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The trophic niches of sympatric sibling *Myotis myotis* and *M. blythii*: do mouse-eared bats select prey?

Raphaël ARLETTAZ

Institute of Zoology and Animal Ecology
University of Lausanne
CH-1015 Lausanne, Switzerland

and Nicolas PERRIN

Ethological Station Hasli
University of Bern
CH-3032 Hinterkappelen, Switzerland

Synopsis

The two sibling species *Myotis myotis* and *M. blythii*, while sympatric in the Swiss Alps, exhibit highly distinct and narrow trophic niches. Does this differentiation arise purely from the use of distinct feeding habitats or, alternatively, do the species exert active prey selection within their feeding habitats? To answer this question, we compared the distribution of prey in the species' diets with that in their respective feeding habitats, looking for discrepancies with respect to taxon and/or size. Although the general correlation is fairly good, some local discrepancies arise: (1) *M. myotis* underexploited small prey items (<0.05 g dry weight), and (2) *M. blythii* overexploited cockchafers (*Melolontha melolontha*) and underexploited ground arthropods. We argue, however, that these discrepancies do not result from active prey selection, but from (1) the low availability of some categories of prey (due to either low detectability or low accessibility) and (2) the opportunistic exploitation of atypical feeding habitats. In fact, our results do not falsify the parsimonious hypothesis that the two species exert no active prey selection within their feeding habitats. We are furthermore not aware of any paper from the bat literature that provides definite support for active prey selection among insectivorous vespertilionids. Their echolocation system may actually preclude it.

Introduction

The greater and the lesser mouse-eared bats, *Myotis myotis* and *Myotis blythii* respectively, are two morphologically and genetically closely related species of vespertilionid bats which occur in sympatry over wide areas (Strelkov 1972; Felten, Spitzenberger & Storch 1977; Bogan, Setzer, Findley & Wilson 1978).

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These sibling species often coexist in their nursery roosts, frequently building up mixed reproductive clusters (Constant 1960; Ariagno 1973; Ruedi, Arlettaz & Maddalena 1990). Recently, they also have been found together within the same mating roost, but there was no evidence for mixed mating pairs (R. Arlettaz & M. Lutz unpubl.). Despite similar karyotypes (Ruedi *et al.* 1990), the two species do not seem to hybridize, since no hybrid was found among more than 400 individuals biochemically identified (Arlettaz, Ruedi & Hausser 1993).

According to the principles of competitive exclusion (or Volterra-Gause principle; Hutchinson 1957) and of limiting similarity (MacArthur & Levins 1967), we would expect such an intimate coexistence of cryptic but genetically distinct bats to occur only if they had evolved ways of partitioning resources. Arlettaz *et al.* (1993) have recently shown that sympatric mouse-eared bats from the Swiss Alps exploit different prey spectra. Carabid beetles (Carabidae) are by far the most frequent prey in the diet of *M. myotis*, whereas *M. blythii* feeds mainly on bush crickets (Tettigoniidae). As these insects live on the ground or close to it, *M. myotis* and *M. blythii* must both be considered as ground-gleaning bats. However, both species may occasionally switch from their normal foraging method, especially when large concentrations of prey suddenly become available, e.g. cockchafers (*Melolontha melolontha*) in April–June (Kolb 1958). These insects are caught on the wing around trees or gleaned from the canopy foliage (R. Arlettaz & R. Güttinger unpubl.).

Previous radiotracking of sympatric mouse-eared bats in the study area has shown distinct interspecific habitat partitioning (R. Arlettaz unpubl.): *M. myotis* forages mostly in forest and orchards, whereas *M. blythii* exploits mountain slopes covered by steppe, a typical climactic grassland found in the driest valleys of the Central Alps. The aim of this study was to test whether the trophic niche separation of the two species of mouse-eared bats results entirely from habitat segregation, or if they also feed selectively on certain arthropod taxa and/or sizes within their foraging habitats.

A non-selective forager feeds on prey according to availability in the foraging environment. Conversely, a selective feeder captures only certain categories or sizes of prey among those it encounters within its feeding habitat: some prey taxa or sizes are neglected or avoided (underexploited), whereas others are represented in the diet in a higher proportion than would be expected from their availability (overexploited). According to Wittenberger (1981: 211), resource availability refers to the amount of resource an animal can actually capture, utilize or otherwise exploit. In bats, food choice may be heavily restricted by the physical characteristics of their specific echolocation calls (Gould 1955; Simmons, Fenton & O'Farrell 1979; Neuweiler 1984, 1990). Prey availability is difficult or impossible to measure accurately (Faure & Barclay 1992). Instead, we compared bat diets with food abundance, looking for discrepancies between prey abundance in the environment and in the diets, with respect to taxon and/or size.

