Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*

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Summary

1. Ecomorphological studies have described local bat communities as densely-packed species assemblages arising from non-deterministic processes. Together with the observation that insectivorous bats readily exploit patchy, often unlimited trophic resources, this has even led to the claim that partitioning of niche space may be absent. However, the paucity of data on resource exploitation *per se* among bat guilds rarely allows these assertions to be verified. In particular, the mechanisms allowing the co-existence of similar species have proved difficult to determine.

2. As a subset of an insectivorous guild, the vespertilionid bats *Myotis myotis* and *M. blythii* offer an opportunity to examine this question. Genetically closely-related, they are morphologically almost identical. Yet, as established by faecal analysis, they exploit distinct trophic niches, preying upon ground- and grass-dwelling prey taxa, respectively. The distinct habitat requirements of their basic prey suggest that ecological segregation may stem primarily from a differential allocation of foraging space.

3. The present study tests the hypothesis that sympatric *M. myotis* and *M. blythii* segregate spatially to an extent which prevents competitive interference. I performed radio-tracking on Swiss sympatric populations. Using multivariate analyses and randomized contingency table procedures, I looked for (i) habitat overlap and overall inter-specific differences in habitat choice, and (ii) the habitat preferences exhibited by individuals when foraging within their own feeding areas.

4. Primary foraging habitats were largely species-specific. Not only were they spatially segregated, but they also differed structurally. All habitats selected by *M. myotis* offered a high accessibility to ground-dwelling prey (freshly-cut meadows, mown grass in intensively cultivated orchards, forests without undergrowth), whereas grassland predominated in all habitats of *M. blythii* (steppe, unmown meadows, pastures). This corroborates the predictions drawn from dietary niches.

5. This study shows that refined mechanisms of resource partitioning, not predictable by the study of morphological characters or echolocation alone, may still account for the organization of parts of insectivorous bat guilds. It also supports the view that habitat selection may prove to be a major mode of resource allocation amongst similar insectivorous bats, particularly for species exploiting limited food supplies.

Key-words: Chiroptera, community ecology, guild structure, niche, species evolution.

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Introduction

Understanding the mechanisms of co-existence of species within local assemblages is one of the major issues addressed by community ecologists (Pianka 1981; Ricklefs 1990). The observation that local bat faunas are packed assemblages usually consisting of a majority of morphologically very similar species, with only a few outlying forms, has led some bat biologists to believe that competitive niche arrangement might play a minor role, if any, in bat community organization, because strong morphological resemblance is

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assumed to reflect similarity of niches (e.g. Fenton 1982; Findley & Black 1983; Aldridge & Rautenbach 1987; Crome & Richards 1988; Willig & Moulton 1989; Findley 1993; Arita 1997). Also, the majority of bat species appear to be opportunistic foragers which readily exploit patchily distributed, ephemeral trophic resources, i.e. locally and temporally unlimited food supplies, which may prevent competitive niche partitioning from occurring. As a consequence, the organization of bat communities would be under the control of non-deterministic processes (Willig & Moulton 1989; Findley 1993; Arita 1997). Yet, this unorthodox view about the structure of bat faunas has not been challenged by appropriate, refined ecological studies. In this respect, ecomorphological and echolocation studies may well provide insights into the structure of bat communities (e.g. Fenton 1982, 1985; Neuweiler 1984; Aldridge & Rautenbach 1987; Findley 1993; Kalko 1995; Arita 1997), but they both represent indirect approaches since they consider the attributes through which organisms acquire resources rather than resource acquisition *per se* (i.e. they use mere characters, and infer mechanisms from patterns; Wiens 1989). For instance, a spacing in resource partitioning has been suggested from the even apportionment of ultrasonic frequencies within bat assemblages including up to 12 syntopic rhinolophoids (Heller & Helversen 1989), but ecological evidence is still lacking. It may be argued that the ecomorphological approach aims first to look at trends within or amongst communities, not to predict subtle differences at the micro-evolutionary level. Recognizing its intrisic limitations is important, however (Saunders & Barclay 1992).

As no comprehensive data about dietary niches, foraging strategy and habitat use are simultaneously available from the same guilds (Saunders & Barclay 1992), it is difficult to appreciate how bat communities are structured (Kalko 1995). Detailed studies of the mechanisms involved in resource exploitation, especially among morphologically similar bats, are thus needed until we can solve this apparent dilemma and start envisioning the micro-evolutionary processes involved in bats' niche evolution (Aldridge 1986; Saunders & Barclay 1992).

Sympatric cryptic species are simplified subsets of communities (Mayr 1977). Among pairs of species which look alike, those which are not only morphologically similar, but also phylogenetically closely related provide the best opportunities not only to challenge the ecomorphological paradigm, but also to investigate the processes shaping niche evolution in general. Henceforth, the terms 'sibling species' deliberately refer to pairs of morphologically similar species that share a recent common ancestor to whom they are more closely related than any other species. Inter-specific differences (either morphological, physiological or behavioural) between those species can reasonably be seen as having some adaptive value in

the context of niche separation. Inter-specific comparisons between such species could therefore eventually yield information about the processes which have been involved in the apportionment of ecological space during the formation of those foraging guilds.

The greater and lesser mouse-eared bats, *M. myotis* (Borkhausen 1797) and *M. blythii* (Tomes 1857), which are the largest species within their genus (Nowak 1991), correspond to this definition of sibling species. First, the separation between these two Palaearctic taxa probably took place during the Pleistocene (Ruedi, Arlettaz & Maddalena 1990; Arlettaz *et al.* 1997a). Secondly, these two species are extremely similar and overlap in all their external morphological features (Arlettaz, Ruedi & Hausser 1991). Their identification thus remains particularly difficult and blood isozyme electrophoresis is currently the only absolute method available to distinguish between live individuals of these two species (Ruedi *et al.* 1990; Arlettaz *et al.* 1997a). Despite the fact that *M. myotis* and *M. blythii* have very similar, if not identical, karyotypes – they should therefore not experience any barrier to gene flow due to chromosomal incompatibilities (Ruedi *et al.* 1990) – and usually occupy the same colonial roosts in sympatry, either for breeding or mating (Arlettaz *et al.* 1994), genetic analyses carried out on several hundred individuals from sympatric populations have as yet failed to establish hybridization (Arlettaz *et al.* 1997a). This suggests the existence of strong behavioural reproductive barriers isolating the two species.

