J. Raptor Res. 34(2):93–101

HOME RANGE AND HABITAT USE BY THE LONG-EARED OWL IN NORTHWESTERN SWITZERLAND

FABIENNE HENRIOUX
Institut de Zoologie, Université de Neuchâtel, Emile-Argand 11, 2007 Neuchâtel, Switzerland

ABSTRACT.—The home ranges and hunting activities of 14 Long-eared Owls (*Asio otus*) were examined using radiotelemetry in an agricultural area of northwestern Switzerland from 1993–96 to determine the species' habitat requirements. Average home-range size was 980 ha and size was significantly correlated with the amount of the range that was inhabited by humans ($r_s = 0.88$, $P < 0.001$). Long-eared Owls used open fields without trees less than expected according to their availability and preferred wooded areas bordering on fields where they perched during the night. Flight activity patterns varied among seasons with rain, fog, and summer and spring winds decreasing flight activity.

KEY WORDS: *Long-eared Owl;* Asio otus; *habitat use; home range; activity; radiotelemetry; Switzerland.*

Rango de hogar y uso de habitat de *Asio otus* en el noroeste de Suiza

RESUMEN.—El rango de hogar y las actividades de caza de 14 *Asio otus* fueron examinados utilizando radiotelemetría en un área de agricultura del noroeste de Suiza desde 1993–1996 para determinar los requerimientos de habitat de la especie. El tamaño de rango de hogar promedio fue de 980 ha y su tamaño fue significativamente correlacionado con la cantidad de rango habitado por los humanos ($r_s = 0.88$, $P < 0.001$). Los buhos utilizaron campos abiertos sin árboles menos de lo esperado de acuerdo a su disponibilidad y prefirieron áreas boscosas al borde de los campos en donde se posaban durante la noche. Los patrones de actividad de vuelo variaron entre estaciones, con la lluvia, la niebla. Los vientos de verano y primavera hicieron disminuir la actividad de vuelo.

[Traducción de César Márquez]

The Long-eared Owl (*Asio otus*) typically nests in forested areas and forages in open habitats (Mikkola 1983, Cramp 1985). In Germany and the United States, some forms of agriculture have resulted in declines in nesting populations (Illner 1988, Bosakowski et al. 1989) but in rice-producing areas of Italy, Long-eared Owls breed successfully in farmland and, there, the population has recently increased (Galeotti et al. 1997). In this area, Long-eared Owls hunt mainly along treelines and edgebanks that border on rice fields. In Switzerland, the species has declined over the past 20 years (Zbinden and Biber 1989, Nötzli and Birrer 1998) and information on its habitat use in agricultural areas is prerequisite for the adoption of useful conservation plans.

Few data have been reported on home ranges of Long-eared Owls. Wijnandts (1984) recorded the home ranges of five owls tracked for <1 mo and Craig et al. (1988) described the home range and activity pattern of two nesting pairs. Galeotti et al. (1997) tracked seven owls during late winter and documented habitat use but, in general, data on hunting habitats are based only on analyses of diet composition (Getz 1961, Nilsson 1987). Information on the habitat requirements of Long-eared Owls is mostly limited to nest sites (Marks 1986, Nilsson 1987, Bull et al. 1989, Holt 1997).

The goal of my study was to investigate how Long-eared Owls exploit areas of intensive agriculture near Basse Broye, northwestern Switzerland. Previous work has shown that they prey mainly on common voles (*Microtus arvalis*) (Roulin 1996) and data on nest-site selection suggest that Long-eared Owls avoid areas inhabited by people and prefer dense forest edges (unpubl. data). In this paper, I present data on the home ranges and foraging habitat use of 14 Long-eared Owls radio-tracked over four years. I also describe the influence of meteorological conditions on foraging flights.

STUDY AREA

My study was carried out from 1993–96 in a 46-km² area in Basse Broye region, northwestern Switzerland (46°52′N, 6°56′E). The landscape is flat with small hills ranging in elevation from 430–520 m. The climate is characterized by cold, dry winters with average winter temperatures and precipitation of 1.4°C and 57.1 mm/mo, respectively. Summers are hot with average temperatures and precipitation of 18°C and 96.6 mm/mo, respectively. Annual average temperatures are 9.5°C and total annual precipitation averages 913 mm.

Open fields cover 78.8% of the total area. In 1969, natural grassland represented a quarter of the agricultural production of the area but it decreased to only 10.9% in 1996 (Federal Office of Statistics). In 1996, 68.1% of the area was devoted to crops such as cereals, tobacco, beets and potatoes. The study area encompasses the south bank of the lake of Neuchâtel which is covered by marshland (4.5% of the study area). Forests represent 7.4% of the total area and areas inhabited by people represent only 9.3% of the area.