Material and methods

Species identification and faecal analysis

This study took place in the Alps of Valais (southern Switzerland, 46°15' N, 7°30' E) from April to August 1992. In order to assess the diet of mouse-eared bats, droppings were collected at a mixed nursery roost located inside the attic of a church. Individuals flying back to the colony late at night or early in the morning were caught at the attic's entrance with the help of a specially designed harp trap (Arlettaz 1987). Bats were identified according to Arlettaz, Ruedi & Hausser (1991) or on the basis of an electrophoretical analysis of blood samples in the laboratory (Ruedi *et al.* 1990). They were kept in linen bags until defecation was completed. A total of 120 (70 *M. myotis* and 50 *M. blythii*) samples were thus gathered and stored in 70% ethanol. Samples were collected between early May and mid-August. Faeces were dissected under a binocular microscope. Remains were identified, usually to family level. The relative volume (to the nearest 5–10%) of the different prey categories within each sample (4–15 pellets each) was estimated. Volume proportions indirectly provide information about the relative 'biomass' of the different prey items; this could not be achieved by frequency analyses (Kunz & Whitaker 1983). The overall relative proportion of each category of prey in the diet was estimated for each species separately.

Food abundance

Food abundance was investigated through pitfall trapping and hand netting of the ground and/or grass arthropod fauna from early April to late July 1992. The different habitats were chosen among previously (1989–1991) radio-delimited hunting grounds of the bats from the colony where faeces were collected. The three sampling sites (woodland, orchards and steppe) were located within a radius of 2 to 15 km from the colony. Each site was set up with three separate (150–600 m distant) groups of five pitfall traps. The distance between two successive pitfall traps was 5–10 m. The trapped arthropods were collected every 10 days from the beginning to the end of the experiment. In steppe (but not in forest and orchards because of the absence of grass on the ground), hand netting was performed on the same dates as collection from pitfall traps, on a 15–30 m long transect along rows of traps. Samples were stored in 70% ethanol. The content of samples was sorted and the frequency of the different category items was estimated for each sample and each sampling period separately. Insects were dried in an oven for 72 h at 65 °C. The dry weight of each category from a single sample and a single sampling period was measured to the nearest 0.001 g. Items from pitfall traps and hand netting were pooled for analysis.

The arthropods sampled were divided into two groups: larger items (>5–7 mm body length) and smaller ones (<5–7 mm). Bauerová (1978) and Pont & Moulin (1985) concluded that 12–15 mm represents the minimum body length of prey captured by the greater mouse-eared bat. Only items belonging to the larger class (>5–7 mm) have therefore been considered in the subsequent analyses on prey selection. A lower threshold than that proposed by these authors was chosen, since the lesser mouse-eared bat can be expected to feed on smaller prey than does its relative, owing to its slightly smaller body size (21.8 vs 25. 1 g: Arlettaz *et al.* 1991). Finally, the biomass of the different categories was converted into a proportion of the total biomass of food abundance.

Prey selection

Taxa

Since the distributions of prey categories were strongly skewed, and even remained clumped after logarithmic transformation, we performed non-parametric and contingency table analyses. The relationships between the relative frequencies of prey categories in diet and habitats were estimated with Spearman's rank correlation. The distributions of prey categories in the bats' diet and in food supply were tested through χ^2 contingency table analysis. Analyses were restricted to the period May–July, when both faeces and insect samples were obtained. Average category proportions from woodland and orchard were used for the comparison in *M. myotis*, since their arthropod faunas are rather similar (comparison of proportions of the prey categories: $r_s = 0.398$, $n = 28$, $P = 0.042$).

Size

In order to test for selection of prey size, the frequency distribution of the body mass of the arthropods captured in the field was compared with the estimated body mass of those found in faeces. Only the predominant prey groups were considered in this analysis, namely Carabidae for *M. myotis* and Tettigoniidae for *M. blythii*, owing to the scarcity of comparative material obtained for other taxa.

The commonest fragment that enabled body size to be estimated from prey in faeces was the last segment of the tarsus. In order to achieve data independency, we considered only the mean length of all the last tarsus segments found within each faecal sample. Regression of the item's dry mass on tarsus last segment length was calculated for insects trapped and/or hand-netted. For Carabidae, the mean length of the last tarsus segment was calculated for each beetle as the average of the three measurements taken on the three types of legs (foreleg, midleg and backleg). In bush crickets, only the fore- and midleg were taken into account, since previous experiments with captive mouse-eared bats have shown that *M. blythii* always discards the weakly attached backlegs

of bush crickets, whilst this never happens with carabid beetles taken by *M. myotis*.

Results

Dietary niches

Twenty-one prey categories were distinguished within the 120 individual samples analysed (May–August): 16 in *M. myotis* and 11 in *M. blythii* (Fig. 1). Carabidae were by far the most abundant prey items in the diet of *M. myotis* (58.5% by volume), followed by Lepidoptera larvae (23.6%) and Gryllotalpidae (10.6%). The bulk of the diet of *M. blythii* consisted of Tettigoniidae (65.1%), Lepidoptera larvae (18.7%) and cockchafers *Melolontha melolontha* (7.7%) (Fig. 1). Altogether, these taxa made up 92.7% and 91.5% of the biomass consumed by *M. myotis* and *M. blythii*, respectively. All the remaining prey taxa were present in the diets of both species at less than 5% by volume. Seasonal variation in the diets only showed discrepancies from the general pattern (Fig. 1) during May, when Gryllotalpidae predominated in the diet of *M. myotis* (45.6% vs 31.9% for Carabidae, the second most important prey), whereas *Melolontha melolontha* was the most important prey of *M. blythii* (48.1%, against 20.6% for Lepidoptera larvae and 18.8% for