Arlettaz, Perrin & Hausser (1997b) have shown that mouse-eared bats occupy very distinct trophic niches throughout their ranges. *Myotis myotis* specializes in the predation of ground-dwelling prey (e.g. flightless carabid beetles), whereas *M. blythii* is primarily a predator of grass-dwelling arthropods, mainly bush crickets; mouse-eared bats are therefore essentially gleaning bats, i.e. capturing prey from substrates. Without being conclusive, that previous study of dietary niches has suggested that ecological segregation might stem primarily from the utilization of foraging habitats which differ spatially and structurally, because of the distinct habitat requirements of their basic prey (Arlettaz *et al.* 1997b). The present study tests the hypothesis that spatial segregation of foraging activity actually takes place between *M. myotis* and *M. blythii* under sympatric conditions. Temporal segregation, another possible mode of resource partitioning is also addressed briefly.

Methods

RADIO-TRACKING

Foraging activity and habitat of sympatric mouse-eared bats were investigated in the Alps of Valais (south-western Switzerland, *c.* 46°15′ N, 7°30′ E) between May and September 1989–92. Twenty-six

radio-tracking sessions (a session is here defined as a period of several successive days with uninterrupted radio-tracking of a given bat) were carried out on 24 individuals (12 *M. myotis* and 12 *M. blythii*—79% of which were adult females), during a total of 199 nights (Table 1). Two individuals were radio-tagged twice, during two consecutive years. Owing to transmitter defect, four individuals were not considered in the subsequent analyses (2 *M. myotis* and 2 *M. blythii*). Therefore, a total of 10 *M. myotis* and 10 *M. blythii* yielded good data.

Individual bats of the two species were captured at the same mixed nursery roosts. Potential habitat around the roosts was therefore similar for both species. Bats were fitted with radiotransmitters fixed around their necks with a silicone collar (Telemetrie-Systeme für die Wildbiologie, Dr F. Kronwitter, Glonnerstrasse 22, D–8011 Oberpframmern, Germany; tag weight was ≈ 1·4–1·8 g). A piece of reflector tape (Scotchlite™) glued on the upper side of transmitters enhanced location and identification of tracked individuals in the field through direct visual observation with the help of a night scope (BIG III, Wild-Leitz and Leica SA, CH–1020 Renens, Switzerland) coupled with an infra-red halogen lamp. At the end of each radio-tracking session, individuals were recaptured at their roost or mist-netted in their feeding grounds, and transmitters removed. Radio-tracking sessions took place between dusk and dawn, without interruption. Bats were tracked from a car until they reached their foraging grounds which were located up to 25 km from the roost. Radio-tracking was then performed on foot, usually by a single observer equipped with a radio-receiver and an H-antenna (Telonics, Telemetry-electrical consultants, 932 E. Impala av., Mesa, Arizona 85204–6699, USA; Yaesu FT-290RII adapted by Karl Wagener, HS + NF–Technik–Telemetrie, Herwarthstrasse 22, D–5000 Köln 1, Germany). Because of the bats' high flight speed (usually 30–40 km/h, but up to 50 km/h; Arlettaz 1996a), complex alpine topography and availability of a single observer, monitoring of bat activity was interrupted frequently and location was achieved essentially by homing-in on the animal (White & Garrott 1990). The accessibility of foraging grounds to the observer also differed between the two species. *Myotis myotis* visited primarily agricultural habitats and forests with a good road network, whereas *M. blythii* exploited, first, steep rocky slopes (up to 43°) with few if any roads, which sometimes

Table 1. The 26 radiotracking sessions carried out on 24 individuals in 1989–1992

Species	Individual (ring number)	Sex, age and reproductive state[1]	Period	Number of nights with radiotransmitter	Number of nights with recorded foraging activity	Number of foraging areas (⩾ five 1-ha cells)
M. myotis	083G	fem. ad. lact.	26–30 Jun 90	5	4	2
M. myotis	096G	fem. ad. lact.	10 Jul 90	1[2]	—	—
M. myotis	090G	fem. ad. lact.	11–16 Jul 90	6	5	2
M. myotis	877G	fem. imm.	03–05 Sep 91	3	3	1
M. blythii	424G	fem. ad. preg.	19–24 Jun 90	6[2]	—	—
M. blythii	430G	male ad.	04–20 Sep 89	17	7	1
M. blythii	434G	fem. ad. lact.	19–27 Jul 90	9[2]	—	—
M. blythii	514G	fem. ad. preg.	03–09 Jul 90	7	4	1
M. blythii	745H	fem. imm.	29 Aug–03 Sep 91	6	3	1
M. myotis	749G	fem. ad. lact.	02–06 Jul 91	5	4	2
M. myotis	759G	fem. ad. lact.	06–08 Jul 91	3	2	2
M. myotis	763G	fem. ad. lact.	08–11 Jul 91	4	3	
	idem	lact.	05–30 Jun 92	26	9	3
M. myotis	778G	fem. ad. lact.	16–18 Jul 91	3	2	1
M. myotis	824G	fem. ad. lact.	29 Jul–01 Aug 91	4	3	
	idem	lact.	14–29 May 92	16	6	4
M. myotis	875G	fem. imm.	23–26 Aug 91	4	2	1
M. myotis	768G	fem. ad. lact.	15–16 Jun 91	2[2]	—	—
M. blythii	710H	fem. ad. lact.	04–21 Aug 91	18	5	3
M. blythii	953G	fem. ad. lact.	11–22 Aug 91	12	2	2
M. blythii	962G	fem. ad. lact.	18–23 Jul 91	6	6	4
M. blythii	995G	fem. ad. lact.	02–04 Aug 91	4	2	1
M. blythii	997G	male imm.	14–23 Aug 91	10	3	1
M. blythii	999G	fem. ad. lact.	23–29 Jul 91	7	3	1
M. myotis	301G	fem. ad. lact.	30 Jul 90–07 Aug 90	9	7	1
M. blythii	466G	fem.ad.lact.	24–29 Jul 90	6	6	1
Total	24			199	91	35

