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Habitat selection by barbastelle bats (*Barbastella barbastellus*) in the Swiss Alps (Valais)

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Abstract

Recent faecal analyses have shown that barbastelle bats *Barbastella barbastellus* are highly specialized moth predators. The predominance of moths (> 99% by volume) in their diet both in wooded areas of the Swiss Alps and in denuded steppe areas of Central Asia further suggests that this narrow diet does not stem from a highly specialized habitat selection, but merely from peculiar species-specific foraging constraints. Non-opportunistic predators relying on a few prey types must find areas providing their basic prey in abundance. Using radiotracking, habitat selection was investigated in a population of barbastelle bats inhabiting xeric forests in the Swiss Alps. In particular, I tested the prediction that the biologically most productive areas within the forest are exploited in priority. Eleven individuals were radiotracked from June through to October 1992, and in June 1993. The home range (59 ha) of the overall radiotracked population was divided in 236 cell units of 0.25 ha each. Within each cell, habitat and vegetation structure was described using 19 environmental variables. Habitat selection by the bats was investigated through stepwise regression analysis, which retained 11 variables showing a significant positive relationship with habitat use. The four variables accounting for 31% of the overall variance were: litter thickness, percentage of shrub layer cover, percentage of pine tree cover, and circumference of oak trunks. The results showed a clear preference by barbastelles bats for richly structured forests, and an avoidance of open woodland on stony outcrops and rocky slopes. This confirms that the biologically most productive parts of the forest were exploited in priority.

Key words: habitat selection, barbastelle bats, Swiss Alps, xeric forests, prey

INTRODUCTION

Over much of western Europe the barbastelle *Barbastella barbastellus* is considered to be one of the most endangered and rarest bat species (Stebbings, 1988; Schober & Grimmberger, 1989; Rydell & Bogdanowicz, 1997). These are probably the main reasons why few ecological studies have been carried out on this poorly understood mammal (see review in Rydell & Bogdanowicz, 1997). Surveys in winter roosts were made mainly in Poland and Slovakia (Urbanczyk, 1983; Uhrin, 1994–95) and Germany (Hoehl, 1960), as well as one in a breeding colony in Germany (Richarz, 1989). Previous faecal analyses in *B. barbastellus* have established a very narrow diet consisting of 99% Lepidoptera. Samples of food availability in the foraging area were made up mainly of Microlepidoptera suggesting that barbastelles bat could prey on smaller tympanate moths (Sierro & Arlettaz, 1997). Here, I attempt to understand the causes of the drastic decline of the barbastelle in western Europe during the twentieth century by investigating habitat use in a small population in Switzerland.

MATERIAL AND METHODS

Habitat use by barbastelles was investigated between June and October 1992, and in June 1993. The bats were mist-netted at the entrance of 2 abandoned magnetite mines. Twelve radiotracking sessions were carried out on 11 individuals, 8 males, and 3 females, from dusk to dawn. Bats were tracked on foot by a single observer equipped with a radio-receiver (Yaesu FT-290RII adapted by Karl Wagener, Herwarthstrasse 22, D-5000 Köln 1, Germany) and a H antenna. Bats were fitted with small glue-on (cyanoacrylate) radiotransmitters (BD-2B; 0.65–0.68 g; Holohil Systems Ltd., Ontario, Canada). Because of topographic constraints, the standard tag had to be modified for our field requirements: life span was reduced to 7 days to increase the detection range up to 1.5 km. The 'homing-in on the animal' method (White & Garrott, 1990) was used to locate

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Table 1. The 19 environmental variables considered in the habitat selection analysis

Variables	Unit
Coord *x*	Longitude
Coord *y*	Latitude
Altitude	metre
Litter thickness	cm
Height of herbaceous layer	1–3 (relative scale)
Herbaceous cover	0–4: 0 = 0–5%; 1 = 5–25%; 2 = 25–50%; 3 = 50–75%; 4 = 75–100%
Shrub layer cover	0–4: 0 = 0–5%; 1 = 5–25%; 2 = 25–50%; 3 = 50–75%; 4 = 75–100%
Arborescent cover	0–4: 0 = 0–5%; 1 = 5–25%; 2 = 25–50%; 3 = 50–75%; 4 = 75–100%
Circumference of pine trunks	Average value of 10 trees chosen randomly
Circumference of oak trunks	Average value of 10 trees chosen randomly
Circumference of spruce trunks	Average value of 10 trees chosen randomly
Circumference of larch trunks	Average value of 10 trees chosen randomly
Circumference of dominant deciduous tree trunks	Average value of 10 trees chosen randomly
Pine cover	% (projected on the ground)
Spruce cover	% (projected on the ground)
Larch cover	% (projected on the ground)
Oak cover	% (projected on the ground)
Deciduous tree cover	% (projected on the ground)
Lichen on trunks	1–3 (relative scale)