METHODS

Bow-nets were used to capture adult Long-eared Owls at night during the nonbreeding season (Bub 1991). A live brown mouse (*Mus musculus*) was used as a lure and was set in a cage with dry leaves as litter to make noise to attract owls. Traps were checked every 30 min. Each trapped owl was fitted with a numbered leg band (standard Swiss Ornithological Station aluminum leg band), and 23 were fitted with transmitters. Six transmitters were back-pack types (Televilt SA, Stora, Sweden; type TXP-2, 16 g) attached using a criss-cross harness (Smith and Gilbert 1981). Seventeen were tail-mounted (15 from Biotrack Ltd, Wareham, U.K., type SS-2, 4 g; one from Holohil, Ontario, Canada, Type RI-2C, 5.8 g; and one from AVM Instrument Co., Livermore CA, USA, Type SM1-H, 5 g) (Kenward 1978). Radio signals were detected with a Yaesu FT 290 receiver (Wagner, Köhn, Germany). Owls were first located using a nondirectional antenna. Bearings were then determined by triangulation from two or more points using a two-element directional antenna. Signals were usually received from distances as great as 1 km. When possible, sex of breeders was determined according to courtship behavior.

Each radio-tracked owl was located once a day and on two nights each week. I checked whether owls were active during the day by continuously tracking five owls over a period of 17 d. Night data were recorded at 15-min intervals during two tracking periods from half an hour before dusk to midnight and from midnight to half an hour after dawn. To avoid biases after owls were captured, tracking began 1 wk after capture (McCrary 1981).

Most bearings were taken from a distance of <200 m and their accuracy was tested by estimating the location of hidden transmitters. My accuracy was sufficient to allow use of a 50 × 50 m grid as a basis for location data.

I lost the signals of nine owls soon after their capture. After unsuccessfully searching for them from an aircraft 15 km around the last daytime perch, I concluded that they had either left the area or their transmitters had failed.

Home-range size and centers of activity were computed with Ranges V (Kenward and Hodder 1996). Maximum home ranges at night were estimated with 100% minimum convex polygon (100% MCP, Mohr 1947) to allow comparisons with earlier studies (Wijnandts 1984, Galeotti et al. 1997). Levels of autocorrelation were assessed as recommended by Swihart and Slade (1985) and found to be negligible at the 75-min intervals used in analyses. Incremental plots were used to determine the number of locations required to calculate the home-range size Six home-range areas became asymptotic at about 15 fixes but the area of two of them increased again at 60 fixes. Other home ranges did not reach an asymptote. Home-range size was thus calculated on the basis of all fixes and data sets with <15 fixes were excluded from the analysis. Multirange utilization plots indicated an inflection point at 60% of fixes (Harris et al. 1990, Kenward and Hodder 1996). Therefore, I estimated core areas using 60% minimum convex polygons, the center of activity being the harmonic center (Dixon and Chapman 1980, Spencer and Barrett 1984). Home ranges were estimated during the breeding period (March–July), post-fledging period (August–September) and common-roost period (October–February) (Wijnandts 1984, Cramp 1985).

For analysis of habitat use, I divided the landscape into seven categories: open fields (>30 m from a wooded area), woodlands (>30 m from open fields), forest edges (defined as a strip of 30 m inside and 30 m outside of forest borders), hedges (or tree lines), inhabited areas (villages or isolated buildings), copses (wooded areas < 1 ha) and marshlands. Habitat composition was counted from a 50 × 50 m grid superimposed on a 1:25 000 topographic maps (Federal Office of Topography) and ground-truthed in the field. Each cell was then indexed according to its predominant habitat. Relative use of habitat type was compared with the amount of each type first within the home range and second within the study area with goodness-of-fit tests. Preference and avoidance of different habitat types was ascertained using Bonferroni Z statistics (Neu et al. 1974, Byers et al. 1984, Alldredge and Ratti 1986). Analysis was performed first with all fixes and second with flight locations only.

The night activity period was defined as the elapsed time between the time an owl was last located at a daytime perch in the evening and the time it was first recorded at a daytime perch the next morning (Forbes and Warner 1974, Wijnandts 1984). Transmitters contained posture switches, so signals indicated when birds were in flight. Flight activity was expressed as the percent of flying locations per hour. Activity analyses were performed seasonally: spring (March–May), summer (June–August), autumn (September–November) and winter (December–February).

RESULTS

Owing to transmitter failures, molt of tail feathers, death or permanent emigration from the study area, only 14 out of 23 owls had sufficient locations for analysis (two females, six males and six owls of unidentified sex) (Table 1). Recapture of owl H1 one year after it was instrumented indicated no sign of either feather wear or skin abrasion. Owls were monitored 20–249 d. Removal of location points to reduce autocorrelation resulted in a total of 869 locations that could be used in analyses of home ranges and habitat use.

Home Range and Habitat Use. Long-eared Owls

Table 1. Home range of radio-tagged Long-eared Owls in the Basse Broye Region of Switzerland from 1993–96. M = male; F = female; ? = unidentified sex.

