred areas. The owls consistently shifted seasonal ranges, concentrating activity at higher elevations during summer months. Despite this shift to higher elevations during breeding, nest sites were all within the lower one third of the study area and were generally on the periphery of the home range. Although not conclusive, our data suggested that the owls used larger home ranges and moved further from one day to the next during a period of declining prey.

As indicated by other authors, we found no evidence of defense of foraging areas. Home ranges of owls overlapped extensively and male boreal owls were found roosting within 200 m of one another. A mixed pattern of sedentary and nomadic behavior was indicated by year to year movements.

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