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Trophic resource partitioning and competition between the two sibling bat species *Myotis myotis* and *Myotis blythii*

RAPHAËL ARLETTAZ*, NICOLAS PERRIN and JACQUES HAUSSER
Institute of Zoology and Animal Ecology, Lausanne University, CH-1015 Lausanne, Switzerland

Summary

1. Niche theory predicts that the stable coexistence of species within a guild should be associated, if resources are limited, with a mechanism of resource partitioning. Using extensive data on diets, the present study attempts: (i) to test the hypothesis that, in sympatry, the interspecific overlap between the trophic niches of the sibling bat species *Myotis myotis* and *M. blythii*—which coexist intimately in their roosts—is effectively lower than the two intraspecific overlaps; (ii) to assess the role played by interspecific competition in resource partitioning through the study of trophic niche displacement between several sympatric and allopatric populations.

2. Diets were determined by the analysis of faecal samples collected in the field from individual bats captured in various geographical areas. Trophic niche overlaps were calculated monthly for all possible intraspecific and interspecific pairs of individuals from sympatric populations. Niche breadth was estimated from: (i) every faecal sample; (ii) all the faecal samples collected per month in a given population (geographical area).

3. In every population, the bulk of the diets of *M. myotis* and *M. blythii* consisted of, respectively, terrestrial (e.g. carabid beetles) and grass-dwelling (mostly bush crickets) prey. All intraspecific trophic niche overlaps were significantly greater than the interspecific one, except in Switzerland in May when both species exploited mass concentrations of cockchafers, a non-limiting food source. This clearcut partitioning of resources may allow the stable, intimate coexistence observed under sympatric conditions.

4. Relative proportions of ground- and grass-dwelling prey, as well as niche breadths (either individual or population), did not differ significantly between sympatry and allopatry, showing that, under allopatric conditions, niche expansion does not take place. This suggests that active interspecific competition is not the underlying mechanism responsible for the niche partitioning which is currently observed between *M. myotis* and *M. blythii*.

Key-words: Chiroptera, community ecology, cryptic species, dietary niches, niche displacement.

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Introduction

Interspecific competition has long been regarded as the main process shaping the structure of natural communities (see the reviews by Connell 1983; Schoener 1983, 1985; Ferson *et al.* 1986). Recent studies, however, provide less evidence in support of its omnipotence as an organizing force in nature (e.g. Shorrocks *et al.* 1984; Tilman 1987; but see Stewart 1996), and tend to emphasize the possibly predominant role played simultaneously by other mechanisms such as environmental stochasticity, predation or parasitism (e.g. Chesson & Huntly 1989; Faivre & Auger 1993; Richner, Oppliger & Christe 1993; Loye & Carroll 1995). By preventing populations from reaching their point of demographic saturation, such alternative factors can modulate the extent of com-

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*Present address: Swiss Ornithological Institute, Rue du Paradis, CH-1967 Bramois-Sion, Switzerland.

petitive interactions and prevent competitive exclusion (Chesson & Huntly 1989). Previously, these alternative mechanisms had been largely underestimated, if not totally neglected. It remains open to debate, however, whether this recent change of perspective is just a consequence of the newest orientations in ecological research (i.e. perhaps a mere question of fashion), or whether it reflects the actual mode of organization of ecological communities (Shorrocks 1993). Further studies on various organisms are thus needed until we can appreciate the real role played by interspecific competition in niche evolution.

According to niche theory, species coexisting at equilibrium within a community must partition the resources of their environment – at least if the environment is assumed stable and its resources limited – until interspecific competition becomes, overall, less significant than intraspecific competition (Hutchinson 1957, 1978; Begon, Harper & Townsend 1986; Ricklefs 1990). However, the intensity of interspecific competition remains difficult to measure accurately in nature. Consequently, the majority of studies on community organization have looked at the extent of overlap in resource utilization, assuming that the lower the interspecific overlap in resource use, the higher the probability of stable coexistence of potential competitors (Begon *et al.* 1986; Ricklefs 1990). The overall niche of a species results from the combination of all the realized niches exhibited by the individuals in all populations. Accordingly, as long as data on resource use by individuals of coexisting species are simultaneously available, it is possible to calculate these two types of overlap: (i) the intraspecific overlap, i.e. the overlap in resource utilization between all individuals from a given species; (ii) the interspecific overlap, i.e. the overlap in resource utilization between every individual of one species and every individual of the other species.

The demonstration of a niche differentiation does not tell anything about the processes involved in partitioning, namely about the role played by interspecific competition. Two different processes may actually lead to such a pattern (Pianka 1981): (i) exploitative or interference competition, either active at present or having played some role in the past (the 'ghost of competition past' of Connell 1980); (ii) differential evolution (e.g. allopatric speciation; Mayr 1977). These mechanisms may be studied either experimentally through 'removal experiments' (Abramsky & Sellah 1982; Neet & Hausser 1990), or by comparative, correlational methods termed 'natural experiments' (Pianka 1981; Begon *et al.* 1986). For obvious reasons, however, removal experiments are particularly inappropriate to bats; for instance, these vertebrates are strictly protected by the legislation of most western countries. Natural experiments compare the morphology (character displacement, Brown & Wilson 1956), the behaviour or the ecology (competitive release and subsequent niche shift, Grant 1972; Alatalo, Gustafsson & Lundberg 1986) of species under sympatric and allopatric conditions; in other words, they attempt to compare fundamental and realized niches *sensu* Hutchinson (1978). When using this method, however, it is crucial to recognize that the only acceptable difference between allopatric and sympatric situations is the absence of potential competitor(s) in allopatry, a condition which is rarely fulfilled in reality. Despite these severe limitations, the assessment of interspecific competition between *Myotis myotis* and *M. blythii* will be approached in this way in this study (Grant 1972; Alatalo *et al.* 1986).

The greater (*Myotis myotis*, Borkhausen 1797) and lesser (*Myotis blythii*, Tomes 1857) mouse-eared bats are genetically closely related species which are morphologically similar (Ruedi, Arlettaz & Maddalena 1990; Arlettaz, Ruedi & Hausser 1991). They overlap over much of their distribution (see map in Arlettaz *et al.* 1997, p. 56), and usually coexist intimately in their roosts, frequently forming mixed nurseries, or even mating side by side (Constant 1960; Ariagno 1973; Ruedi *et al.* 1990; Arlettaz *et al.* 1994). Yet, despite similar karyotypes (Ruedi *et al.* 1990), the two species apparently do not cross breed, since no hybrid was found among more than 400 individuals identified biochemically (Arlettaz, Ruedi & Hausser 1993; Arlettaz *et al.* 1997). This suggests that *M. myotis* and *M. blythii* have evolved interspecific reproductive barriers. Additionally, subtle, but possibly adaptive, morphological differences between these two species – e.g. skull morphology (Ruedi *et al.* 1990; Arlettaz *et al.* 1997); wing morphology (Norberg & Rayner 1987); snout histology (Haffner & Ziswiler 1990); ear shape (Arlettaz *et al.* 1991) – suggest that some niche separation does occur between *M. myotis* and *M. blythii* (Findley 1993).

This study focuses on diet, one major dimension of the niche (Schoener 1974a, 1986). The first part will be devoted to the comparative trophic ecology of *M. myotis* and *M. blythii* under sympatric conditions; the second part will approach interspecific competition by comparing the trophic niches of sympatric vs. allopatric populations, looking for a possible niche release in allopatry. To our knowledge, this is the first attempt to investigate trophic niche displacement of potentially competing species over a wide geographical area, including several sympatric and allopatric populations.

Materials and methods

Henceforth, the term 'sympatric' indicates faecal samples collected at mixed maternity roosts, whereas 'syntopic' denotes faecal samples collected from individuals of either species captured while foraging side by side on the same feeding ground. 'Allopatric' bears here the sense given by Mayr (1977), designating droppings collected in geographical areas occupied by only one of the two species (Arlettaz *et al.* 1997).