Owl	Sex	Tracking Period	Total No. of Locations	No. of Independent Locations	Home-Range Area (ha)[a] 100% MCP[b]	60% MCP	Range Span[c] (m)
H1	?	930702–931115	332	73	766	292	6104
H2	?	930715–930830	100	20	544	93	5055
H4	?	940104–940124	111	24	97	38[d]	1553
H6	M	940413–940608	228	52	1017	16[d]	4904
H7	M	941011–950406	515	117	295	88	3043
H8	F	950205–950502	104	37	128	1[d]	1595
H9	M	950206–950713	210	80	829	338[d]	6435
H10	M	950208–950720	219	78	417	155[d]	3453
H12	?	950803–960409	225	62	1559	484	6261
H14	?	950830–951002	70	26	161	42[d]	1866
H15	M	951023–960621	483	131	1629	541[d]	7349
H16	F	951031–960609	121	45	3174	77[d]	10048
H17	M	951203–960718	275	71	1916	1445	7669
H23	?	960813–961120	233	53	1188	577[d]	5882

[a] Based on independent locations.
[b] MCP = minimum convex polygon.
[c] Calculated from 100%.
[d] Core areas comprise the daytime perch.

Table 2. Variation of home-range size of Long-eared Owls among breeding periods in the Basse Broye region, Switzerland from 1993–96. N = number of telemetry locations; M = male; F = female; ? = unidentified sex.

	Sex	Breeding Period N	Breeding Period 100% MCP (ha)	Common Roost Period N	Common Roost Period 100% MCP (ha)	Post-fledging Period N	Post-fledging Period 100% MCP (ha)
H1	?	18	221	21	386	34	202
H2	?					14	182
H4	?			24	97		
H6	M	52	1017				
H7	M	16	239	101	233		
H8	F	18	24	19	83		
H9	M	71	829				
H10	M	58	417	20	121		
H12	?					52	1075
H14	?					26	161
H15	M	52	1188	79	1258		
H16	F	19	12	26	3174		
H17	M	36	1322	35	1070		
H23	?			16	357	37	1174
Mean			585.4		753.2		558.8
SD			509.5		1003.6		517.8

occupied home ranges that varied in size from 97 to 3174 ha ($\bar{x}$ = 979.9 ± 864.2, ±SD) (Table 1). All ranges were elongated and the range span averaged 5086.9 ± 2529.8 m. I calculated one core area for each owl. It covered in average 298.9 ± 386.9 ha. Core areas included daytime perches of nine owls, six of which were breeders. There was no significant correlation between home-range size and number of fixes (Spearman rank correlation: $r_s = 0.38$; $P = 0.18$).

I detected no significant differences in home-range size between periods (Kruskall-Wallis test: $\chi^2 = 0.38$, df = 2, $P = 0.83$) (Table 2). Females had smaller home ranges than males only during the breeding period (Mann-Whitney U test: $U = 0$, $P = 0.04$). All range sizes were positively correlated with proportions of areas inhabited by humans (Spearman rank correlation: $r_s = 0.88$; $P < 0.001$). No other habitat characteristic influenced home-range sizes ($P > 0.05$).

When testing the difference between the proportion of locations in each habitat and habitat availability in both the study area and the home range, habitat use by 11 of the 14 Long-eared Owls varied significantly from availability ($\chi^2 = 39.9$, df = 6, $P < 0.001$) (Table 3) with owls avoiding open

Table 3. Percent habitat composition of study area and home ranges (HR), and percent of telemetry locations (TL) in each habitat of Long-eared Owls tracked from 1993–96 in the Basse Broye region of Switzerland. + preferred, − avoided, Bonferroni confidence intervals, $P < 0.05$/number of habitat categories in the home range.

	OPEN FIELD		FOREST		FOREST EDGE		HEDGE		COPSE		MARSHLAND		INHABITED AREA	
	HR	TL	HR	TL	HR	TL	HR	TL	HR	TL	HR	TL	HR	TL
H1	70.9	32.9−	4.3	0.0	8.0	39.7+	0.4	2.7	0.7	1.4	1.1	13.7+	14.6	9.6
H2	42.9	55.0	40.6	15.0	10.6	20.0	0.0	10.0	0.0	0.0	—	—	5.9	0.0
H4	90.0	29.2	2.2	0.0	5.9	0.0	0.4	4.2	1.3	54.1	—	—	0.2	12.5
H6	85.3	46.2−	1.7	0.0	4.4	51.9+	0.2	1.9	—	—	—	—	8.4	0.0
H7	78.9	38.5−	2.4	0.0	2.4	2.6	0.5	9.4+	1.6	29.9+	6.7	8.5	7.5	11.1
H8	97.2	2.7−	—	—	—	—	2.7	40.5+	0.1	56.8+	—	—	—	—
H9	84.3	26.3−	1.6	0.0	7.7	46.2+	1.1	11.3+	—	—	0.0	5.0+	5.3	11.2
H10	93.6	26.9−	0.1	0.0	1.6	0.0	3.0	56.4+	1.1	15.4+	—	—	0.6	1.3
H12	80.3	54.9−	4.5	1.6	6.1	24.2+	0.2	12.9+	0.2	3.2	0.0	1.6	8.7	1.6
H14	98.8	65.4	—	—	—	—	0.0	26.9	0.6	7.7	—	—	0.6	0.0
H15	75.7	19.1−	5.3	0.0−	7.7	41.2+	0.2	28.2+	0.4	9.2+	0.0	0.8	10.7	1.5−
H16	75.9	6.7−	1.6	4.4	3.5	64.5+	0.6	22.2+	0.3	0.0	0.0	0.0	18.1	2.2−
H17	76.4	42.2−	1.3	0.0	4.4	21.1+	0.1	15.6+	0.6	2.8	0.5	2.8	16.7	15.5
H23	84.3	43.4−	2.4	15.1+	4.7	20.8+	0.3	11.3+	0.5	7.5+	—	—	7.8	1.9−
Median	82.3	35.7	2.3	0.0	5.3	22.7	0.4	12.1	0.6	7.6	0.3	2.8	7.8	1.9
Study area	75.9		3.4		5.4		1.0		0.5		4.5		9.3	