[1]fem. = female; ad. = adult, imm. = immature; lact. = lactating.
[2]radiotransmitter defect: individuals not retained for analysis owing to scarce data.

rendered radio-tracking, even on foot, quite hazardous (see habitat photographs in Arlettaz 1995). To avoid any inter-specific methodological bias in data collection, habitat use was therefore defined by considering the proportion of the different types of habitat visited by a bat, and not by considering the time spent in the different habitat types. Despite obvious potential shortcomings, this simple spatial approach permitted direct inter-specific comparisons about habitat use. Five different types of activity were recognized:

1. resting at day roost;
2. night resting in foraging area;
3. commuting flight;
4. foraging activity; and
5. unidentified activity.

Commuting and foraging were easily distinguished, since (i) foraging usually consisted of gleaning from the ground, thus giving a signal of variable intensity due to micro-topography and frequent changes in flight direction; and (ii) commuting consisted of fast straight flights, possibly at some meters above the ground, thus providing a strong, constant signal (Arlettaz 1995). Contacts were classified with respect to the estimated accuracy of localization, which corresponded to the proximity of the bat to the observer. Only locations referring to foraging activity (type 4) and with an accuracy of $\leqslant \approx 50$ m, including visual observations, were considered for habitat selection analysis.

Bats selected for radio-tracking were first identified in the field according to the morphological method outlined in Arlettaz *et al.* (1991). Correctness of identification was then ascertained in the laboratory on the basis of protein analysis of blood samples (Ruedi *et al.* 1990; Arlettaz *et al.* 1997a). Radio-tracking was carried out under licence from the Nature Conservancy Service of the State of Valais.

HABITAT MAPPING AND FORAGING AREAS

Foraging habitats were divided in 1-ha cells according to the official reference grid of the Swiss Federal Topographic Service. Each foraging contact was attributed exclusively to one of these grid cells, and each cell was described by the dominant habitat type. Overall, 30 habitat types were recognized (Table 2). As far as possible, habitat mapping took place during the day following radio-tracking nights, usually from certain vantage topographic points; however, in the case of steep, remote habitats, aerial photographs provided by the Swiss Topographic Service were consulted.

The area exploited by each radio-tracked bat was estimated by summing the number of 1-ha cells (either isolated or not, see below) visited at least once by a given foraging individual (White & Garrott 1990). One habitat cell was considered in these calculations even if the bat visited only parts of it. Because individual bat foraging areas amounted to several dozens

of hectares each (see below), we considered any potential shortcomings inherent in this method as background noise which would not have substantially biased overall inter-specific comparisons.

The altitude of foraging grounds and the distance of foraging grounds to the nursery roost were estimated from the geometric centre of the minimum area polygon drawn for each foraging ground (Harris *et al.* 1990; White & Garrott 1990). For one given individual, I arbitrarily considered as one separate foraging ground every group of at least five neighbouring 1-ha cells which was isolated from the next closest group by at least 800 m; groups of less than five cells were not considered for the study of the altitude of feeding grounds and their distance to the roost. If there were more than one foraging ground per individual, I took their average altitude and distance to the roost for every individual bat.

HABITAT OVERLAP

Intra- and inter-specific overlaps in the use of the different types of foraging habitats were estimated from the proportions of the 30 habitat types visited (Table 2), with the Freeman–Tukey statistic (Matusita 1955; Krebs 1989):

$$FT_{ij} = \sum_{r=1}^{k} (p_{ir} \cdot p_{jr})^{1/2} \qquad \text{eqn 1}$$

where FT_{ij} is Freeman's and Tukey's measure of habitat overlap between individual i and individual j; for intra-specific overlap, i and j belong to the same species; for inter-specific overlap, i and j belong, respectively, to species A and B; k = total number of habitat types; p_{ir} and p_{jr} = proportions habitat r is of total habitat utilized by individuals i and j, respectively.

This measure of overlap ranges from 0 (no habitats used in common) to 1 (complete overlap). For intra-specific habitat overlap, the overlap coefficient is calculated for every possible pair of individuals of one species. For inter-specific habitat overlap, the statistic is calculated for every possible inter-specific pair of individuals.

For comparing the magnitude of habitat overlap between and within species, I relied on randomization procedures to avoid statistical pseudo-replication inherent in pairwise comparisons [see Manly (1991) and Arlettaz *et al.* (1997) for more details about the concept]. Mean intra-specific overlaps were calculated for both species, as well as mean inter-specific overlap. In order to test for differences between means, the following two-step procedure was repeated 5000 times: (i) random permutations of rows and columns of the habitat overlap matrix (as would be done for a Mantel test; Manly 1991); (ii) calculation of the intra- and inter-specific means of the shuffled matrix. The test probability was then the proportion of shuffled matrices that gave niche overlap as large as or larger

Table 2. Habitat categories (I–X) and habitat types (1–30) mapped within the different bat foraging areas, from the more open environments (top) to the cluttered ones (bottom). The dominant tree species are indicated for some habitats