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SPECIES IDENTIFICATION AND FAECAL ANALYSIS

Sympatry

Trophic niches of sympatric mouse-eared bats were investigated in the Alps of Valais (south-western Switzerland), and, for comparison, in southern Portugal. Diets were determined by the analysis of 349 faecal samples, one sample consisting of all the droppings excreted by an individual at the time of its capture, i.e. usually 5–15 droppings per sample. Bats returning to mixed maternity colonies just before dawn were captured at roost entrances with the help of specially designed harp-traps (Arlettaz 1987; Palmeirim & Rodrigues 1993). Nursery colonies were located inside church attics (Switzerland) or underground sites (Portugal). Under syntopic conditions, individuals were mist-netted in the field while foraging side by side (Arlettaz 1996). Bats were identified in the field according to the morphological method outlined in Arlettaz *et al.* (1991); atypical individuals exhibiting intermediate morphological characters were identified subsequently by protein (isozyme) analysis of blood samples (Ruedi *et al.* 1990). Individual bats were kept in linen bags until they had defecated. Faecal samples were stored in 70% ethanol, and then teased apart under a binocular microscope (magnification up to 40 ×). Arthropod fragments were identified, usually to order or family level, by comparison with a reference collection of whole specimens, and by using various insect identification guides and/or guides to faecal analysis (e.g. McAney *et al.* 1991). The relative volume (to the nearest 5–10%) of the different prey categories within each sample was estimated visually. The reliability of faecal analysis for the quantification of bat diet has recently been questioned (Robinson & Stebbings 1993; against, e.g. Kunz & Whitaker 1983; Dickman & Huang 1988). We think that this criticism is not relevant either to the method adopted here, or to these two species in particular, because: (i) we rely on individual instead of collective faecal samples, and each faecal sample comprises, on average, only two prey categories (Arlettaz *et al.* 1993); (ii) most variability in diet is thus due to inter-individual variation rather than to within-sample variation (Arlettaz 1995); (iii) prey consists mostly of large chitinous arthropods; (iv) moths, whose scales remain longer in the digestive tract and thus could be a serious source of bias, contribute only marginally to diets; (v) the identification of all arthropod fragments, including soft body parts (e.g. caterpillars), is possible, although it requires much experience.

Dietary data from the core study area in south-western Switzerland were split into two entities: Lower Valais (one single mixed nursery roost) and Upper Valais (two mixed nurseries). The former area is characterized by an intensively cultivated landscape, whereas the latter is still largely cultivated according to traditional farming practices. Moreover, no biological connection seems to exist between these two bat populations, separated by about 60 km, since no individual exchange was recorded between them, although more than 2500 individuals were ringed in the two populations over 15 years (RA, unpublished data).

Allopatry

The diet of allopatric populations of mouse-eared bats was investigated in the same way. For *M. myotis*, 67 faecal samples were collected in Morocco, Malta, Sardinia, Corsica and northeastern Switzerland. By contrast, allopatric *M. blythii* were sampled in only one geographical area (Kirghizstan, $n = 58$ samples); this is because it was discovered progressively, during successive expeditions to various geographical areas (see below), that the existing view about the identity of Palaearctic mouse-eared bat populations was erroneous (see Arlettaz *et al.* 1994; Arlettaz *et al.* 1997); for instance, North Africa and the main western Mediterranean islands are presently inhabited by *M. myotis* alone and not by mixed populations or pure populations of *M. blythii* (Arlettaz *et al.* 1997; contra, e.g. Bogan *et al.* 1978; Felten, Spitzenberger & Storch 1977).

TROPHIC NICHE OVERLAP

Traditional statistical approaches of the niche require normal distribution curves for the use of resources by species populations (e.g. prey size; MacArthur & Levins 1967; Pianka 1973, 1981); hence they cannot be applied to most studies of communities which are usually described from discretely distributed resources, namely nominal data like prey categories (Pianka 1973; Schoener 1974b; this study). Another approach of community structure is therefore needed. As replicates of interspecific and intraspecific overlap measures yield means and variances, differences between the two niche overlaps can be tested by conventional statistics and variances do not need to be extrapolated theoretically. This approach, first suggested by Horn (1966) and, to our knowledge, applied only by Neet (1989a, b), was used in this study.

Sympatry

Intraspecific and interspecific niche overlaps were estimated from all individual faecal samples collected in the three sympatric populations, by using the Freeman–Tukey statistic (Matusita 1955):

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

where FT_{ij} = Freeman's and Tukey's measure of niche overlap between individual i and individual j; for intraspecific overlap, i and j belong to the same spec-

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ies; for interspecific overlap, i and j belong, respectively, to species A and B; k = total number of resource states r (here prey categories); p_{ir}, p_{jr} = proportion of the resource r in the total resources utilized by individual i and j, respectively.

This measure of overlap ranges from 0 (no resource used in common) to 1 (complete overlap). For intraspecific niche overlap, the index was calculated monthly for every possible pair of individuals of one species; for interspecific niche overlap, the statistic was calculated monthly for every possible pair of individuals, each member of a pair belonging to a different species.

Syntopy

Trophic niche overlap was estimated in a similar way for bats captured under syntopic conditions. The interspecific niche overlaps of syntopically foraging bats were then compared to the overall overlap obtained from sympatry—*sensu lato* since some samples coming from syntopy cannot a priori be excluded from the faecal samples collected at mixed nursery roosts.

TROPHIC NICHE BREADTH

Trophic niche breadth was estimated from faecal samples by using Levins' index (Krebs 1989):

$$B = \frac{1}{\Sigma p_i^2} \qquad \text{eqn 2}$$

where B = Levins' measure of niche breadth; p_i = proportion of items of category i in the diet. This index ranges from 0 to n, n corresponding to the total number of resource states (here prey categories). As the same level of taxonomic precision was used for determining the diets of both species, species-specific diet breadths could be compared directly.

Trophic niche breadth was calculated both at the individual level (i.e. one index per individual faecal sample, which therefore represents the niche of one individual over, at most, one night) and at the population level (i.e. one index calculated for pools of all faecal samples collected from one geographical area during a given month), because broader niches may result either from a higher diversity in the prey categories captured by every individual, or from different individual dietary specializations. Thereafter, these indices will be called, respectively, 'Individual Levins' B index' and 'Month-population Levins' B index'.

NICHE DISPLACEMENT

Diet composition (i.e. relative proportion of the major groups of prey), niche overlap and niche breadth of sympatric vs. allopatric populations were compared statistically to see whether niche displacement (niche release and/or expansion) takes place under allopatric conditions.

STATISTICS

In order to test niche overlap between and within species, we had to rely on randomization procedures to avoid statistical pseudoreplication inherent in pairwise comparisons. We calculated mean within-species overlap for both species, and mean interspecific overlap. In order to test for differences between means, we repeated 5000 times the following two-step procedure: (i) random permutations of rows and columns of the niche overlap matrix (as would be done for a Mantel test; Manly 1991); (ii) calculation of the intraspecific and interspecific means of the shuffled matrix. The test probability is then the proportion of shuffled matrices that gave niche overlap as large as, or larger than, the observed (the program used for this test is available, upon request, from the authors). Other statistical tests conducted were Mann–Whitney U-tests—with Bonferroni adjustment where necessary (Altman 1991) and derived z-scores calculated for larger samples—and Kruskal–Wallis oneway ANOVAS (SYSTAT for the Macintosh; Wilkinson, Hill & Vang 1992).

Results

DIETS

Overall, 25 prey categories were determined from faecal samples, 23 categories in the diet of *M. myotis* and 19 in the diet of *M. blythii* (Tables 1–6). All but seven categories were found in the diet of both species.

Sympatry

Few prey categories dominated ($\geqslant$ 10% volume) the overall (May–September) diets of *M. myotis* under sympatric conditions: Carabidae, Lepidoptera larvae and *Gryllotalpa gryllotalpa* in Lower Valais (representing altogether 93% of prey by volume, see Table 1); Carabidae, Lepidoptera larvae, *Gryllus campestris*, *Melolontha melontha* and Staphylinidae in Upper Valais (84%,Table 2); Carabidae and Tettigoniidae in Portugal (79%, Table 3). *M. blythii*'s diet comprised mostly Tettigoniidae and Lepidoptera larvae in Lower Valais (84%, Table 1); Tettigoniidae and *M. melolontha* in Upper Valais (76%, Table 2); Tettigoniidae in Portugal (99%, Table 3).