fields and preferring wooded areas bordering on fields (Fig. 1). Eight owls selected forest edges, nine selected hedges and five selected copses. Forests were rarely used (0–15.1% of locations) but one owl used forests significantly more than expected and another one used them less (Table 3). Two owls used marshlands more than expected and three avoided inhabited areas. The same pattern of habitat use was found when only flight locations were considered, but differences were less significant. Seven owls showed a habitat preference ($\chi^2 = 17.1$, df = 6, $P < 0.004$; Fig. 2), six avoided open fields and five preferred wooded areas bordering on fields.

Activity and Flight Period. Night activity began an average of 38 ± 17 min after local sunset and ended 53 ± 33 min before local sunrise. In all seasons, there were significant positive correlations between the time of dusk and the onset of nightly activity (Table 4). Except in winter, the same significant positive relationship was found between the time of dawn and the cessation of nightly activity.

Twenty-eight percent of the nocturnal locations were recorded when the owls were in flight. The patterns in flight behavior indicated that the owls flew throughout the night (Fig. 3). There were slight seasonal differences with owls flying mainly between dusk and 2300 H in spring and summer, from dusk to 2200 H and 0200 H to dawn in autumn, and from midnight to 0300 H in winter.

Precipitation and fog significantly limited flight activity (Table 5). Wind limited flight activity in spring and summer but increased it in winter. In spring, flying also increased with increasing temperatures.

DISCUSSION

The home ranges of the owls I studied were intermediate in size when compared to those reported by Wijnandts (1984) and Galeotti et al. (1997). However, they were more variable in size than previously reported perhaps due to individual variation and variability in environmental factors (Marquiss and Newton 1981, Newton 1986). During the breeding season, females occupied areas restricted to the vicinity of their nests, which was in accordance with Craig et al. (1988). The largest range was measured for a 1-yr old female (H16) banded as a nestling the year before that returned to its natal area to breed. Male Long-eared Owls are known to breed as yearlings close to their natal sites (Marks et al. 1994), but, to my knowledge, this is the first documentation for a female.