Habitat category	Habitat type	Dominant tree species
I. Rocky	1 Cliff	
	2 Stony outcrop	
	3 Scree	
II. Urbanized	4 Human settlements	
III. Arable	5 Open fields	
	6 Vineyard	
IV. Water	7 Stream, river	
V. Steppe	8 Steppe on stony outcrop or scree	
	9 Open steppe ($< 50\%$ bushes)	
	10 Bushy steppe ($> 50\%$ bushes)	*Quercus pubescens*
	11 Wooded steppe ($< 50\%$ trees)	*Quercus pubescens, Betula pendula, Larix decidua, Pinus sylvestris*
VI. Pasture	12 Steppic pasture	
	13 Xeric pasture or abandoned meadow	
	14 Wet pasture	
VII. Dense meadow	15 Meagre meadow	
	16 Mesophilous meadow	
VIII. Mown meadow	17 Meagre meadow	
	18 Mesophilous meadow	
IX. Orchard	19 Traditional orchard	Apple
	20 Traditional orchard	Apricot
	21 Intensively cultivated orchard	Apple, pear
X. Deciduous forest ($> 50\%$ deciduous)	22 Xerothermic forest	*Quercus pubescens*
	23 Xerothermic forest	*Sorbus aria, Fraxinus excelsior*, etc.
	24 Chestnut forest	*Castanea sativa*
	25 Riparian forest	*Populus alba, P. nigra, Salix* sp.
X. Mixed forest	26 Xerophilous forest	*Larix decidua, Picea abies, Betula pendula, Sorbus aria, Castanea sativa, Pinus sylvestris*
X. Coniferous forest ($> 50\%$ coniferous)	27 Pine forest	*Pinus sylvestris*
	28 Spruce forest	*Picea abies*
	29 Larch forest	*Larix decidua*
	30 Mixed coniferous forest	*Larix decidua, Picea abies, Abies alba, Pinus sylvestris*

than the observed (the program used was written by J. Goudet, and may be obtained upon request from its creator at the same institutional address as the author).

HABITAT SELECTION

Species-specific habitat utilization. Differences in the habitats visited by *M. myotis* and *M. blythii* were visualized in the multivariate space using a principal component analysis performed on the 10 main habitat categories (first column in Table 2) obtained by a logical regrouping of the 30 fundamental habitat types recognized (second column in Table 2).

Habitat selection within individual foraging grounds. Habitat preferences and avoidances were established by comparing the absolute frequencies of the different habitats (number of 1-ha cells) which were visited or not by the bats inside the minimum area convex polygon(s) delimited for (each of) their main foraging ground(s). It was assumed that habitats of non-visited cells were actually avoided since foraging bats had to fly over them when moving from one part of their foraging ground to another. All cells with $\geqslant 50\%$ of their area (i.e. 0·5 ha) enclosed within one given polygon were considered. It was possible to distinguish between positive and negative selection, in which habitat is over-exploited with respect to its frequency of occurrence or under-exploited (avoided), respectively. Statistical tests performed on the overall species data sets consisted of randomized contingency table procedures (program MACACTUS, G. F. Estabrook, University of Michigan Herbarium, Ann Arbor, MI 48109, USA; Estabrook & Estabrook 1989). This method provides a level of probability (to the nearest 0·001) for every deviation between observed and expected frequencies, that is for every box or every habitat group in a contingency table. In order to avoid very small expected values in contingency tables, some habitat types had to be regrouped within higher habitat sorts prior to performing statistical comparisons (those habitat sorts are depicted on *x*-axes in Fig. 3).

Results

FORAGING ACTIVITY AND FEEDING AREAS

Bats carried transmitters for a total of 199 nights (average: 7·7 nights per session), but only 91 nights

(46%) provided satisfactory data on foraging activity (average: 4·1 nights per successful session). The general chronology of foraging activity did not differ between the two species. All tagged individuals left roosts after dusk and had returned before dawn. Hunting activity was essentially unimodal, even during lactation, and concentrated in the darkest hours of the night. This excludes inter-specific resource partitioning by temporal segregation.

Thirty-five foraging grounds were delimited (Table 1). Sixty-eight (13 out of 19) of the foraging grounds of *M. myotis* were on the north-facing slope (i.e. south of the river Rhône), 26% in the plain and only 6% on the south-facing slope (north of the river Rhône). In contrast, 56% (9 out of 16) of *M. blythii*'s foraging areas were situated on the south-facing slope, 6% in the plain and 38% on the north-facing slope. Overall, inter-specific differences in the use of the plain and the slopes were highly significant ($\chi^2 = 11\cdot5$, d.f. = 2, $P = 0\cdot003$) and randomized contingency tables showed that *M. myotis* avoided the south-facing slope ($P = 0\cdot014$) which, conversely, was selected by *M. blythii* ($P = 0\cdot037$). Since 1·5 foraging grounds, on average, were delimited per individual (Table 1), these patterns denote overall species-specific trends in space use and not mere individual specializations.

There was no inter-specific difference in the size of the individual's foraging areas: they amounted to $36\cdot2 \pm 17$ ha (mean $\pm$ SD) in *M. myotis* and to $38\cdot1 \pm 11$ ha in *M. blythii* (Mann–Whitney $U = 38\cdot5$, $n = 10$ and 10, $P = 0\cdot384$). The altitude of the foraging grounds did not differ statistically between the two species: 877 ± 328 m a.s.l. (mean $\pm$ SD) in *M. myotis* and 1012 ± 317 m a.s.l. in *M. blythii* ($t = -0\cdot936$, $n = 10$ and 10, $P = 0\cdot362$). The highest feeding areas were located at 2000 m a.s.l. for *M. blythii* and around 1600 m a.s.l. in *M. myotis*, whereas the roosts were at between 470 and 675 m altitude. The distance of foraging areas from nursery roost was significantly greater in *M. myotis* than in *M. blythii*: 8680 ± 6061 m vs. 3862 ± 1548 m (mean $\pm$ SD) ($t = 2\cdot435$, $n = 10$ and 10, $P = 0\cdot026$). The farthest feeding grounds were situated at 25, 18·5, 17, 14 and 13 km from the nursery colony in *M. myotis*, but only at 9, 6·5 and 5·5 km for *M. blythii*.