Referring to Arlettaz & Perrin (1995), some prey taxa were considered as primarily ground-dwelling arthropods (hereafter 'ground prey'), whereas others were classified among typically grass-dwelling prey ('grass prey'); there are several taxa, however, which could not be attributed exclusively to one of these two major prey groups (for more details about this classification, see Tables 1–6). At a first glance, this dichotomic classification might appear somewhat

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Table 1. Mean percentage volume (± SE) of the different prey categories and groups of prey categories (bottom) found in faecal samples (n = 120) of sympatric *Myotis myotis* and *M. blythii* in Lower Valais (Switzerland, 46°15′N, 7°30′E) from May to September. Sample sizes and results of univariate *U*-tests on interspecific differences in diet composition are also given (NS, $P \geqslant 0{\cdot}05$; $^{*}P < 0{\cdot}05$; $^{**}P < 0{\cdot}01$; *P*-values adjusted using Bonferroni correction). Prey categories representing more than 10% by volume are shown in italics. Taxa are arranged according to systematic order

	May					June					July					August					September					May–September				
	M. myotis $n = 16$		*M. blythii* $n = 8$			*M. myotis* $n = 5$		*M. blythii* $n = 7$			*M. myotis* $n = 5$		*M. blythii* $n = 9$			*M. myotis* $n = 34$		*M. blythii* $n = 18$			*M. myotis* $n = 10$		*M. blythii* $n = 8$			*M. myotis* $n = 70$		*M. blythii* $n = 50$		
	Mean	SE	Mean	SE	*P*	Mean	SE	Mean	SE	*P*	Mean	SE	Mean	SE	*P*	Mean	SE	Mean	SE	*P*	Mean	SE	Mean	SE	*P*	Mean	SE	Mean	SE	*P*
Opiliones	0		0			0		0			0		0			0·1	0·1	0		NS	0		0			0·1	0·1	0		NS
Aranaea†	0		0			3·0	3·0	0		NS	0		0			0		0·1	0·1	NS	0		0			0·2	0·2	0·1	0·1	NS
Myriapoda†	1·3	1·3	0		NS	3·0	2·0	0		NS	0		0			1·5	0·9	0		NS	8·0	6·1	0		NS	2·4	1·0	0		NS
Gryllotalpa†	*45·6*	12·1	0		NS	0		0			0		0			0·3	0·3	0		NS	0		0			*10·6*	3·5	0		NS
Gryllus†	0		0			0		0			0		0			0·1	0·1	0		NS	0		0			0·1	0·1	0		NS
Tettigoniidae‡	0		*18·8*	11·5	*	0		*79·3*	13·6	NS	0		*57·8*	16·8	NS	0		*82·7*	8·1	*	0		*67·5*	15·9	**	0		*65·1*	6·2	*
Acrididae‡	0		0			0		0			0		0			0·6	0·4	1·2	0·9	NS	0		*26·9*	13·6	NS	0·3	0·2	4·7	2·5	NS
Forficulidae†	0·1	0·1	0		NS	0		0			0		0			0		0			5·0	4·0	0		NS	0·7	0·6	0		NS
Heteroptera‡	0·3	0·3	0		NS	0		0			0		0			0		0			0		0			0·1	0·1	0		NS
Lepidoptera imagos	0		0			0		0			0		0			0·4	0·2	0		NS	0		0·6	0·6	NS	0·2	0·1	0·1	0·1	NS
Lepidoptera larvae	*19·4*	9·3	*20·6*	12·5	NS	0		*15·7*	14·1	NS	0		*42·2*	16·8	NS	*29·1*	7·1	*14·4*	7·9	NS	*35·5*	12·5	2·5	2·5	NS	*23·6*	4·5	*18·7*	5·1	NS
Tipulidae	0		6·9	6·2	NS	1·0	1·0	0		NS	0		0			0		0			1·5	1·5	0·6	0·6	NS	0·3	0·2	1·2	1·0	NS
Other Diptera	0		1·3	1·3	NS	0		0·7	0·7	NS	0		0			0		0			0		0			0		0·3	0·2	NS
Formicidae†	0		0			4·0	2·4	0		NS	0		0			0		0			0		0			0·3	0·2	0		NS
Ichneumonidae	0		3·2	2·1	NS	0		4·3	3·0	NS	0		0			0		0			0		0·6	0·6	NS	0		1·2	0·6	NS
Other Hymenoptera	0		1·3	1·3	NS	0		0			0		0			0		0			0		1·3	1·3	NS	0		0·4	0·3	NS
Carabidae†	*31·9*	10·3	0		NS	*86·0*	5·1	0		*	*86·6*	12·0	0		**	*65·3*	7·0	1·0	0·7	*	*50·0*	11·5	0		*	*58·5*	4·9	0·4	0·3	*
Melolontha	0		*48·1*	18·3	*	0		0			0		0			0		0			0		0			0		7·7	3·7	NS
Other Scarabaeidae	0		0			1·0	1·0	0		NS	0		0			0·1	0·1	0·1	0·1	NS	0		0			0·1	0·1	0·1	0·1	NS
Staphylinidae†	1·6	1·1	0		NS	0		0			*12·2*	12·2	0		NS	1·4	0·9	0·6	0·6	NS	0		0			1·9	1·0	0·2	0·2	NS
Coleoptera larvae†	0		0			2·0	2·0	0		NS	1·2	1·2	0		NS	1·0	1·0	0		NS	0		0			0·7	0·5	0		NS
Ground prey	*80·3*	9·3	0		**	*98·0*	1·2	0		**	*100·0*	0	0		**	*69·7*	7·0	1·6	0·9	**	*63·0*	12·3	0		**	*75·3*	4·5	0·6	0·3	**
Grass prey	0·3	0·3	*18·8*	11·5	*	0		*79·3*	13·6	*	0		*57·8*	16·8	*	0·6	0·4	*83·9*	8·2	**	0		*94·4*	*3·7*	**	*0·4*	*0·2*	*69·8*	6·0	**

†Taxa classified as primarily ground-dwelling prey.
‡Taxa classified as primarily grass-dwelling prey.

Table 2. Mean percentage volume (± SE) of the different prey categories and groups of prey categories (bottom) found in faecal samples (n = 201) of sympatric *Myotis myotis* and *M. blythii* in Upper Valais (Switzerland, 46°20′N, 8°00′E) from May to September. Sample sizes and results of univariate *U*-tests on interspecific differences in diet composition are also given (NS, $P \geqslant 0{\cdot}05$; $*P < 0{\cdot}05$; $**P < 0{\cdot}01$; *P*-values adjusted using Bonferroni correction). Prey categories representing more than 10% by volume are shown in italics. Taxa are arranged according to systematic order