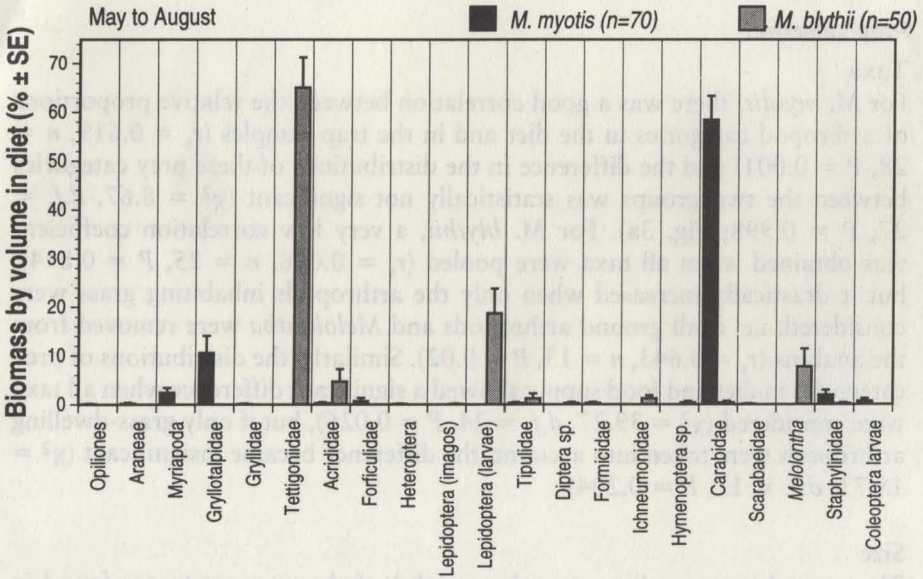

Fig. 1. Percentage (biomass by volume) of the 21 prey categories found in the diets of *M. myotis* and *M. blythii* from May to August. Error bars show the intraspecific variation in diet composition (SE = standard error of the mean). Taxa are arranged according to systematic order.

bush crickets). Overall, the trophic niches of the greater and lesser mouse-eared bats were narrow, with a few prey categories dominating the diet.

Relative biomass and phenology of prey

A total of 13 666 arthropod items were identified. The habitats of *M. myotis* and *M. blythii* contained 28 and 25 prey categories, respectively. Larger arthropod items (>5–7 mm body length) made up 77.4% of the total biomass (51.9% of the total frequency) of arthropods in woodland, 85.7% (60.5%) in orchards, and 80.9% (40.1%) in steppe (Fig. 2). However, since the frequency of occurrence of the different prey categories was highly correlated with their respective biomass within all three habitats (woodland, $r_s = 0.956$, $n = 20$, $P = 0.0001$; orchards, $r_s = 0.962$, $n = 14$, $P = 0.0005$; steppe, $r_s = 0.918$, $n = 25$, $P = 0.0001$), data on relative biomass also provide overall information about the relative frequency of the prey categories. Carabidae were by far the commonest prey in forested areas and orchards throughout the season (Fig. 2a,b). In orchards, *Gryllotalpa* was also common (Fig. 2b). Arachnida (essentially Aranaeidea) were predominant in orchards only early in the season, when no bat faeces were collected (April, Fig. 2b). Bush crickets (Tettigoniidae) comprised most of the biomass in steppe from June onwards. Their delayed larval development makes them a rare prey item early in the season (Fig. 2c).

Prey selection

Taxa

For *M. myotis*, there was a good correlation between the relative proportions of arthropod categories in the diet and in the trap samples ($r_s = 0.619$, $n = 28$, $P = 0.001$) and the difference in the distributions of these prey categories between the two groups was statistically not significant ($\chi^2 = 8.67$, $d.f. = 27$, $P = 0.998$; Fig. 3a). For *M. blythii*, a very low correlation coefficient was obtained when all taxa were pooled ($r_s = 0.046$, $n = 25$, $P = 0.814$), but it drastically increased when only the arthropods inhabiting grass were considered, i.e. if all ground arthropods and *Melolontha* were removed from the analysis ($r_s = 0.643$, $n = 13$, $P = 0.02$). Similarly, the distributions of prey categories in diet and food supply showed a significant difference when all taxa were considered ($\chi^2 = 39.27$, $d.f. = 24$, $P = 0.026$), but if only grass-dwelling arthropods were taken into account, the difference became insignificant ($\chi^2 = 15.73$, $d.f. = 12$, $P = 0.204$).

Size

The mean biomasses (in grams dry weight) of the prey categories found in the three habitats are shown in Fig. 4. The main prey eaten by either bat species was not only the most abundant, but also the largest among European arthropod fauna.