HABITAT OVERLAP

The two intra-specific overlaps [*M. myotis*: FT = $0\cdot299 \pm 0\cdot26$ (mean $\pm$ SD), $n = 45$; *M. blythii*: FT = $0\cdot428 \pm 0\cdot23$, $n = 45$] were significantly greater than the inter-specific one (FT = $0\cdot180 \pm 0\cdot16$, $n = 100$; $P < 0\cdot03$ in the first case, and $P < 0\cdot001$ in the second case; randomization tests), whereas the magnitude of intra-specific overlap did not differ between species ($P = 0\cdot15$; randomization test, not illustrated).

HABITAT SELECTION

Species-specific habitat use. The overall utilization of the 10 main habitat categories (Table 2) differed significantly between the two species ($\chi^2 = 430$, d.f. = 9, $P < 0\cdot001$). Inter-specific differences (all $P < 0\cdot01$; Fig. 1) appeared for steppe, pastureland and dense meadow which were predominantly exploited by *M. blythii*, and for freshly mown meadow, orchard and forest that were more frequently visited by *M. myotis*. There were no obvious differences between the habitat choice of the four tagged yearlings (2 *M. myotis* and 2 *M. blythii*) and that of adult individuals, but no statistical tests could be performed because of the small sample sizes available.

A principal component analysis performed on the frequencies (i.e. number of 1-ha cells) of the 10 main habitat categories showed a distinct clustering of individuals of the two species in the multivariate space, with no inter-specific overlap (Fig. 2). The first two factors accounted for 54% of variance (32 and 22%, respectively). The first component was positively correlated with freshly cut meadow ($r = 0\cdot656$, $P = 0\cdot002$) and forest ($r = 0\cdot512$, $P = 0\cdot021$), but negatively correlated with steppe ($r = -0\cdot846$, $P < 0\cdot001$). The second component was positively correlated with pasture ($r = 0\cdot582$, $P = 0\cdot007$), but negatively associated with orchard ($r = -0\cdot846$, $P < 0\cdot001$).

Individual selection. The percentage frequencies of the habitats available and effectively used within the main foraging areas are shown in Fig. 3. *Myotis myotis* positively selected freshly cut meadow ($P < 0\cdot001$), intensively cultivated orchard, mixed forest (both $P < 0\cdot01$), and (lowland) *Pinus sylvestris* forest ($P < 0\cdot05$). It avoided dense meadow and *Larix decidua* forest ($P < 0\cdot001$), mixed coniferous forest, human settlements and open fields (all $P < 0\cdot01$), vineyards and *Picea abies* forest ($P < 0\cdot05$). *Myotis blythii* showed a very highly significant preference for open steppe and dense meadows ($P < 0\cdot001$), and selected for rocky steppe and pastures ($P < 0\cdot05$). It avoided rocky areas, human settlements, vineyards, xeric deciduous forest ($P < 0\cdot001$), open fields, chestnut forest and mixed forest ($P < 0\cdot05$).

Discussion

SPATIAL SEGREGATION DURING FORAGING

This study demonstrates that the differences in diets between *M. myotis* and *M. blythii* (Arlettaz *et al.* 1997b) correlate with a sharp spatial segregation of foraging activities, with the inter-specific overlap in habitat use being much smaller than the two intra-specific ones (0·18 vs. 0·30 and 0·43, respectively). According to niche theory, this is sufficient to permit
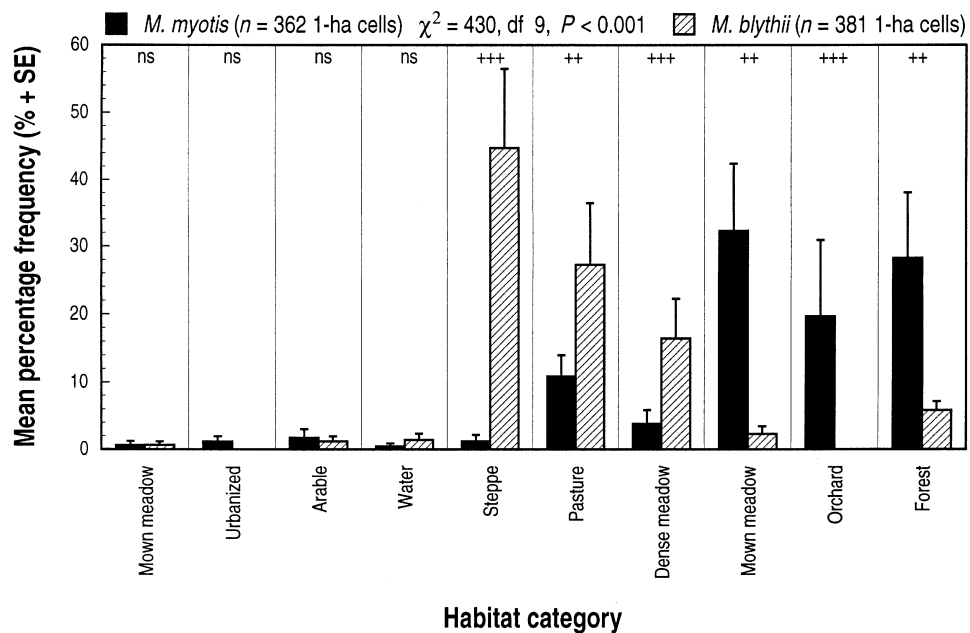
Fig. 1. Inter-specific differences in the mean percentage frequency of utilization of the 10 main habitat categories (see Table 2); habitats are ranked according to their approximate degree of clutter, from left to right. Chi-square and randomization tests were carried out on overall absolute frequencies (not on percentages) of visited habitat categories (number of 1-ha cells, see Methods; ns = non-significant; $++ = P < 0.01$; $+++ = P < 0.001$).
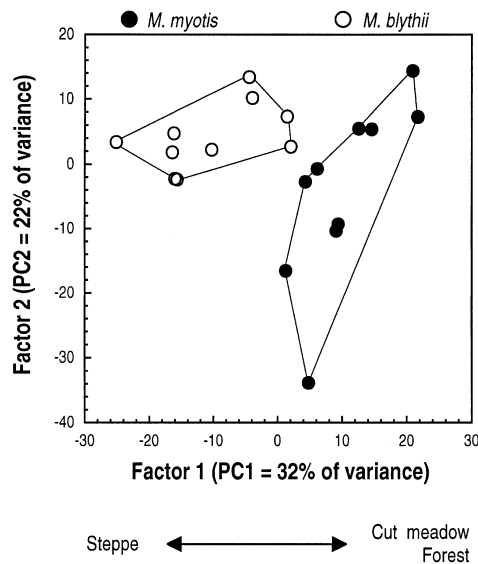