	May					June					July					August					September					May–September				
	M. myotis $n = 18$		*M. blythii* $n = 11$			*M. myotis* $n = 23$		*M. blythii* $n = 22$			*M. myotis* $n = 16$		*M. blythii* $n = 10$			*M. myotis* $n = 10$		*M. blythii* $n = 37$			*M. myotis* $n = 15$		*M. blythii* $n = 39$			*M. myotis* $n = 82$		*M. blythii* $n = 119$		
	Mean	SE	Mean	SE	*P*	Mean	SE	Mean	SE	*P*	Mean	SE	Mean	SE	*P*	Mean	SE	Mean	SE	*P*	Mean	SE	Mean	SE	*P*	Mean	SE	Mean	SE	*P*
Opiliones	0		0			0		0			0		0			0		0			2·1	1·4	0		*	0·4	0·3	0		NS
Aranaea†	0		0			0·3	0·3	2·1	1·6	NS	1·3	0·9	4·0	3·1	NS	0		1·2	0·6	NS	0		0			0·3	0·2	1·1	0·4	NS
Myriapoda†	0		0			0·4	0·4	0		NS	0·6	0·6	0		NS	0		0			0		0			0·2	0·2	0		NS
Gryllotalpa†	0		0			5·7	4·0	0		NS	0		0			0		0			0		0			1·6	1·1	0		NS
Gryllus†	*20·8*	9·2	0		NS	*10·7*	6·0	6·5	3·2	NS	0		4·2	4·0	NS	*15·5*	6·3	0·4	0·3	*	*13·3*	4·6	0		**	*11·9*	2·9	1·7	0·7	*
Tettigoniidae‡	0		0			0		8·6	4·3	NS	0·3	0·3	*43·1*	13·5	*	0		*74·9*	5·7	*	0		*91·8*	3·6	**	0·1	0·1	*58·6*	4·1	*
Acrididae‡	0		0			0		0			1·9	1·3	9·0	7·1	NS	3·5	1·5	8·6	2·7	NS	3·5	1·2	0		**	1·4	0·4	3·4	1·1	NS
Mantidae‡	0		0			0		0·1	0·1	NS	0		0			0		0			0		0			0		0·1	0·1	NS
Forficulidae†	0		0			0		0			0·6	0·6	2·0	2·0	NS	7·0	3·4	9·6	3·4	NS	*36·5*	7·1	7·2	3·5	**	7·6	2·0	5·5	1·6	NS
Lepidoptera imagos	1·7	0·9	0		NS	0		7·9	5·5	NS	3·1	2·5	2·5	2·0	NS	0		1·6	1·1	NS	0		0·5	0·5	NS	1·0	0·5	2·3	1·1	NS
Lepidoptera larvae	*41·1*	9·9	4·5	3·1	*NS*	*10·7*	4·2	*18·7*	6·9	NS	8·8	5·3	*19·7*	9·8	NS	6·0	4·0	*2·3*	1·2	NS	3·9	1·6	0·5	0·5	*	*15·2*	3·1	6·4	1·7	*
Tipulidae	0		0			0		4·5	4·5	NS	0·6	0·6	4·5	4·0	NS	0		0			0		0			0·1	0·1	1·2	0·9	NS
Other Diptera	0·3	0·3	0		NS	0		2·0	1·4	NS	0		0			0		0			0		0			0·1	0·1	0·4	0·3	NS
Formicidae†	0		0			0·1	0·1	0		NS	4·4	3·3	0		NS	0		0			0		0			0·9	0·7	0		NS
Ichneumonidae	0		0			0		0			0		3·0	3·0	NS	0·5	0·5	1·1	0·8	NS	0		0			0·1	0·1	0·6	0·4	NS
Other Hymenoptera	0		0			0·2	0·2	0		NS	0		0·5	0·5	NS	0		0·1	0·1	NS	0		0			0·1	0·1	0·1	0·1	NS
Carabidae†	7·8	5·1	0		NS	*25·6*	7·1	0·5	0·5	*	*67·4*	8·8	3·0	3·0	*	*56·8*	6·6	0·1	0·1	*	*37·4*	*8·3*	0		**	*35·8*	4·0	0·4	0·3	*
Melolontha	*22·2*	9.6	*95·5*	3·1	**	*21·3*	8·6	43·6	10·1	NS	0		0			0		0			0		0			*10·9*	3·4	*16·9*	3·3	NS
Other Scarabaeidae	1·7	1·7	0		NS	0		0			4·5	3·9	3·9	2·7	NS	3·2	3·2	0		NS	0		0			1·6	0·9	0·3	0·2	NS
Staphylinidae†	3·3	2·0	0		NS	*25·0*	6·5	2·7	2·7	*	6·6	3·3	0·6	0·5	NS	7·5	4·7	0		*	3·3	2·3	0		NS	10·5	2·3	0·6	0·5	*
Curculionidae	0		0			0		2·7	2·7	NS	0		0			0			0		0		0			0		0·5	0·5	NS
Coleoptera larvae†	1·1	1·1	0		NS	0		0			0		0			0		0			0		0			0·2	0·2	0		NS
Ground prey	*33·1*	9·7	0		**	*67·8*	8·4	*11·8*	5·1	**	*80·8*	7·3	13·8	5·2	**	*86·8*	4·0	*11·4*	3·3	**	*90·5*	2·5	7·2	3·5	**	69·2	4·2	9·2	1·9	**
Grass prey	0		0			0		8·7	4·3	**	2·2	1·4	*52·1*	12·4	**	3·5	1·5	*83·5*	4·3	**	3·5	1·2	*91·8*	3·6	**	1·5	0·4	*62·0*	4·0	**

†Taxa classified as primarily ground-dwelling prey.
‡Taxa classified as primarily grass-dwelling prey.

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Table 3. Mean percentage volume (± SE) of the different prey categories and groups of prey categories (bottom) found in faecal samples (n = 28) of sympatric *Myotis myotis* and *M. blythii* in Portugal (37°30′N, 8°30′W) in June. Sample sizes and results of univariate *U*-tests on interspecific differences in diet composition are also given (NS, $P \geqslant 0{\cdot}05$; $*P < 0{\cdot}05$; $**P < 0{\cdot}01$; *P*-values adjusted using Bonferroni correction). Prey categories representing more than 10% by volume are shown in italics. Taxa are arranged according to systematic order

	Myotis myotis $n = 13$		*Myotis blythii* $n = 15$		
	Mean	SE	Mean	SE	*P*
Aranaea†	2·3	1·2	0·7	0·7	NS
Gryllus†	5·4	4·6	0		NS
Tettigoniidae‡	*13·5*	7·6	*98·7*	0·9	**
Hymenoptera	5·4	5·4	0		NS
Carabidae†	*65·0*	11·6	0·7	0·7	**
Scarabaeidae	8·5	4·2	0		NS
Coleoptera larvae	5·4	5·4	0		NS
Ground prey	*75·0*	8·9	1·3	0·9	**
Grass prey	*13·5*	0·8	*98·7*	0·9	**

†Taxa classified as ground-dwelling prey.
‡Taxa classified as grass-dwelling prey.

arbitrary. It is further substantiated, however, by the observation that free-ranging mouse-eared bats capture most of their prey from bare ground or from grass vegetation, but not from other structures such as tree or bush foliage, trunks or walls, which is usually the case for most other European gleaning bat species (Arlettaz 1996). Accordingly, overall food preferences clearly showed both a prevalence of primarily ground prey (e.g. 75% and 69% in Lower and Upper Valais, respectively) in the diet of *M. myotis* and a predominance of grass prey (e.g. 70% and 62%) in the diet of *M. blythii* (Tables 1–3).

In all three sympatric populations, overall significant differences between the diets of *M. myotis* and *M. blythii* were recorded for the two main groups, ground prey and grass prey, as well as for the two main species-specific prey taxa already mentioned (namely Carabidae and Tettigoniidae, respectively) (Tables 1–3). Further overall interspecific differences were found for Gryllidae, Lepidoptera larvae and Staphylinidae, which were more frequently eaten by *M. myotis* in Upper Valais (Table 2). The seasonal (monthly) variation in diet composition did not deviate strikingly from these general patterns (Tables 1 and 2), but, in Lower and Upper Valais, more cockchafers, *M. melolontha*, were captured by *M. blythii* in May, and *M. myotis* took more Acrididae and Forficulidae in Upper Valais in September.

Syntopy

The diets of *M. myotis* and *M. blythii* mist-netted while foraging syntopically, which remains a rare event (Arlettaz 1996), are presented in Table 4. In most cases, syntopic dietary niches deviated greatly from sympatric diets (compare Table 4 with Tables 1–3): Tipulidae, Lepidoptera (imagos and larvae), Scarabaeidae (either *M. melolontha* or other species) were found in comparatively much larger quantities. Accordingly, under these circumstances, typical ground prey and grass prey did not predominate in the diets of the two species (for more details about foraging strategy, see Arlettaz 1996).