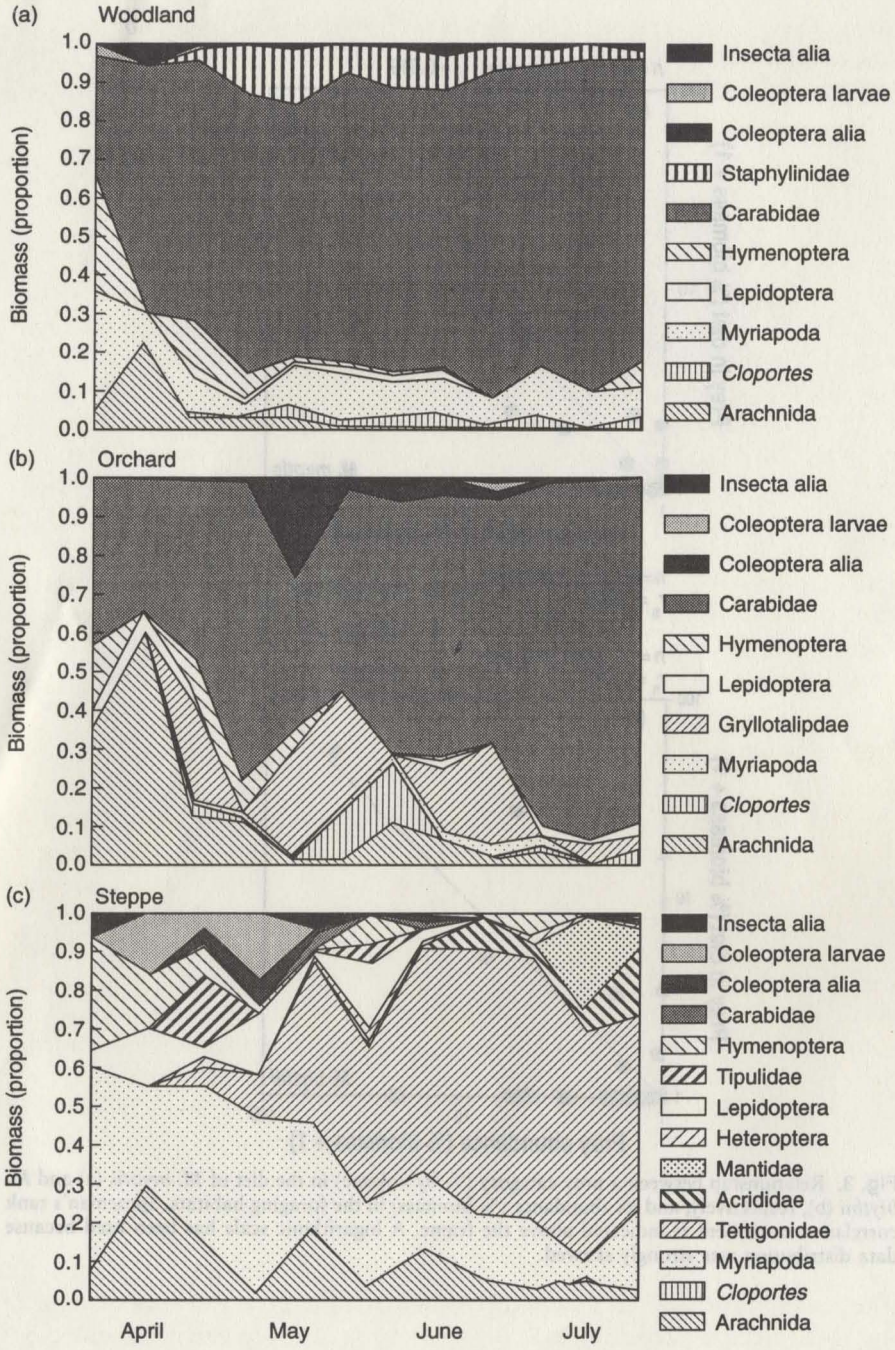

Fig. 2. Relative proportion and phenology of the main arthropod categories sampled in forest (a), in orchards (b) and in steppe (c). Taxa are arranged according to systematic order, from bottom to top.

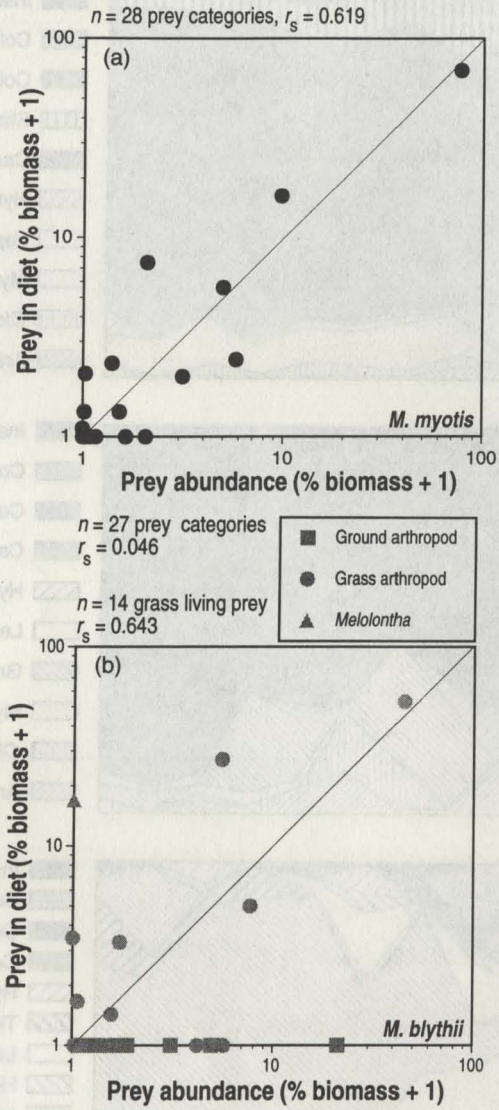

Fig. 3. Relationship between a prey category (% by volume) in the diet of *M. myotis* (a) and *M. blythii* (b), respectively, and its abundance (% biomass) in the foraging habitats. Spearman's rank correlation coefficient is indicated above the frame. A logarithmic scale has been used because data distribution was strongly skewed.