Fig. 2. Relationship between the first two factors (PC1 and PC2) obtained from a principal component analysis performed on the absolute frequencies (number of 1-ha cells) of the different habitat categories visited by the 20 radio-tracked mouse-eared bats (each symbol depicts a radio-tracked bat). The variables which are significantly (positively or negatively) correlated with factors are indicated along axes.

the stable co-existence observed in sympatry (Pianka 1981).

In the study area, *M. myotis* avoided the south-facing slope north of the river Rhône, whilst *M. blythii* preferred to forage there. In the upper Rhône valley, xeric grassland habitats (including steppe, a climactic grassland found in the driest valleys of the Alps) are widespread on the south-facing slope, but nearly absent on the north-facing one, south of the river Rhône, which is much more wooded. Given that *M. blythii* captures mostly grass-dwelling prey (bush crickets), whereas *M. myotis* feeds mainly on terrestrial prey (carabid beetles), this major spatial segregation across the valley correlates with the trophic requirements of these two bat species (Arlettaz *et al.* 1997b).

Within their individual foraging habitats, *M. myotis* selected freshly cut meadows and intensively cultivated orchards. Both habitats yield ground surfaces that are not cluttered by dense grass: hay meadows are exploited by the bats only during the first nights after mowing (Arlettaz 1996a), and orchards provide extensive surfaces of short grass which is frequently cut by farmers. The avoidance of meadows, prior to mowing, and larch forests, which have a dense grass undergrowth, further illustrates the bats' preference for uncluttered substrates. Among the woodland, only lowland forests with no undergrowth (neither grass nor bushes) were selected. Moreover, some forests exploited by *M. myotis* were heavily grazed by cattle. In conclusion, each type of habitat visited by *M. myotis* offers a high accessibility to terrestrial arthropods, apparently enabling a flying bat to land on the substrate to catch prey (Arlettaz 1996a). Despite a seemingly appropriate micro-habitat structure, some other habitats avoided by greater mouse-eared bats—such as high altitude coniferous forests, open fields and vineyards—probably yield insufficient numbers of suitable prey owing to their low arthropod productivity (personal field observations).
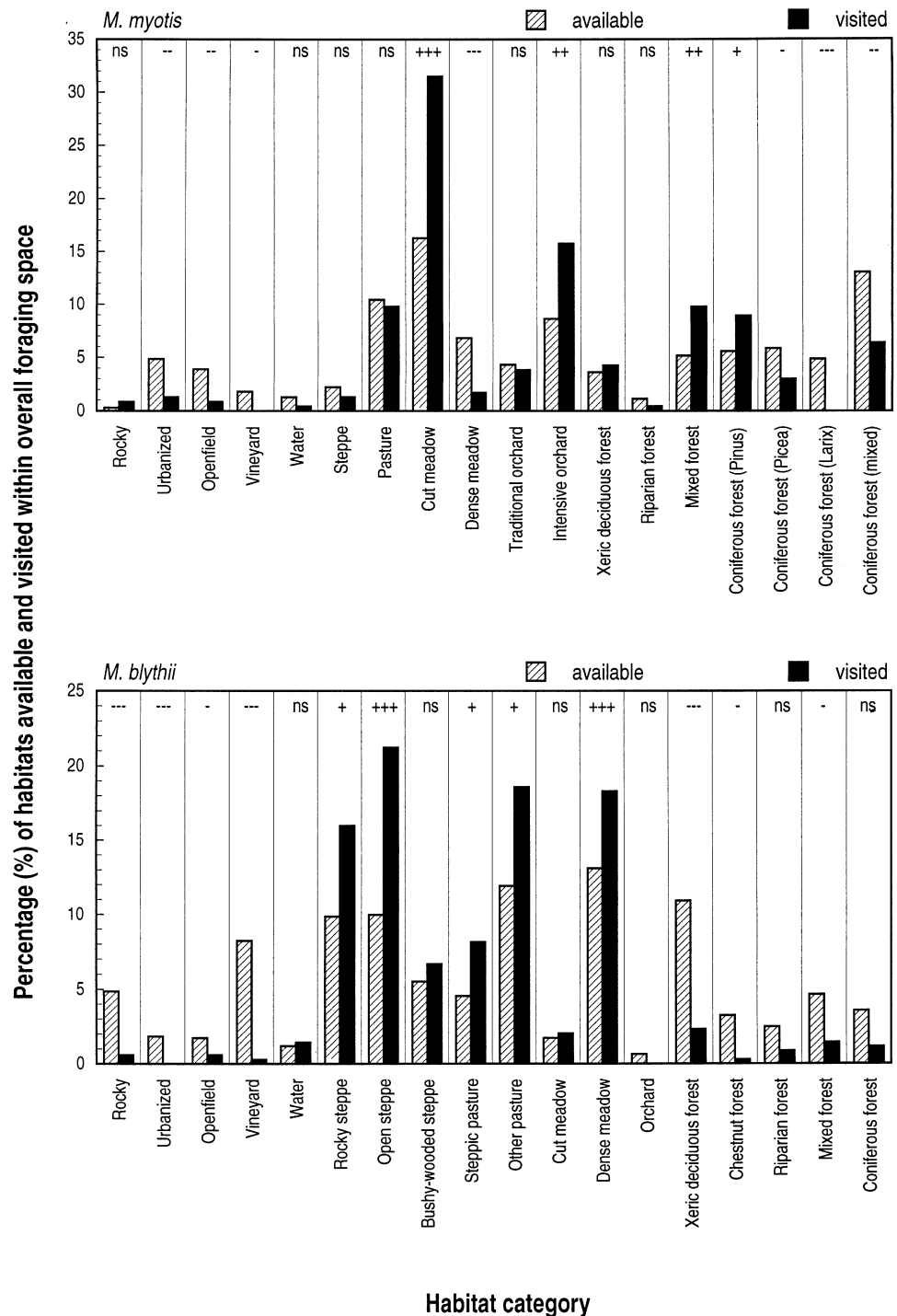
Fig. 3. Percentage frequency of the different habitat types available to, and visited by *M. myotis* (top) and *M. blythii* (bottom) in their individual foraging grounds (minimum area polygons, see Methods). Tests were run using absolute frequency data (number of 1-ha cells). The symbols indicate the direction of selection: + = over-exploitation (habitat preference), – = under-exploitation (habitat avoidance); ns = non-significant; one symbol: $P < 0.05$; two symbols: $P < 0.01$; three symbols: $P < 0.001$. In order to avoid very small expected values in contingency tables, habitat types have been grouped (see *x*-axis) differently in each species prior to running tests.