Allopatry

Diet composition of northern (Switzerland) and southern (Mediterranean) allopatric populations of *M. myotis* (Table 5) showed a high proportion of ground prey (70–93%, according to region), one apparent noticeable exception being Corsica (34%). There, Homoptera appeared in large numbers (49%) in July. Faecal analyses established that the majority of those Homoptera (all represented by cicadas) were captured as larvae, i.e. probably while emerging from the soil. Thus, if Homoptera are included in ground prey, the latter would represent as much as 82% of the total food of Corsican *M. myotis*.

Individual *M. blythii* from Kirghizstan (Table 6) conformed to sympatric ones, since they also ate more grass prey than ground prey. However, while typical grass prey, mostly Tettigoniidae, contributed to 69% of the diet in September, they represented as few as 17% in October. This may be attributed to night ambient temperatures frequently falling below 0 °C at that time of the year (R.A., personal observation), thus probably inhibiting bush cricket activity.

TROPHIC NICHE OVERLAP

Sympatry

The month per month comparison between intraspecific (*M. myotis* and *M. blythii*) and interspecific overlaps within the three sympatric populations yielded significant differences (randomization tests, $P < 0{\cdot}01$) for every possible monthly intra-interspecific pair ($n = 22$), except for *M. myotis* in Upper Valais in May ($P = 0{\cdot}18$) (Fig. 1). Interestingly, the level of intraspecific overlap did not differ significantly between species [FT = 0·595 ± 0·06 for *M. myotis*, FT = 0·635 ± 0·07 for *M. blythii* (mean ± SE); $U = 51{\cdot}5$, $n = 11$ & 11, $P = 0{\cdot}554$], suggesting that both species face a similar intensity of intraspecific competition.

Syntopy vs. sympatry

Under syntopic conditions, the average intraspecific niche overlap was 0·63 ± 0·1 (mean ± SE) in *M. myotis* ($n = 4$), and 0·50 ± 0·5 in *M. blythii* ($n = 2$), whereas the average interspecific overlap was

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Table 4. Mean percentage volume (± SE) of the different prey categories and groups of prey categories (bottom) found in faecal samples (n = 38) of sympatric *Myotis myotis* and *M. blythii* mist-netted at the same foraging grounds (syntopy) in Lower Valais (first case) and Upper Valais (all five subsequent cases) (Switzerland). Date, type of foraging habitat and sample sizes are also given. Prey categories representing more than 10% by volume are shown in italics. Taxa are arranged according to systematic order

	5 September 1991 Intensive orchard			17 July 1991 Freshly cut meadow			2 August 1991 Freshly cut meadow			12 June 1992 Grassland and hedges		26 June 1992 Freshly cut meadow		15 July 1992 Freshly cut meadow			
	M. myotis $n = 10$		*M. blythii* $n = 1$	*M. myotis* $n = 6$		*M. blythii* $n = 1$	*M. myotis* $n = 7$		*M. blythii* $n = 1$	*M. myotis* $n = 1$	*M. blythii* $n = 2$	*M. myotis* $n = 1$	*M. blythii* $n = 1$	*M. myotis* $n = 5$		*M. blythii* $n = 2$	
	Mean	SE	Mean	Mean	SE	Mean	Mean	SE	Mean	Mean	Mean	Mean	Mean	Mean	SE	Mean	SE
Aranaea†	4·0	2·7	0	0		0	0		0	0	0	0	0	0		10·0	10·0
Tettigoniidae‡	0		*13·0*§	3·3	3·3	0	0		0	0	0	0	0	*19·0*	15·4	*50·0*	50·0
Acrididae‡	0		0	0		0	1·7	1·7	0	0	0	0	*40·0*	0		10·0	10·0
Lepidoptera imagos	0		0	0		9·0	4·1	2·7	*30·0*	0	0	0	0	0		*15·0*	15·0
Lepidoptera larvae	2·6	2·6	*67·0*	3·2	1·8	0	*21·4*	12·7	*70·0*	0	0	*50·0*	*50·0*	*67·0*	17·3	0	
Tipulidae	*89·1*	4·4	*20·0*	0		0	0		0	0	0	0	0	0		0	
Other Diptera	0		0	0		0	2·6	1·5	0	0	0	0	0	0		0	
Formicidae†	0		0	0		1·0	0		0	0	0	0	0	0		0	
Other Hymenoptera	0		0	0		0	2·9	2·9	0	0	0	0	0	0		0	
Carabidae†	4·3	3·0	0	3·2	2·3	0	*42·7*§	15·9	0	0	0	*30·0*§	0	*12·0*	5·8	0	
Melolontha	0		0	0		0	0		0	*100·0*	*100·0*	0	*10·0*	0		0	
Other Scarabaeidae	0		0	*75·7*	5·5	*91·0*	*16·2*	12·1	0	0	0	*20·0*	0	2·0	2·0	0	
Staphylinidae†	0		0	14·7	14·7	0	8·1	6·5	0	0	0	0	0	0		*15·0*	15·0
Ground prey	8·3	*3·6*	0	*17·8*	15·2	0	*50·9*	14·6	0	0	0	*30·0*	*40·0*	*12·0*	5·8	*25·0*	25·0
Grass prey	0	*13·0*	3·3	3·3	3·3	0	1·7	1·7	0	0	0	0	0	*19·0*	15·4	*60·0*	40·0

†Taxa classified as ground-dwelling prey.
‡Taxa classified as grass-dwelling prey.
§These prey may have been captured outside the aggregative food patches, i.e. in primarily feeding habitats (see Arlettaz 1996).

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Table 5. Mean percentage volume (± SE) of the different prey categories and groups of prey categories (bottom) found in faecal samples (n = 67) of allopatric *Myotis myotis* in Morocco (34°75′N, 2°40′W; 33°80′N, 4°00′W; 32°′N, 2°50′W), Malta (35°80′N, 14°40′E), Sardinia (40°′N, 8°37′E; 40°22′N, 8°40′E; 40°33′N, 8°45′E), Corsica (42°40′N, 7°72′E; 42°21′N, 7°54′E), North-eastern Switzerland (47°23′N, 9°13′E). Date of sample collection (month) and sample size are also given. Prey categories representing more than 10% by volume are shown in italics. Taxa are arranged according to systematic order

	Morocco August $n = 23$		Malta April $n = 2$		Sardinia October $n = 8$		Corsica July $n = 13$		NE Switzerland May–August $n = 19$	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Scorpiones	3·5	3·5	0		0		0		0	
Aranaea†	*17·0*	6·4	0		5·0	5·0	*10·8*	7·8	0·8	0·5
Myriapoda†	1·7	1·0	0		5·3	3·4	0		0·9	0·4
Gryllotalpa†	0		0		0		*17·7*	9·8	0	
Gryllus†	*33·9*	8·1	*17·5*	7·5	8·4	6·3	0		0	
Tettigoniidae	6·1	3·6	0		1·3	1·3	*15·4*	10·4	0	
Acrididae‡	1·3	1·3	0		0		0		0	
Forficulidae†	2·2	2·2	5·0	5·0	2·6	2·6	0		0	
Homoptera	0		0		0		*48·5*	13·1	0	
Lepidoptera imagos	1·3	1·0	7·5	2·5	5·9	5·0	0		0	
Tipulidae	0		0		0		0		*15·8*	8·6
Other Diptera	0		0		0		2·3	2·3	0·2	0·2
Carabidae†	*14·8*	7·0	*70·0*	0·0	*34·0*	11·6	5·4	4·6	*78·5*	8·9
Melolontha	0		0		0		0		3·8	3·8
Other Scarabaeidae	*13·5*	6·7	0		0		0		0	
Staphylinidae†	0		0		*35·9*	13·1	0		0	
Coleoptera larvae†	4·8	4·3	0		1·8	1·8	0		0	
Ground prey	*77·8*	7·5	*92·5*	2·5	*92·9*	4·9	*33·8*§	11·7	*80·2*	9·0
Grass prey	7·4	3·7	0		1·3	1·3	*15·4*	10·4	0	

†Taxa classified as ground-dwelling prey.
‡Taxa classified as grass-dwelling prey.
§82% if Homoptera (Cicadidae) are included in ground-dwelling prey, most remains concerning larvae.