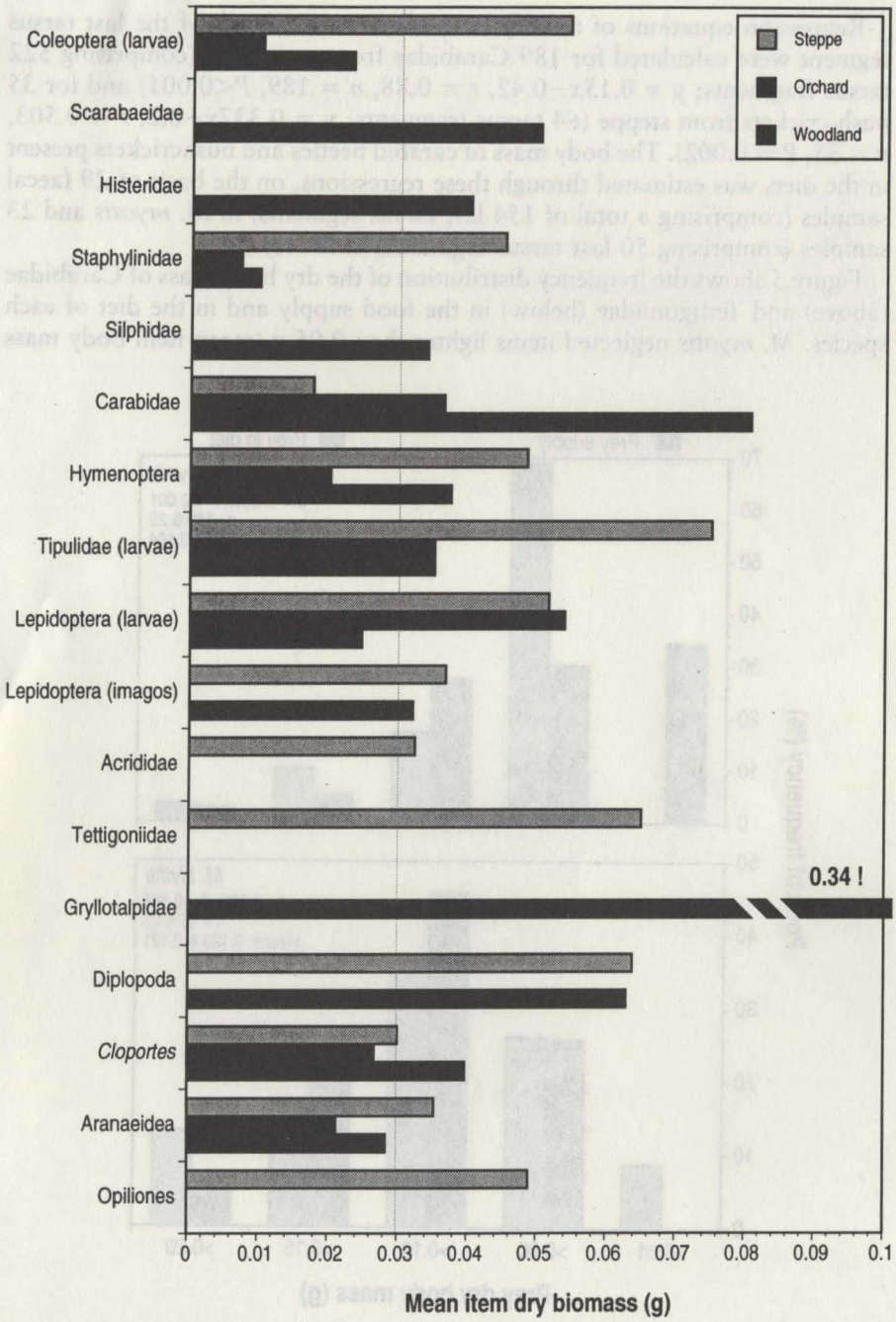

Fig. 4. Mean item biomass (g) of the main arthropod categories sampled in the field. Prey items whose average biomass was less than 0.03 g (line) in each of the three habitats are not shown. Taxa are arranged according to systematic order, from bottom to top.

Regression equations of the dry body mass vs the length of the last tarsus segment were calculated for 189 Carabidae from woodland (comprising 522 tarsus fragments; $y = 0.15x - 0.42$, $r = 0.88$, $n = 189$, $P < 0.001$) and for 35 bush crickets from steppe (64 tarsus fragments; $y = 0.337x - 0.2$, $r = 0.503$, $n = 35$, $P = 0.002$). The body mass of carabid beetles and bushcrickets present in the diets was estimated through these regressions, on the basis of 29 faecal samples (comprising a total of 154 last tarsus segments) in *M. myotis* and 23 samples (comprising 50 last tarsus segments) in *M. blythii*.