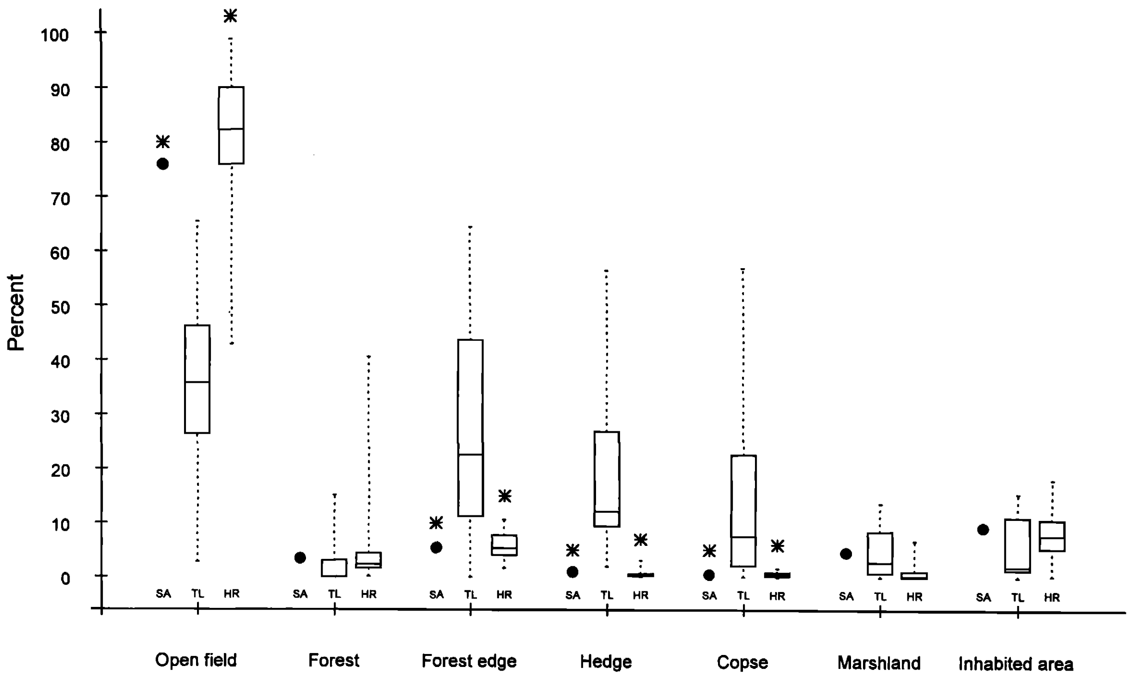

Figure 1. Habitat use of Long-eared Owls in the Basse Broye region of Switzerland estimated by comparison between percent of telemetry locations (TL: boxplot) and availability of habitats in the study area (SA: plot) and home ranges (HR: boxplot). Asterisk indicates significant difference between TL and HR or SA obtained for a minimum of five owls (Bonferroni confidence intervals: $P < 0.05$/number of habitat variables).

Higher prey availability can decrease home range size. (Kenward 1982, Zabel et al. 1995, Marzluff et al. 1997). This could explain why eight of the owls I tracked had home ranges that continuously got larger. Perhaps, the patchy distribution of their primary prey species, the common vole, forces some owls to constantly hunt new areas (Goszczynski 1981, Korpimäki 1992, F. Henrioux unpubl. data). Habitat can also influence home range size of raptors (Marquiss and Newton 1981, Newton 1986, Babcock 1995, Redpath 1995). I found home range size to increase with increased amounts of inhabited areas and they avoided inhabited areas both as nesting and as foraging sites. No other relationship was found between the size of home ranges and the amount of other habitats but this may have been due to the fact that there was little difference in the availability of the habitats among the home ranges (Zabel et al. 1995).

My analyses indicated that Long-eared Owls avoided uniform habitats like open fields without trees and preferred forest edges, copses and hedges. As in Italy (Galeotti et al. 1997), the availability of this type of habitat has decreased in Switzerland as intensive agriculture has eliminated isolated trees and fences in open fields. Based on visual observations and analyses of diet composition, Long-eared Owls were known to hunt in open fields (Getz 1961, Glutz von Blotzheim and Bauer 1980, Mikkola 1983, Cramp 1985, Marks et al. 1994), the edges of which are prime foraging habitat.

My activity observations agreed with those of Wijnandts (1984) and Galeotti et al. (1997) who found that Long-eared Owls mostly perched during the night, but they were inconsistent with those of Glue and Hammond (1974) and Marks et al. (1994) who found that Long-eared Owls hunted mainly in flight. Perch-and-wait hunting is common in raptors (Kenward 1982, Watson 1986, Plumpton and Andersen 1997) and I observed Long-eared Owls hunting from perches several times at the edges of open fields as they waited for common voles. Hunting occurred mainly after sun-