Table 6. Mean percentage volume (± SE) of the different prey categories and groups of prey categories (bottom) found in faecal samples ($n = 58$) of allopatric *Myotis blythii* in Kirghizstan (40°21′N, 73°37′E; 40°33′N, 72°30′E) in September and October. Sample sizes are also given. Prey categories representing more than 10% by volume are shown in italics. Taxa are arranged according to systematic order

	September $n = 29$		October $n = 29$	
	Mean	SE	Mean	SE
Aranaea†	0·3	0·3	0	
Gryllus†	*10·5*	5·6	0	
Tettigoniidae‡	*64·5*	7·7	9·7	4·9
Acrididae‡	3·4	2·4	0	
Heteroptera‡	0·7	0·7	7·2	4·8
Lepidoptera imagos	*17·1*	6·2	0·7	0·5
Lepidoptera larvae	2·8	2·4	*46·9*	8·8
Diptera	0		1·4	1·4
Formicidae†	0		1·7	1·7
Other Hymenoptera	0		*30·0*	8·2
Carabidae†	0·3	0·3	0·7	0·7
Scarabaeidae	0		1·7	1·7
Staphylinidae†	0·3	0·3	0	
Ground prey	*11·6*	5·5	2·4	1·8
Grass prey	*68·6*	7·7	*16·9*	6·5

†Taxa classified as primarily ground-dwelling prey.
‡Taxa classified as primarily grass-dwelling prey.

0·53 ± 0·1 ($n = 6$; Fig. 2). Thus, intraspecific and interspecific overlap measures appeared of the same order of magnitude under syntopic conditions (Kruskal–Wallis oneway ANOVA: KW = 0·26, $P = 0·88$; dark bars in Fig. 2), contrary to what was observed for all but one situation of sympatry, where interspecific overlap was constantly much lower (Kruskal–Wallis oneway ANOVA: KW = 21·52, $P < 0·001$; summarized by white bars in Fig. 2).

Statistical comparisons (Mann–Whitney *U*-tests) between the average niche overlaps measured in each syntopic locality (dark bars in Fig. 2) and the niche overlaps measured monthly in each sympatric population (white bars) showed no statistically significant differences in intraspecific overlap both for *M. myotis* ($U = 23$, $n = 4$ & 11, $P = 0·90$) and *M. blythii* ($U = 11$, $n = 2$ & 11, $P = 1·00$), but a very significant difference in interspecific overlap ($U = 4$, $n = 6$ & 11, $P = 0·004$) (Fig. 2). This establishes that dietary overlap was much greater when the two species were foraging side by side.

TROPHIC NICHE BREADTH

Interspecific differences in sympatry

Individual Levins' *B* index was larger in *M. myotis* (1·570 ± 0·06; mean ± SE, $n = 165$) than in *M. blythii*

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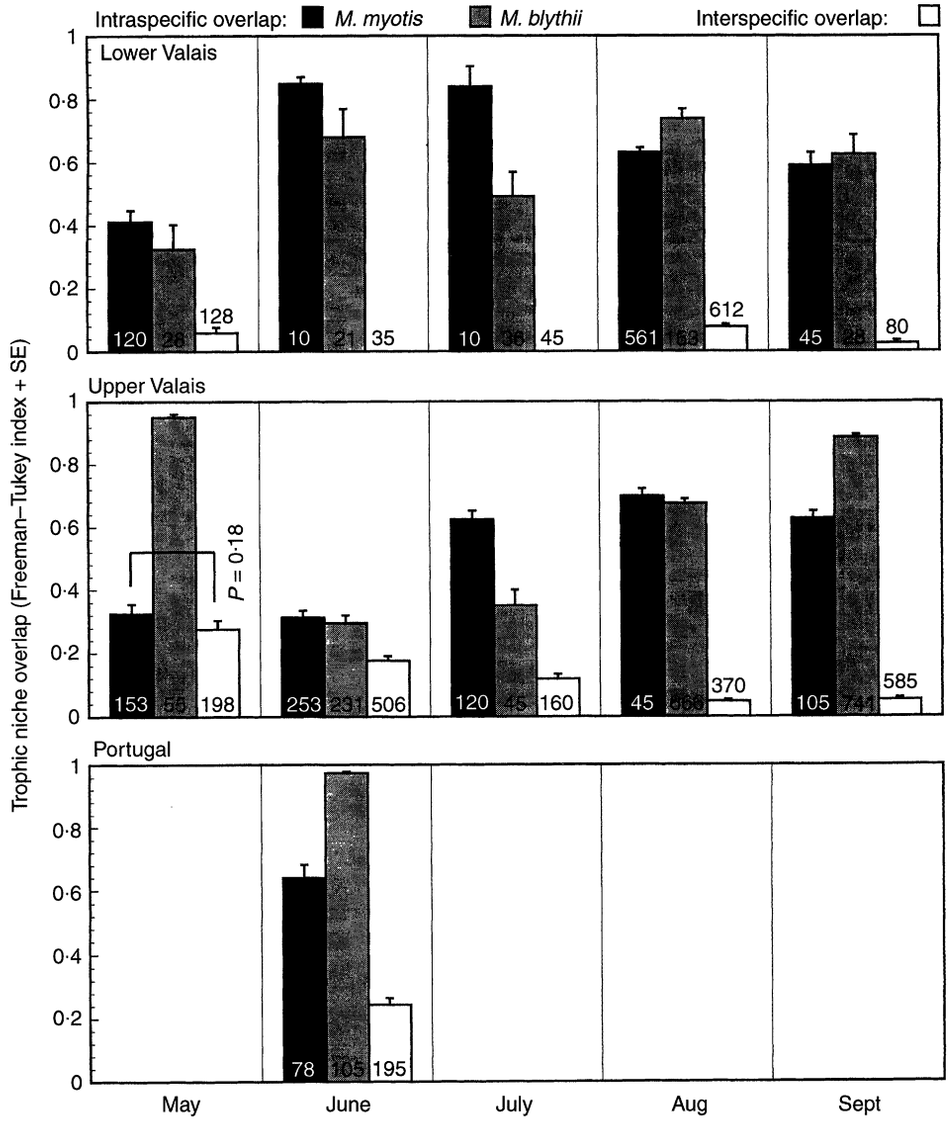

Fig. 1. Monthly intraspecific vs. interspecific trophic niche overlaps (Freeman–Tukey index + SE) in the three sympatric populations of Lower Valais, Upper Valais (Switzerland) and Portugal. Differences between intraspecific and interspecific overlaps are all highly significant ($P < 0{\cdot}001$, $n = 16$ pairs) or significant ($P < 0{\cdot}01$, $n = 5$; randomization tests), except in Upper Valais in May for the *Myotis myotis* intraspecific overlap—interspecific overlap pair which is non-significant (this pair is indicated in the middle plot by its probability level). Sample sizes (number of pairs of individuals used for estimating niche overlaps) are printed at the foot of columns. Tables 1–2 provide data on geographical origin of faecal samples.

($1{\cdot}301 \pm 0{\cdot}05$, $n = 184$), both when all individual faecal samples from all three sympatric populations were pooled (Mann–Whitney U-test, $z = -5{\cdot}23$, $P = 0{\cdot}0001$; Fig. 3), and when each sympatric population was considered separately (U-tests, all three z-scores giving P-values $< 0{\cdot}03$; not illustrated).

Month-population Levins' B indices did not differ between species either when the three sympatric populations were pooled (Mann–Whitney U-test: $U = 83$, $n = 11$ & 11, $P = 0{\cdot}14$), or when only the two Swiss populations were considered ($U = 65$, $n = 10$ & 10, $P = 0{\cdot}26$).

Allopatric populations

Values of Individual Levins' B index and Month-population Levins' B index will be discussed below, in comparison with sympatric populations.