Figure 5 shows the frequency distribution of the dry body mass of Carabidae (above) and Tettigoniidae (below) in the food supply and in the diet of each species. *M. myotis* neglected items lighter than 0.05 g (mean item body mass

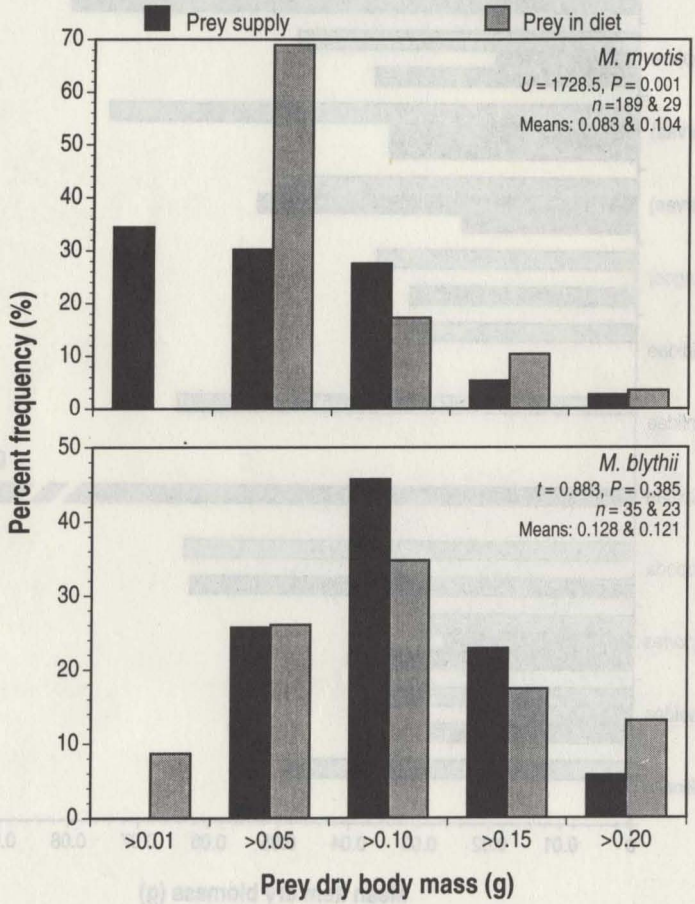

Fig. 5. Relative frequency distribution (%) of the different body mass classes of prey in the food supply and in the diet for *M. myotis* (above) and *M. blythii* (below). Results of statistical tests on means are indicated.

of carabid beetles from supply: = 0.83 g; from diet: = 0.104 g; $U = 1728.5$, $n = 189$ & 29, $P = 0.001$). On the other hand, *M. blythii* did not show any size preference for larger bush crickets (mean item body mass of bush crickets from supply: = 0.128 g; from diet: = 0.121 g; $t = 0.883$, $n = 35$ & 23, $P = 0.385$). On average, bush cricket prey were larger than carabid beetle prey. However, the lightest prey body mass from *M. myotis*' faecal samples was 0.063 g, which corresponds to a body length of 14.8 mm (regression of body length vs dry body mass of carabid beetles: $y = 70.888x+10.314$, $r = 0.96$, $n = 36$, $P < 0.001$), whereas the overall smallest estimated prey body mass of *M. blythii* was 0.043 g, which represents a body length of 13.5 mm (regression of body length against dry body mass of bush crickets: $y = 51.387x+11.324$, $r = 0.913$, $n = 27$, $P < 0.001$). The minimum size of the prey items captured by the lesser mouse-eared bat *M. blythii* would hence be slightly smaller than the size of prey eaten by its larger sibling species.

Discussion

Although the overall correlation between food abundance and diet was fairly good, some discrepancies arose: *M. myotis* underexploited small prey items (<0.05 g dry weight, or <14.8 mm body length), whereas *M. blythii* underexploited ground arthropods and overexploited cockchafers (*M. melolontha*). This may suggest selective feeding. However, these discrepancies may also stem from violations of two assumptions: first, food abundance may differ from actual food availability and second, foraging may have taken place in habitats other than those in which arthropods were sampled.

Because of their special acoustic sensory systems involved in predation, investigating prey availability in insectivorous bats is difficult (Faure & Barclay 1992). The absence of smaller prey items in the diet of *M. myotis* may be an effect of low detectability. Moreover, the use of passive acoustical cues for locating prey by *M. myotis* (Deutschmann 1991) probably further reduces the availability of smaller items, much more so than for echolocating foragers (Barclay 1985–1986; Barclay & Brigham 1991). Nevertheless, active food selection in terms of prey profitability cannot be definitely excluded in *M. myotis*. We have seen that *M. myotis* is able to catch molecrickets (Gryllotalpidae) which are, on average, four times heavier than carabid beetles (Fig. 4); handling costs thus probably do not differ substantially between carabid beetles of different sizes, and the capture of larger items would be energetically advantageous. *M. blythii* clearly neglected arthropods on the soil surface and preferred the grass-dwelling ones; this suggests that this species has evolved species-specific adaptations to detect prey in grass vegetation instead of on the ground.