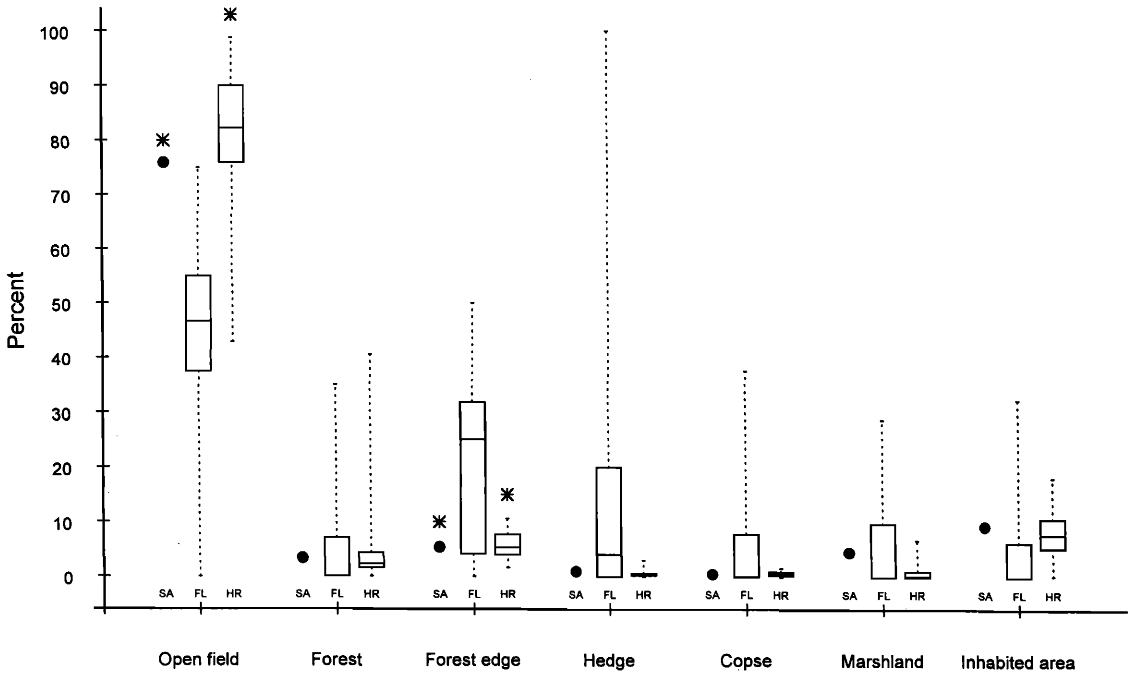

Figure 2. Habitat use in flight by Long-eared Owls in the Basse Broye region of Switzerland estimated by comparison between percent of flight locations (FL: boxplot) and availability of habitats in the study area (SA: plot) and home ranges (HR: boxplot). Asterisk indicates significant difference between FL and HR or SA obtained for a minimum of five owls (Bonferroni confidence intervals: $P < 0.05$/number of habitat variables).

set and before sunrise, so the owls I studied were nocturnal like other Long-eared Owls (Glass 1971, Moritz 1979, Wijnandts 1984, Marks et al. 1994, Galeotti et al. 1997). In spring, summer and winter, they flew at all times of the night but, in autumn, they became less active around midnight. Such periods of inactivity have been reported elsewhere and may be associated with the coldest nighttime temperatures and times when prey are least active in autumn (Glutz von Blotzheim and Bauer 1980, Wijnandts 1984).

Wijnandts (1984) found that flight was reduced during precipitation and fog. In addition, I found that wind was an important meteorological variable

Table 4. Time intervals between onset time of activity and sunset, and sunrise and cessation time, as taken for nocturnal activity period of Long-eared Owls in the Basse Broye region of Switzerland. Spearman correlation coefficients (r_s) are given between onset and cessation times of activity and sunset and sunrise.

	SPRING	SUMMER	AUTUMN	WINTER	ALL YEAR
Mean interval between activity onset and sunset	32 min	41 min	38 min	44 min	38 min
SD	14 min	17 min	11 min	26 min	17 min
r_s	0.91	0.94	0.95	0.64	0.98
P	<0.001	<0.001	<0.001	<0.005	<0.001
Mean interval between sunrise and end of activity	47 min	51 min	48 min	70 min	53 min
SD	30 min	19 min	34 min	46 min	33 min
r_s	0.84	0.77	0.65	−0.22	0.9
P	<0.001	<0.001	<0.005	>0.05	<0.001

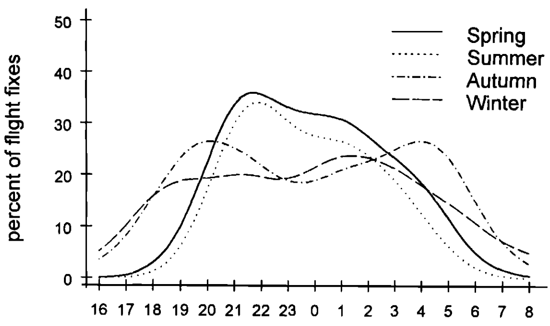

Figure 3. Seasonal flight activity pattern of Long-eared Owls tracked in the Basse Broye region of Switzerland from 1993–96.

that reduced flight activity in spring and summer, but favored it in winter. During winter, long windy periods may force owls to move more often causing them to hunt more in flight.

ACKNOWLEDGMENTS

I am grateful to L.F. Bersier and C. Mermod who kindly read the manuscript. I am indebted to J.M. Weber and C. Mermod who provided the scientific assistance for the project. For advice and encouragement throughout the project, I thank the staff of the Institute of Zoology, University of Neuchâtel and, in particular, N. Ferrari, M. Liberek, J.S. Meia and S. Meyer. I wish to thank the Broyard Group for Ornithological Research and, in particular, T Blanc and C. Henninger for their reports on owl sighting and for their advice on field methods. The Federal Office of Environment, Forests and Landscapes, the Conservation of the Fauna of the Canton of Vaud, and Pro Natura financially supported the study.

LITERATURE CITED

ALLDREDGE, J.R. AND J.T. RATTI. 1986. Comparison of some statistical techniques for analysis of resource selection. *J. Wildl. Manage.* 50:157–165.

BABCOCK, K.W. 1995. Home range and habitat use of breeding Swainson's Hawks in the Sacramento valley of California. *J. Raptor Res.* 29:193–197.

BOSAKOWSKI, T., R. KANE AND D.G. SMITH. 1989. Decline of the Long-eared Owl in New Jersey. *Wilson Bull.* 101: 481–485.

BUB, H. 1991. Bird trapping and bird banding. Cornell Univ. Press, Ithaca, NY U.S.A.