Interestingly, *M. myotis* in the Swiss Alps did not show the preference for forested habitats reported by Rudolph (1989) and Audet (1990) in Germany. This probably results from a greater habitat and/or food diversity in the Alps, due in particular to the per-

sistence of ancient farming practices which help to preserve a rich invertebrate fauna within grassland habitats (Arlettaz 1996a,b; Arlettaz *et al.* 1997b). However, it cannot be ruled out, *a priori*, that *M. myotis* may experience somewhat sub-optimal for-

aging conditions in mountainous environments (e.g. lack of productive mature deciduous forests typical of lowland areas), forcing it to seek prey in more open areas.

In their individual foraging grounds, *M. blythii* selected steppe and unmown meadows. They also appeared to choose the relatively dense steppe vegetation more frequently than the sparse xeric grassland which grows on stony outcrops. In contrast, they avoided the patches of xeric deciduous forests as well as the chestnut forests covering some south-facing slopes. Clearly, there is an association between *M. blythii* and relatively dense grass vegetation. Like *M. myotis*, *M. blythii* avoided rocky areas, human settlements, open fields and vineyards. This is again likely due to the very low arthropod productivity of these habitats.

The individual foraging grounds of *M. myotis* were, on average, situated at greater distances from the nursery roosts than the individual feeding grounds of *M. blythii* (9 vs. 4 km), although they covered similar areas and were situated at comparable altitudes. Freshly mown meadows appeared to be the most important habitat of *M. myotis* in the study area; interestingly, cut meadows also represented the most ephemeral food patches amongst all habitats recorded either in *M. myotis* or *M. blythii* (Arlettaz 1996a). Since they offer highly attractive food sources for *M. myotis*, owing both to massive occurrences of very profitable prey and high accessibility to ground prey (Arlettaz 1996a), it is not surprising that greater mouse-eared bats commuted such long distances to reach these habitats. Again, however, possible suboptimal feeding habitats in the Alps could also constrain *M. myotis* to forage farther away from roosts.

Set in a broader zoogeographical context, the present data provide an ecological explanation to the new view about the distribution of *M. myotis* and *M. blythii* in the Palaearctic region (Arlettaz *et al.* 1997a). *M. myotis* typically inhabits environments offering bare-ground habitats, from the central European beech forest to the denuded or even desert areas of North Africa, including also the main Mediterranean islands, whereas *M. blythii* is restricted to the mainland and appears primarily to be a species of the warm steppe which has extended its range throughout Eurasia.

WHAT UNDERLIES HABITAT SEGREGATION?

Considering their foraging strategy, I described mouse-eared bats as opportunistic predators which were able to maximize energy intake by searching for the most abundant/profitable prey (Arlettaz 1996a). However, this applied only to situations when mouse-eared bats exploited ephemeral food patches, particularly freshly-mown hay meadows (Arlettaz *et al.* 1997b). Nonetheless, if the bats can so readily take advantage of sudden concentrations of prey, why do they still allocate most of their foraging time to well segregated, species-specific habitats, as demonstrated in the present study? There are two possible answers.

First, it might be the pressure of inter-specific competition which may be the source of a differential use of space. Yet, this would contradict the conclusion by Arlettaz *et al.* (1997b) that inter-specific competition is not a major drive in trophic partitioning between these bats. As there is no evidence for niche shift – towards the occupation of the other species' niche – between sympatric and allopatric populations in either species, those authors excluded inter-specific competition as a factor of niche differentiation in sympatry. Given that the prey which form the bulk of the diets of mouse-eared bats are largely habitat-specific over their entire geographical range, the same conclusions readily apply to the bats' foraging habitats. As a consequence, it is unlikely that inter-specific competition is the key mechanism responsible for habitat segregation under sympatric conditions.