Mouse-eared bats sometimes switch from their ground- or grass-gleaning behaviour to aerial feeding (R. Arlettaz unpubl.). Some apparent selection may be explained by such changes in foraging strategy. The most striking

example is the cockchafers, which were overexploited by *M. blythii*. In May, these beetles were found in large numbers in bats' diet but never in the pitfall traps or during hand netting. In fact, cockchafers do not occur on slopes covered by steppe because the soil is so shallow that their underground larvae do not find suitable conditions; in the study area, this beetle occurs exclusively in cultivated landscapes (A. Schmidt pers. comm.). Every three or four years, cockchafer populations explode, attracting mouse-eared bats, which then switch from their normal feeding behaviour to forage by hawking around tree crops (R. Arlettaz & R. Guttinger unpubl.). The relative discrepancy between the abundance of the second most important prey type, caterpillars, and their proportions in the diet may also indicate foraging activity which took place away from the traditionally used habitats. Flexibility in feeding behaviour of *M. myotis* was suspected by Kolb (1958), who also observed seasonal peaks in given categories of prey such as *M. melolontha, Tortrix viridana* or *Geotrupes*.

Our results do not falsify the hypothesis that the two species exert no active prey selection within their foraging habitats. Which peculiarities, if any, may then explain the narrow trophic niches observed in mouse-eared bats? *M. myotis* and *M. blythii* are among the largest vespertilionid bat species and they are by far the largest representatives of their genus, which includes 93 species (Nowak 1991). They are ground- and grass-gleaning bats, which may restrict the types of prey they can detect. They select species-specific foraging habitats where they use passive acoustical cues for prey detection (Deutschmann 1991). Hence, mouse-eared bats are specialized predators because they have evolved particular morphological, behavioural and physiological adaptations which restrict the resources they could use. Faure & Barclay (1992) termed such bats 'passive specialists'.

Bauerová (1978) compared the diet of *M. myotis* with prey abundance. Unfortunately, she set up pitfalls in half-open habitats, in the immediate surroundings of the colony, where she believed foraging took place, whereas recent radiotracking experiments showed that the main foraging grounds are located between 1.5 and 25 km away from the nursery roost but never in the immediate vicinity of the colony (Rudolph 1989; Audet 1990; R. Arlettaz unpubl.). Bauerová (1978) limited her analysis of ground-dwelling arthropods to carabid beetles and compared the proportions of the different species with their presence in the diet. Proportions of taxa were similar, but bats seemed to neglect the smaller items. Although there is a probable bias in her data on food supply, since smaller carabid beetles are much more frequent in open habitats than in forest (Thiele 1977), the apparent selection of carabid beetles of larger body size by *M. myotis* agrees with the present study.

The contrasted pattern observed in mouse-eared bats (narrow niches but absence of evidence for actively selective feeding) is not unique within insectivorous bat communities. At least one similar case is reported by

Faure & Barclay (1992), who considered *Myotis evotis* as a non-selective feeder despite the prevalence of moths in its diet. As pointed out by Fenton (1982), 'although the data from a number of studies have been used to support the suggestion that some insectivorous bats [actively] specialize to some level on particular types of insects, the evidence does not justify these suggestions'. Most microchiropteran species whose diet is documented exhibit broader niches than do mouse-eared bats or long-eared *Myotis*. Doubt must thus be expressed about reports of selective feeding in insectivorous bats unless reliable data on food abundance, or better food availability, can support it (Kunz 1988; Faure & Barclay 1992).

In a sample of 80 papers dealing with trophic ecology in insectivorous bats, 61 articles described diet composition but not food supply. Nevertheless, among them, nine addressed the question of dietary selectivity: four pleaded for a selective diet and five against. Although the 19 remaining papers all provided further information about food supply, eight did not address precisely the question of dietary selection. Six of the other 11 papers clearly concerned non-selective feeders (Swift & Racey 1983; Swift, Racey & Avery 1985; Barclay 1985–1986; Hoare 1991; Barclay & Brigham 1991; Fenton, Rautenbach, Chipese, Cumming, Musgrave, Taylor & Volpers 1993). Four further papers do not present definite evidence for trophic selectivity: (1) Brigham & Fenton (1991) hesitated between active and passive selection; (2) Anthony & Kunz (1977) demonstrated an apparent temporary prey selectivity in *M. lucifugus*; (3) Brigham & Saunders (1990) suggested that *Eptesicus fuscus* is probably a selective forager, but they did not make a clear distinction between food abundance and food availability. As they themselves hypothesized, small dipterans were thus overrepresented in their data on food 'availability', yet may well not be detectable by the bats, i.e. not actually available *sensu stricto*. Furthermore, Coleoptera, which made up the bulk of the diet, were scarce in traps, but, as hypothesized by Brigham & Saunders (1990) and stated by Jones (1990), there is no reliable technique for sampling correctly the abundance of flying beetles. (4) Sample & Whitmore (1993) reported an overexploitation of Lepidoptera but an avoidance of Coleoptera by *Plecotus townsendii*. However, as this species is probably a forest foliage-gleaner (Dalton, Brack & McTeer 1986; Krull 1992; and Sample & Whitmore 1993; *contra* Bell in Kunz & Martin 1982), passive specialization *sensu* Faure & Barclay (1992) may thus also act in this species. In fact, there is only a single paper that, in our opinion, seems to demonstrate feeding selectivity in an insectivorous bat species. Jones (1990) found that *Rhinolophus ferrumequinum* actually prefers preying on moths when abundant, avoiding other types of insects during moth population peaks in midsummer. The sophisticated echolocation systems of rhinolophids (mainly finely tuned constant-frequency calls) may allow much better prey discrimination than do other acoustic systems evolved in other bat families. Is this the reason why most, if not all, vespertilionids seem to feed unselectively?