the bats in the field. Field data were recorded on a Walkman tape-recorder equipped with a tie-microphone. In order to facilitate location of the tracked individuals in the field, a piece of reflector tape (Scotchlite^{TM}) was glued on the upper side of transmitters. This facilitated direct visual observations through a night scope (BIG III, Wild-Leitz@ Leica SA, rue de Lausanne 60, CH-1020 Renens, Switzerland) coupled with an infrared halogen lamp. Very bright 8×56 Habicht binoculars were used in the twilight for watching the first foraging flights of emerging barbastelles. Regular ultrasound listenings with a bat detector Mini II (Summit, 6 Key Hill Drive, Hockley, Birmingham, B18 5NY, U.K.) confirmed visual contacts. Because the mine is only a temporary summer roost for males and a mating place in autumn, females are rarely found there (sex-ratio 80% biased towards the males, $n = 49$). All radiotracking sessions concerned a single individual at a time, except once, when a male and a subadult female were radiotracked during 2 nights alternately. The aim was to take the opportunity of a female capture for discovering a possible breeding colony. The MC Paal package (*Micro-computer Programs for the Analysis of Animal Locations*; M. Stüwe, Front Royal, U.S.A., v. 1.2.1985), through its minimal convex polygon model, allowed me to delimit the total home range explored by the radiotagged barbastelles. Then, the whole surface was divided in 236 grid cells of 0.25 ha. Cells with foraging activity (i.e. more than 2 min of flight activity) were classified as 'visited', the others as 'non visited'.

Vegetation surveys concerning 19 environmental variables were mapped for each cell in August 1993 (Table 1). Since the caterpillars of most moth species found in the light traps (Sierro & Arlettaz, 1997) feed upon epiphytes, the lichen cover growing on tree trunks was noted during the surveys. This matrix was submitted to a stepwise regression analysis on CANOCO (ter Braak, 1990) using a forward selection procedure. First, the covariable influence was checked before operating with a multiple regression analysis that selected the most significant variable. Then, a simple regression was processed with this retained variable; the percentage of explained variation was tested through permutation test ($n = 99$). After having added this variable to the model the residue of the first regression was processed by another simple regression. This procedure was used as many times as necessary until the percentage of variation did not increase significantly. Seven variables with less or equal 1% of explanation were set aside for the discussion about habitat selection.

Study area

The survey took place in a remote area (Mt Chemin: 46° 6′N, 7° 6′E) of an alpine valley in the canton of Valais (southwestern Switzerland), on a wooded slope between 900 and 1300 m altitude. The characteristic vegetation of the area is a xeric pine forest *Pinus sylvestris*, irregularly mixed with steppe *Stipo-Poion*, oaks *Quercus pubescens*, and spruces *Picea abies* in the coolest parts (Ozenda, 1985; Plumettaz Clot, 1988; Werner, 1988). Apart from a small village (Chemin-dessus) 500 m from the trapping site the study area is virtually uninhabited; furthermore, there are no bright streetlamps to attract bats.

RESULTS

Nine individuals provided information on foraging areas during 19 nights (average: 2.11 nights per successful experiment) (Table 2). Two sessions on the same male in July 1992 and June 1993 gave no data; this individual disappeared as soon as released. Heavy storms of foehn (dry and mild local wind typical in the valleys of central Alps) and even slight drizzles prevented the bats from flying. The radiotagged individuals always sheltered in rock crevices; only once was a roost site found in a tree.

For a very short period of time, using the night scope during two radiotracking sessions, visual contact was kept with the barbastelles flying above the tree canopy. The radiotransmitter contacts always came from the air above the tree crowns, which topped 6 to 8 m at most of the hunting grounds. The foraging flight was straight,

Table 2. The 12 radiotracking experiments carried out on 11 barbastelle bats (eight males and three females) at Mt. Chemin (Valais, Switzerland)

Code	Sex and age	Dates of signal emission	Nights with recorded foraging activity
N 134	Male adult	16–17.6.92	1
N 141	Male subadult	22–23.6.92	1
K 724	Male adult	3.7.92	0
		8.6.93	0
N 139	Male adult	31.7–5.8.92	4
N 143	Male adult	4.8.92	0
N 144	Female subadult	11–13.8.92	2
K 592	Male adult	10–13.8.92	3
N 145	Female subadult	6.9.92	1
N 133	Male adult	14–16.9.92	3
N 148	Female adult	8–9.10.92	2
N 201	Male adult	27–30.6.93	2
Total	11 individuals		19

Table 3. Environmental variables retained by the stepwise regression analysis

Environmental variables	Variance		
	F-ratio	%	*P*
1. Litter thickness	59.36	19	0.01
2. Shrub layer cover	21.53	7	0.01
3. Pine tree cover	11.85	4	0.02
4. Circumference of oak trunks	5.22	2	0.03
5. Herbaceous cover	2.13	1	0.04
6. Lichen cover	2.13	1	0.04
7. Altitude	2.13	1	0.04
8. Circumference of pine trunks	2.13	1	0.04
9. Circumference of spruce trunks	2.13	1	0.04
10. Deciduous tree cover	2.13	1	0.04
11. Larch cover	2.13	1	0.04
Total		38	

with deep wingbeats and sudden downward turns, probably to catch prey.