BULL, E.L., A.L. WRIGHT AND M.G. HENJUM. 1989. Nesting and diet of Long-eared Owls in conifer forests, Oregon. *Condor* 91:901–912.

BYERS, C.R., R.K. STEINHORST AND P.R. KRAUSMAN. 1984. Clarification of a technique for analysis of utilization-availability data. *J. Wildl. Manage.* 48:1050–1053.

Table 5. Influence of meteorological factors on flight activity of Long-eared Owls in the Basse Broye region of Switzerland. N = number of total locations; %: percent of flight locations.

	SPRING		SUMMER		AUTUMN		WINTER		ALL YEAR	
	N	%	N	%	N	%	N	%	N	%
Precipitation										
No rain	698	35	605	31	854	28	622	21	2779	29
Rain	141	24	14	50	123	15	115	25	393	22
χ^2	6.2 (P = 0.01)		2.3 (P = 0.1)		9.4 (P = 0.002)		1.2 (P = 0.3)		6.8 (P = 0.009)	
Wind										
No wind	507	35	457	34	592	26	285	13	1841	29
Wind	332	30	162	23	385	26	452	27	1331	27
χ^2	17.3 (P = 0.002)		10.4 (P = 0.02)		2.0 (P = 0.7)		29.9 (P < 0.001)		12.3 (P = 0.02)	
Fog										
No fog	813	0.33	619	0.32	868	0.28	631	0.24	2931	0.29
Fog	26	0.23	0	0	109	0.13	106	0.08	241	0.12
χ^2	1.2 (P = 0.3)		—	—	11.0 (P < 0.001)		14.2 (P < 0.001)		34.4 (P < 0.001)	
Temperature										
−9 to 0°C	138	0.27	—	—	80	0.28	450	0.2	668	0.23
1 to 10°C	450	0.27	80	0.25	502	0.25	287	0.23	1319	0.25
11 to 20°C	237	0.49	432	0.32	395	0.28	—	—	1064	0.34
21 to 30°C	14	0.29	107	0.34	—	—	—	—	121	0.33
χ^2	35.3 (P < 0.001)		1.9 (P = 0.4)		1.2 (P = 0.5)		0.7 (P = 0.4)		36.5 (P < 0.001)	

CRAIG, E.H., T.H. CRAIG AND L.R. POWERS. 1988. Activity patterns and home-range use of nesting Long-eared Owls. *Wilson Bull.* 100:204–213.

CRAMP, S. [ED.]. 1985. The birds of western Paleartic. Vol. 4. Oxford Univ. Press, Oxford, U.K.

DIXON, K.R. AND J.A. CHAPMAN. 1980. Harmonic mean measure of animal activity areas. *Ecology* 61:1040–1044.

FORBES, J.E. AND D.W. WARNER. 1974. Behavior of a radio-tagged Saw-Whet Owl. *Auk* 91:783–795.

GALEOTTI, P., G. TAVECCHIA AND A. BONETTI. 1997. Home-range and habitat use of Long-eared Owls in open farmland (Po Plain, northern Italy), in relation to prey availability. *J. Wildl. Res.* 2:137–145.

GETZ, L.L. 1961. Hunting areas of the Long-eared Owl. *Wilson Bull.* 73:79–82.

GLASS, M.L. 1971. Some remarks on the evening departure during winter of the Long-eared Owl (*Asio otus*). *Dansk Ornithologisk Forenings Tidsskrift.* 65:173–179.

GLUE, D.E. AND G.J. HAMMOND. 1974. Feeding ecology of the Long-eared Owl in Britain and Ireland. *Br. Birds* 67:361–367.

GLUTZ VON BLOTZHEIM, U.N. AND K.M. BAUER. 1980. Handbuch der Vögel Mitteleuropas, Band 9. Strigiformes. Akademische Verlagsgesellschaft, Wiesbaden, Germany.

GOSZCZYNSKI, J. 1981. Comparative analysis of food of owls in agrocenoses. *Ekol. Polska* 29:431–439.

HARRIS, S., W.J. CRESSWELL, P.G. FORDE, W.J. TREWHELLA, T. WOOLLARD AND S. WRAY. 1990. Home-range analysis using radio-tracking data—a review of problems and techniques particularly as applied to the study of mammals. *Mammal Rev.* 20:97–123.

HOLT, D.W. 1997. The Long-eared Owl (*Asio otus*) and forest management: a review of the literature. *J. Raptor Res.* 31:175–186.

ILLNER, H. 1988. Langfristiger Rückgang von Schleiereule *Tyto alba,* Waldohreule *Asio otus,* Steinkauz *Athene noctua* und Waldkauz *Strix aluco* in der Agrarlandschaft Mittelwestfalens 1974–1986. *Vogelwelt* 109:145–151.

KENWARD, R.E. 1978. Radio transmitters tail-mounted on hawks. *Ornis Scand.* 9:220–223.