The second series of arguments pertains to possible species-specific functional adaptations evolved as proximate factors in resource partitioning. Energetic advantages – which should be measurable in terms of food intake, and ultimately as reproductive success and fitness – must be linked with these putative adaptations, making the sharp habitat segregation a fixed strategy. I predict above all that subtle differences in flight morphology enable one species, *M. blythii*, to exploit habitats structurally more complex. Gleaning a prey item from grass stalks requires a better flight ability than landing upon a prey on the ground. Species would therefore concentrate their foraging effort on the energetically more suitable habitat configuration. However, this seems insufficient to explain why *M. blythii* does not exploit easily accessible bare-ground habitats. Additional mechanisms providing bats with different search images may also be involved. Prey palatability may differ; for instance, carabid beetles, the basic prey of *M. myotis*, have a strong smell and may not be edible for *M. blythii*. Also, different auditory capabilities may indirectly influence patterns of habitat selection. As mouse-eared bats are primarily passive-listening predators (own unpublished data), auditory sensitivities tuned to the frequency emitted by their basic prey, such as the mating calls of bush crickets in the case of *M. blythii*, could drive the two species to different kinds of habitats in search of their preferred prey.

MODES OF CO-EXISTENCE WITHIN BAT GUILDS

Community studies that have alluded to resource use by insectivorous bats have usually involved groups which did not particularly include rather similar species (Black 1972, 1974; Kunz 1973; Fenton *et al.* 1977, 1980; Fenton & Bell 1979; Fenton 1982, 1985; Swift & Racey 1983; Fenton & Rautenbach 1986; McKenzie & Rolfe 1986; Aldridge & Rautenbach 1987; Rydell

1989; Barclay 1991; Barataud 1992). It is therefore not surprising that coarse-grained niche differences have been established in most cases, except maybe when resources were apparently not limited in supply (Bell 1980). In order to recognize fine-grained patterns behind species co-existence, the following discussion is deliberately restricted to pairs of cryptic and sibling species, as comprehensive ecological and behavioural data on entire guilds is still lacking (Kalko 1995).

Despite the fact that pairs of cryptic bat species exist all over the world, they have been the subject of ecological studies mainly in the depauperate faunas of the temperate zones of the northern hemisphere. In the Palaearctic region, there has been only one further pair of cryptic bat species subjected to intensive studies, although several such pairs would be available. Jones & Van Parijs (1993), Jones (1997) and Barratt *et al.* (1997) have shown that the 45- and 55-kHz phonic types in the taxon *Pipistrellus pipistrellus* are, in fact, two sympatric, cryptic species of bats. Jones (1997) has predicted that species-specific differences in tuning of ultrasound call frequencies of the two phonic types could allow syntopic resource partitioning through the capture of different sizes of prey, but faecal analyses have provided equivocal evidence (Barlow 1997). Indeed, Barratt *et al.* (1995) have established that the two phonic types of *P. pipistrellus* are actually not sibling species, as defined in this paper, but more distantly related, cryptic species (Jones 1997). It is therefore questionable whether the inter-specific differences in sonar systems relate directly to niche differentiation (the disruptive selection hypothesis by Jones & Van Parijs 1993), or whether they merely represent plesiomorphic characters which have been acquired independently of niche segregation, for instance, during the gradual speciation events (character drift). Furthermore, according to Vaughan, Jones & Harris (1997), the means by which sympatric co-existence is achieved could instead be differential use of space, although the mechanism behind this is still to be uncovered.

In North America, Husar (1976) has suggested that *Myotis evotis* and *M. auriculus* diverge in their diets only while occurring sympatrically, but do not under allopatric conditions. However, these two species co-occur over a small part of their distributions (only three localities according to Findley 1960) and must, hence, be considered as competitive parapatric species rather than members of the same guild. Although that study would probably be the most convincing example of competitive exclusion between bat species, Husar (1976) did not present decisive data about actual food supply at the various foraging locations so that it is questionable whether dietary changes between sympatric and allopatric conditions were actually the consequence of niche release alone. Woodsworth (1981), Herd & Fenton (1983) and Saunders & Barclay (1992) have established that the pairs *Myotis leibii*–*M. californicus*, *M. lucifugus*–*M. yumanensis* and *M.*

lucifugus–*M. volans*, respectively, segregated more or less through distinct patterns of habitat use.

The scarce evidence gathered so far suggests that sibling bat species partition niche space primarily by exploiting distinct micro-habitats (McKenzie & Rolfe 1986; Kalko 1995). Microchiroptera, at least insectivorous species, would not therefore differ substantially from other vertebrates (Pianka 1969, 1973; Schoener 1968, 1986; MacArthur 1972; Rosenzweig 1981, 1987; Bell 1984; but see Grant 1986; Brown 1989). Interestingly, most pairs of cryptic and sibling species for which habitat segregation has been established conclusively belong to the taxon *Myotis*. Contrary to the majority of temperate zone bats that capture airborne prey, the genus *Myotis* includes many species that glean prey from substrates (Beck 1994; Arlettaz 1996a,c). While aerial-hawking bats readily exploit ephemeral, patchy trophic resources, such as swarming insects which provide temporally and spatially unlimited food supplies, gleaning bats are apparently less prone to do so, probably because similar concentrations are far less common among 'substrate-dwelling' arthropods. One can therefore wonder if the exploitation of more predictable trophic resources, as in the case of *Myotis*, may imply more structured modes of community organization among insectivorous bats?

It seems clear that ecomorphology would hardly have been able to predict the subtle nature and the contrasted patterns of resource and space use by *M. myotis* and *M. blythii*. Morphologically almost indistinguishable, the sibling mouse-eared bats project far apart into ecological space. We can therefore wonder how many species described as merging in morphospace do actually differ radically in their use of resources.

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