NICHE DISPLACEMENT

Diets

Monthly differences in the proportions of the two dominant prey groups, ground prey and grass prey, did not differ significantly between sympatric and allopatric populations either in *M. myotis* (ground prey: $U = 36{\cdot}5$, $n = 11$ & 8, $P = 0{\cdot}54$; grass prey: $U = 47{\cdot}5$, $n = 11$ & 8, $P = 0{\cdot}76$), or in *M. blythii* (ground prey: $U = 6$, $n = 11$ & 2, $P = 0{\cdot}31$; grass prey: $U = 16$, $n = 11$ & 2, $P = 0{\cdot}32$; Fig. 4).

Trophic niche breadth

Neither Individual Levin's B indices (*M. myotis*; Mann–Whitney U-test, $z = -1{\cdot}716$, $n = 165$ & 65, $P = 0{\cdot}09$; *M. blythii*: $z = -0{\cdot}405$, $n = 184$ & 58,

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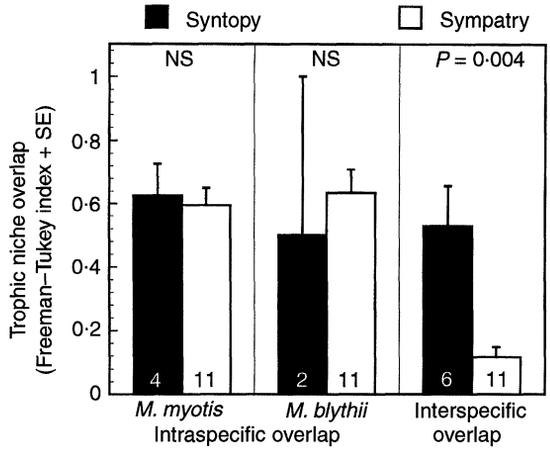

Fig. 2. Comparison of average trophic niche overlaps between syntopy and sympatry *sensu lato* (see text for more details). The diets of the two species appear closer under syntopic conditions. Sample sizes are indicated at the foot of columns and results of Mann–Whitney *U*-tests on the top of frame.

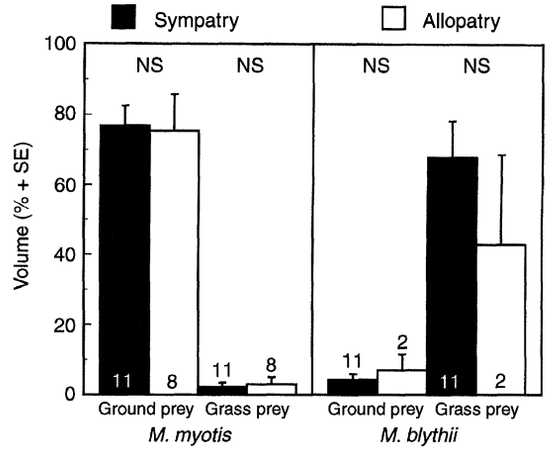

Fig. 4. Comparison of the mean monthly proportions of the two main groups of prey (ground prey and grass prey) in the diets of sympatric and allopatric populations of *Myotis myotis* and *M. blythii*. Here one sample unit consists of all individual faecal samples collected within one geographical population over one given month. Sample sizes are indicated at the foot of columns; all Mann–Whitney *U*-tests are non-significant.

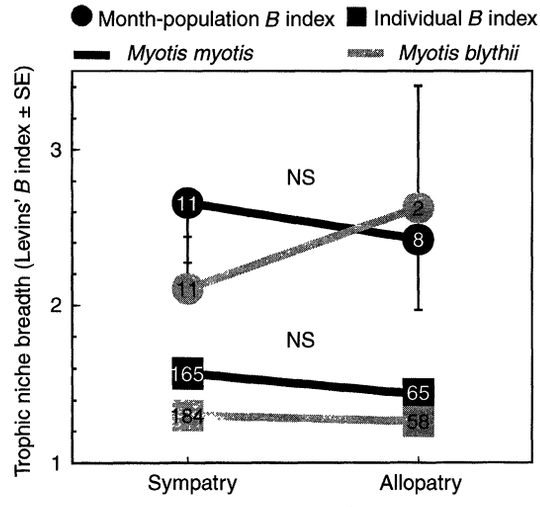

Fig. 3. Comparison of the mean monthly trophic niche breadth (top: Month-population *B* index; bottom: Individual *B* index) of sympatric and allopatric populations of *Myotis myotis* and *M. blythii*, showing that niche expansion does not take place in allopatry. Sample sizes are indicated on the symbols. Both Mann–Whitney *U*-tests are non-significant. For Individual *B* index, SE bars are so small that they are hidden behind the symbols.

$P = 0{\cdot}69$) nor Month-population Levin's *B* indices (*M. myotis*; $U = 35$, $n = 11$ & 8, $P = 0{\cdot}55$; *M. blythii*: $U = 16$, $n = 11$ & 2, $P = 0{\cdot}32$) differed between allopatry and sympatry in either species (Fig. 3).

Discussion

DIETARY NICHES DENOTE SPECIES-SPECIFIC MICRO-HABITAT PREFERENCES

This study shows that two morphologically similar species of bat, which coexist in a stable and intimate manner when sympatric – forming mixed clusters in their colonies – exploit highly distinct niches, as predicted by niche theory.

As in previous studies, Carabidae represent here the most important prey of *M. myotis* in continental Europe (Kolb 1958; Bauerova 1978; Gebhard & Hirschi 1985; Audet 1990; Arlettaz *et al.* 1993). In contrast, carabid beetles did not predominate in southern allopatric populations of mouse-eared bats in Morocco, Sardinia and Corsica, but were replaced by other ground prey, namely Gryllidae, Araneae or Staphylinidae. All these findings suggest that *M. myotis* is primarily adept at catching prey on the soil surface (Arlettaz 1996; Arlettaz *et al.* 1997).

Bush crickets (Tettigoniidae) appear the most important prey of *M. blythii* throughout its geographical range. The predominance of bush crickets and other grass prey in the diet of *M. blythii* points to its dependence on grass vegetation and grassland habitats. Interestingly, Tettigoniidae are much more frequent than Acrididae in the diet of *M. blythii*, although they appear to be much less abundant than field crickets in grassland habitats; this is probably because bush crickets are more active at night (including calling), and therefore potentially more readily detectable by hunting mouse-eared bats.

Clearly, the division of prey into two main groups, ground prey and grass prey, provides the best way to separate the diets of *M. myotis* and *M. blythii* (Arlettaz & Perrin 1995). This denotes interspecific differences in the main habitats prospected by the two species, and possible species-specific preferences for distinct habitat micro-structures as well. The cricket *Gryllus campestris* probably presents the best example in support of a differential micro-habitat specialization in the two mouse-eared bat species. Although crickets are ground-dwelling orthopterans linked with grass-

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land, they occur in significantly larger proportions in the diet of *M. myotis* than in the diet of *M. blythii*. This, again, shows that *M. myotis* is adapted to catch prey from the ground (Rudolph 1989; Audet 1990; Arlettaz 1996), whereas *M. blythii* mainly gleans its food from grass. Moreover, Gryllidae are probably caught by *M. myotis* in open grassland (e.g. overgrazed pastures) rather than in dense grass vegetation since this prey contributes to an important part of the diet in xeric submediterranean or subdesert environments like Upper Valais, Morocco and Malta. The prevalence of *G. gryllotalpa* in the diet of *M. myotis* in Lower Valais and Corsica may be interpreted correspondingly; in both regions, molecrickets were captured in wet, alluvial habitats, namely over lawns of intensively cultivated orchards on the plain of Lower Valais (RA, unpublished data), and presumably over pastures along streams in Corsica.

In conclusion, *M. myotis* and *M. blythii* should be basically considered as, respectively, ground and grass-gleaning predators. Undeniably, a primary micro-habitat specialization (and hence habitat segregation) also provides the most convincing ecological explanation for the differences in the geographical distributions of both species (Arlettaz *et al.* 1997). Similar conclusions have been reached by Saunders & Barclay (1992), who showed that dietary segregation between the sibling North American bat species *Myotis lucifugus* and *M. volans* results from the use of distinct foraging habitats.