The bats foraged in pinewood between 650 and 1200 m altitude. They did not visit the subalpine forested pastureland (1280–1420 m), which was sparsely covered with old larches *Larix decidua*, or the pure spruce *Picea abies* forest. The average individual home range was 8.8 ha (SD ± 5.8 ha, $n = 9$). The barbastelles showed high fidelity to their feeding grounds.

From the four ecological variables selected through the stepwise regression analysis (Table 3), litter thickness appeared to be the most significant (19% of overall variance, $P = 0.01$); due to the steep gradient, the litter accumulated on the flat areas. The second variable retained was the shrub layer (7%, $P = 0.01$); bushes consisted of typically xerothermophilous species: *Prunus spinosa*, *P. mahaleb*, *P. avium*, *Crataegus monogyna*, *Berberis vulgaris*, *Viburnum lantana*, *Juniperus communis, Acer opalus* and *Sorbus aria*. Also, the analysis retained the percentage of pine trees (4%, $P = 0.02$) and the circumference of oak trunks (2%, $P = 0.03$). These four environmental variables contributed 31% of the overall variance. Seven other explanatory variables were selected at the lower end (Table 3): herbaceous cover, lichen on trunks, altitude, circumference of spruces, percentage of deciduous trees, and percentage of larches; each accounted for 1% ($P = 0.04$) of the total variance in habitat selection. The selected variables comprised 38% of the overall variance. Finally, it should be noted that the variable 'arborescent cover' was strongly correlated (47%) with pine cover and litter thickness, as pine is the dominant tree species in the study area. The eight remaining variables (x and y coordinates, height of herbaceous layer, arborescent cover, circumference of larch trunks, circumference of dominant deciduous tree trunks, spruce cover, oak cover and lichen on trunks) played no role in habitat selection.

DISCUSSION

The main feature of the habitat used by the barbastelles seems to be the predominance of pine forest, whereas meadows, wooded outcrops and human settlements were avoided. The selection for a high litter thickness as the first environmental variable suggests a requirement for high phytomass production favouring the development of a large amount of insect prey. The shrub layer enhances the importance of a complex stratified structure with numerous bush species. This richness could be essential for a large prey diversity during the vegetation period. Thermophilous bushes have proved to be the most attractive as host plants for Lepidoptera: in the British fauna, 64 Macrolepidoptera and 60 Microlepidoptera species feed on *Crataegus monogyna,* and 48 and 43 species respectively, on *Prunus spinosa* (Kennedy & Southwood, 1984). Recent forestry practices that have turned underwooded forests into selectively cut timber forests or plantations have impoverished insect numbers and diversity.

The selection of pine tree cover suggests a predilection of the barbastelle for forested areas, but not necessarily for pine because other localities harbouring this species in Switzerland are located in mixed forests of spruce *P. abies*, beech *Fagus sylvatica*, lime *Tilia platyphyllos*, and fir *Abies alba* in the Jura mountains (Chapuisat & Ruedi, 1993), near the Sarnen Lake (central Switzerland) (A. Theiler & A. Sierro, pers. obs.) and in a hedgerows landscape in Grisons (east Switzerland) (Lutz, 1995). Moreover, the pine forests have been recognized as poorer habitat for Microlepidoptera (Kaltenbach & Küppers, 1987). Nevertheless, the preference for tree covered areas also indicates an important ecological requirement for conservation measures in Europe.

The last environmental variable selected – the circumference of oak trunks – may indicate the preference for old woodland with high general diversity, and highlights the influential role of the mixed composition of the forest used by the barbastelles for foraging. Futhermore, this hypothesis is supported by a large-scale analysis in which Kennedy & Southwood (1984) pointed out that *Quercus* sp. is the most attractive host tree for the Macrolepidoptera (106 species) and the second for Microlepidoptera (83 species) of the British fauna. As the barbastelles specialize on small moths (Beck, 1995; Rydell *et al.*, 1996, Sierro & Arlettaz, 1997), especially Microlepidoptera, they presumably select sites with high moth density.

The habitat around an old mine, where 12 *Barbastella b. leucomelas* were mist-netted in Kirghizstan (Central Asia) was only constituted of rocky steppe (R. Arlettaz, pers. obs.) and woodland was absent. Therefore, there seems to be no definite link between habitat and the presence of barbastelle bats, nor with the abundance of Microlepidoptera.

The reasons for the drastic decline of the barbastelle in much of western Europe remain unclear. Exhibiting a very narrow diet (Sierro & Arlettaz, 1997), the barbastelle appears particularly vulnerable to the impoverishment of its food supply. When one considers that most of agricultural pests are found among Microlepidoptera (Kaltenbach & Küppers, 1987; Charmillot *et al.*, 1994) it may be supposed that the wide scale use of organochlorine insecticides may have led this bat to the brink of extinction. This may be particularly true in some regions formerly inhabited by the species that are close to intensive farming areas, especially in the lowlands of western Switzerland where the barbastelle was considered as fairly common during the mid-twentieth century (Bovey 1954). Small populations of barbastelles survive today in Switzerland in remote, mountainous areas, spared by the intensification of agriculture and forestry practices.

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