———. 1982. Goshawk hunting behaviour, and range size as a function of food and habitat availability. *J. Anim. Ecol.* 51:69–80.

——— AND K.H. HODDER. 1996. Ranges V. An analysis system for biological location data. Institute of Terrestrial Ecology, Wareham, U.K.

KORPIMÄKI, E. 1992. Diet composition, prey choice, and breeding success of Long-eared Owls: effects of multiannual fluctuations in food abundance. *Can. J. Zool.* 70:2373–2381.

MARKS, J.S. 1986. Nest-site characteristics and reproductive success of Long-eared Owls in southwestern Idaho. *Wilson Bull.* 98:547–560.

———, D.L. EVANS AND D.W. HOLT. 1994. Long-eared Owl (*Asio otus*). Pages 1–24 *in* A. Poole and F. Gill [EDS.], The birds of North America. Acad. Nat. Sci., Philadelphia, PA and Am. Ornithol. Union, Washington, DC U.S.A.

MARQUISS, M. AND I. NEWTON. 1981. A radio-tracking study of the ranging behaviour and dispersion of European Sparrowhawks *Accipiter nisus. J. Anim. Ecol.* 51· 111–113.

MARZLUFF, J.M., B.A. KIMSEY, L.S. SCHUECK, M.E. MCFADZEN, M.S. VEKASY AND J.C. BEDNARZ. 1997. The influence of habitat, prey abundance, sex, and breeding success on the ranging behavior of Prairie Falcons. *Condor* 99:567–584.

MCCRARY, M.D. 1981. Effects of radio-tagging on the behavior of Red-shouldered Hawks. *North Am. Bird Bander* 6:138–141.

MIKKOLA, H. 1983. Owls of Europe. T. & A.D. Poyser Ltd, Calton, U.K.

MOHR, C.O. 1947. Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* 37. 223–249.

MORITZ, D. 1979. Zur Tagesaktivität der Waldohreule (*Asio otus*). *Orn. Mitt.* 6:137–139.

NEU, C.W., C.R. BYERS AND J.M. PEEK. 1974. A technique for analysis of utilization-availability data. *J. Wildl Manage.* 38:541–545.

NEWTON, I. 1986. The Sparrowhawk. T. & A.D. Poyser Ltd, Calton, U.K.

NILSSON, I.N.. 1987. The relationships between habitat, food and reproductive output in Long-eared Owl *Asio otus* and Tawny Owl *Strix aluco* in southern Sweden *Acta Reg. Soc. Sci. Litt. Gothoburgensis. Zoologica* 14:124–130.

NÖTZLI, F. AND S. BIRRER. 1998. Hibou moyen-duc. Pages 196–197 *in* H. Schmid, R. Luder, B. Naef-Daenzer, R Graf and N. Zbinden [EDS.], Atlas des oiseaux nicheurs de Suisse. Distribution des oiseaux nicheurs en Suisse et au Liechtenstein en 1993–1996. Station Ornithologique Suisse, Sempach, Switzerland.

PLUMPTON, D.L. AND D.E. ANDERSEN. 1997. Habitat use and time budgeting by wintering Ferruginous Hawks *Condor* 99:888–893.

REDPATH, S.M. 1995. Impact of habitat fragmentation on activity and hunting behavior in the Tawny Owl, *Strix aluco. Behav. Ecol.* 6:410–415.

ROULIN, A. 1996. Alimentation hivernale de la chouette effraie (*Tyto alba*), du hibou moyen-duc (*Asio otus*), du busard Saint-Martin (*Circus cyaneus*) et du faucon crécerelle (*Falco tinnunculus*). Bulletin de la Société Vaudoise des Sciences Naturelles 84:19–32.

SMITH, D.G. AND R. GILBERT. 1981. Backpack radio transmitter attachment success in screech owls (*Otus asio*) *North Am. Bird Bander* 6:142–143.

SPENCER, W.D. AND R.H. BARRETT. 1984. An evaluation of the harmonic mean measure for defining carnivore activity areas. *Acta Zool. Fennica* 171:255–259.

SWIHART, R.K. AND N.A. SLADE. 1985. Testing for independence of observations in animal movements. *Ecology* 66:1176–1184.

WATSON, J.W. 1986. Range use by wintering Rough-legged Hawks in southeastern Idaho. *Condor* 88:256–258.

WIJNANDTS, H. 1984. Ecological energetics of the Long-eared Owl (*Asio otus*). *Ardea* 72:1–92.

ZABEL, C.J., K. MCKELVEY AND J.P. WARD, JR. 1995. Influence of primary prey on home-range size and habitat-use patterns of Northern Spotted Owls (*Strix occidentalis caurina*). *Can. J. Zool.* 73:433–439.

ZBINDEN, N. AND O. BIBER. 1989. La situation de l'avifaune en Suisse dans les années 1980. Station Ornithologique Suisse, Sempach, Switzerland.

Received 1 May 1999; accepted 31 January 2000