TROPHIC NICHE OVERLAP

The significantly smaller interspecific than intraspecific niche overlap found under sympatric conditions demonstrates a distinct species-specific utilization of trophic resources by *M. myotis* and *M. blythii*. This splitting clearly enables the stable, intimate coexistence which is usually observed between these two species in sympatry. A single exception to this general pattern is noteworthy: in May, in Upper Valais, the intraspecific niche overlap of *M. myotis* did not differ significantly from the interspecific one, so that coexistence of the two species was theoretically unstable if resources were limiting. Conditions enabling exploitative out-competition from *M. myotis* (the species exhibiting the more diverse diet at that time) towards *M. blythii* (less diverse diet; see Fig. 1) were clearly met. However, this single possible competitive event took place when food resources could no longer be assumed to be limiting. Indeed, cockchafers *M. melolontha*, which contributed to 96% of the diet of *M. blythii* in May, emerge in huge numbers at this time.

Under syntopic conditions, the interspecific overlap appeared markedly closer to the two intraspecific ones. Since diets were more similar then, competition between the two species should theoretically have been more likely when *M. myotis* and *M. blythii* were foraging side by side within the same habitats, which remains a fairly rare event (Arlettaz 1996). Although these data should be interpreted with caution, particularly because of the small sample size, we see two alternative explanations. First, one of the two intraspecific overlap measures available for syntopic *M. blythii* again concerned cockchafers, i.e. a non-limiting trophic resource, which would invalidate the intra-interspecific overlap model. Secondly, if the two species basically exploit foraging habitats which are spatially isolated (R. Arlettaz, unpublished data), then they would select different kinds of prey, except when they happen to forage side by side.

TROPHIC NICHE BREADTH

Since the taxonomic precision of faecal analyses was the same for both species, the slightly broader trophic niche of *M. myotis*, as compared to *M. blythii*, may result either from a larger habitat spectrum, or from a richer prey diversity within the habitats of the greater species.

NICHE DISPLACEMENT AND COMPETITION

There was no evidence for niche expansion and/or niche shift in allopatric populations compared to sympatric ones, even on the Mediterranean islands, where it would have been most likely because of the syndrome of insularity (Blondel 1986). Grass prey were not captured to a greater extent by *M. myotis* in allopatry, and, likewise, ground prey were not more abundant in the diet of allopatric *M. blythii*. To some extent, the same was true for Carabidae and Tettigoniidae. Moreover, trophic niches were not broader in allopatry than in sympatry. Interestingly, this absence of niche displacement agrees with the results obtained from the study of the geographical variation of external characters, namely ear morphology, among various populations of mouse-eared bats (Arlettaz *et al.* 1997). In Microchiroptera, ear shape appears to be related chiefly to their different modes of echolocation, i.e. with the attributes of predation (Fenton 1972; Obrist *et al.* 1993); one may thus assume that such a trait should be subjected to intense natural selection. Yet, Arlettaz *et al.* (1997) showed that ear morphology of *M. myotis* and *M. blythii* did not differ between allopatric and sympatric populations to the extent that is predicted by the model of character displacement (Grant 1972). Both ecological and morphological data thus strongly suggest that interspecific competition is not a major drive in the niche partitioning which is observed today between sympatric *M. myotis* and *M. blythii*.

In the only other study of niche diplacement between similar bat species, Husar (1976) has suggested that *M. evotis* and *M. auriculus* have distinct diets in sympatry, but similar diets in allopatry. Contrary to mouse-eared bats, those two species occupy

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geographically distinct ranges with a minute zone of overlap (Findley 1960); they must hence be considered as competitive parapatric species instead of true sympatric species.

THE TRADITIONAL LIMITATIONS OF A NON-EXPERIMENTAL APPROACH

Violations of the basic assumptions underlying the model of 'ecological character displacement' (Grant 1972; Alatalo *et al.* 1986) cannot definitely be excluded in this study. On the one hand, habitats in at least one of the five allopatric populations of *M. myotis* (North Africa) differ significantly from sympatry; on the other hand, a new potential competitor for *M. blythii* appears in the bat fauna of Central Asia. We discuss those possible violations, presenting arguments for and against.

Revisiting the zoogeography of the two species in their western Palaearctic range, Arlettaz *et al.* (1997) showed that *M. blythii* is currently absent from the main western Mediterranean islands and from North Africa. Paleontological data suggest that this species is a recent colonizer in south-western Europe (Sevilla 1989), originating from the East of the continent (Arlettaz *et al.* 1997). We may, therefore, assume that *M. blythii* has possibly never crossed the Straits of Gibraltar (*c.* 15 km) for mere historical reasons. However, it cannot be excluded, a priori, that the current absence of *M. blythii* in North Africa could also have resulted from a recent secondary extinction, caused, for instance, by the progressive eradication of suitable grassy habitats which constitute the primary feeding grounds of that species (R. Arlettaz, unpublished data). Interestingly, huge pure colonies of *M. blythii* exist in southernmost Spain (Tarifa), not far away from the neighbouring pure Moroccan populations of *M. myotis* (Arlettaz *et al.* 1997). Indeed, extensive areas of steppe and cow pastures are widespread in southern Spain and yield dense populations of bush crickets (R.A., personal observation). By contrast, comparable habitats are (nowadays?) missing throughout Morocco, including the somewhat wetter northern part along the Atlantic coast (R.A., personal observation), possibly as a consequence of overgrazing by goats and sheep. Yet, the possibility of a recent extinction in North Africa is further weakened, in our opinion, by the observation that the main Mediterranean islands, some of which seem to offer suitable foraging (grassy) habitats, have apparently never been colonized successfully by *M. blythii* (Arlettaz *et al.* 1997). This adds a sound argument in support of the historical scenario.

Extensive steppe grassland and denuded habitats both occur in southern Kirghizstan. There, bush crickets are abundant only in the steppe, and do not inhabit desert areas. In Kirghizstan, however, denuded habitats are indeed exploited by another vespertilionid bat species that resembles *M. myotis* in many respects: the long-eared desert bat *Otonycteris hemprichi*. Interestingly, these two species show noticeable convergences in wing morphology (Norberg 1981; Norberg & Rayner 1987; Norberg & Fenton 1988), as well as in diet and foraging behaviour (Horacek 1991; Arlettaz *et al.* 1995). The latter study showed that the proportion of ground prey in the diet of Kirghiz *Otonycteris* amounts to 88% by volume. Any attempt of *M. blythii* to expand its niche towards ground prey theoretically could be hampered by this new potential competitor. However, *Otonycteris* is clearly restricted to the extreme arid lowlands of southern Kirghizstan, close to the Fergana Basin (Ouzbekistan; Horacek 1991; Rybin, Horacek & Cerveny 1989), whereas *M. blythii* has a much larger distribution there. In fact, among the 58 faecal samples we collected from Kirghiz *M. blythii*, only 11 (19%) originate from areas where the two species do occur in sympatry. Since the diet of those 11 individuals consisted of as much as 28% of terrestrial prey (which is a high proportion; see Tables 1–3 and 5–6), the competitive pressure exerted by *Otonycteris* upon *M. blythii* is apparently not so strong where the two species virtually forage together. This suggests that interspecific competition is unlikely to be the cause of niche segregation between these two phylogenetically unrelated bat species, and that, again, mere species-specific habitat preferences may better explain partitioning of niche space.

Conclusion

This study demonstrates that the stable coexistence of these two sibling bat species, usually coexisting intimately where sympatric, is enabled by a clearcut partitioning of food resources. It also suggests that exploitative interspecific competition plays no role at present in this partitioning process. It remains unclear, yet, whether competition played some dynamic role in niche segregation in the past, and possibly, in the speciation of *M. myotis* and *M. blythii*. However, because sympatric speciation through disruptive selection via habitat specialization and assortative mating (Rice 1987; Diehl & Bush 1989) is unlikely as regards mouse-eared bats, in particular owing to their strong colonial habits, with mating roosts often 'mixed' in sympatry (Arlettaz *et al.* 1994), we speculate that niche separation between *M. myotis* and *M. blythii* took place allopatrically during speciation events (Mayr 1977).

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