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References

Anthony, E. L. P. & Kunz, T. H. (1977). Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology* **58**: 775–786.

Ariagno, D. (1973). Observations sur une colonie de petits et de grands murins (*Myotis oxygnathus* et *Myotis myotis*). *Annls Spéléol.* **28**: 125–130.

Arlettaz, R. (1987). Le molosse: première capture au gîte en Suisse. *Rhinolophe* No. 3: 10–14.

Arlettaz, R., Ruedi, M. & Hausser, J. (1991). Field morphological identification of *Myotis myotis* and *Myotis blythi* (Chiroptera, Vespertilionidae): a multivariate approach. *Myotis* **29**: 7–16.

Arlettaz, R., Ruedi, M. & Hausser, J. (1993). Ecologie trophique de deux espèces jumelles et sympatriques de chauves-souris: *Myotis myotis et Myotis blythi* (Chiroptera: Vespertilionidae). Premiers résultats. *Mammalia* **57**: 519–531.

Audet, D. (1990). Foraging behavior and habitat use by a gleaning bat, *Myotis myotis* (Chiroptera: Vespertilionidae). *J. Mammal.* **71**: 420–427.

Barclay, R. M. (1985–1986). Foraging strategies of silver haired (*Lasionycteris noctivagans*) and hoary (*Lasiurus cinereus*) bats. *Myotis* **23–24**: 161–166.

Barclay, R. M. R. & Brigham, R. M. (1991). Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? *Am. Nat.* **137**: 693–703.

Bauerová, Z. (1978). Contribution to the trophic ecology of *Myotis myotis*. *Folia zool.* **27**: 305–316.

Bogan, M. A., Setzer, H. W., Findley, J. S. & Wilson, D. E. (1978). Phenetics of *Myotis blythi* in Morocco. In *Proceedings of the fourth international bat research conference*: 217–230. (Eds Olembo, R. J., Castelino, J. B. & Mutere, F. A.). Kenya Literature Bureau, Nairobi.

Brigham, R. M. & Fenton, M. B. (1991). Convergence in foraging strategies by two morphologically and phylogenetically distinct nocturnal aerial insectivores. *J. Zool., Lond.* **223**: 475–489.

Brigham, R. M. & Saunders, M. B. (1990). The diet of big brown bats (*Eptesicus fuscus*) in relation to insect availability in southern Alberta, Canada. *NW. Sci.* **64**: 7–10.

Constant, P. (1960). Contribution à l'étude de *Myotis myotis* et *Myotis blythi oxygnathus*. *Sous le Plancher* **2–3**: 32–34.

Dalton, V. M. T., Brack, V., Jr. & McTeer, P. M. (1986). Food habits of the big-eared bat, *Plecotus townsendii virginianus*, in Virginia. *Va J. Sci.* **37**: 248–254.

Deutschmann, K. (1991). *Verhalten von* Myotis myotis *(Borkh., 1797) beim Fang fliegender Insekten und der Lokalisation von Beute am Boden.* Unpubl. Master's thesis: University of Tübingen, Germany.

Faure, P. A. & Barclay, R. B. (1992). The sensory basis of prey detection by the long-eared bat, *Myotis evotis*, and the consequences for prey selection. *Anim. Behav.* **44**: 31–39.

Felten, H., Spitzenberger, F. & Storch, G. (1977). Zur Kleinsäugerfauna West-Anatoliens. Teil IIIa. *Senckenberg. biol.* **58**: 1–44.

Fenton, M. B. (1982). Echolocation, insect hearing, and feeding ecology of insectivorous bats. In *Ecology of bats*: 261–285. (Ed. Kunz, T. H.). Plenum Press, New York and London.

Fenton, M. B., Rautenbach, I. L., Chipese, D., Cumming, M. B., Musgrave, M. K., Taylor, J. S. & Volpers, T. (1993). Variation in foraging behaviour, habitat use, and diet of large slit-faced bats (*Nycteris grandis*). *Z. Säugetierk.* **58**: 65–74.

Gould, E. (1955). The feeding efficiency of insectivorous bats. *J. Mammal.* **36**: 390–407.

Hoare, L. R. (1991). The diet of *Pipistrellus pipistrellus* during the pre-hibernal period. *J. Zool., Lond.* **225**: 665–670.

Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harb. Symp. quant. Biol.* **22**: 415–427.

Jones, G. (1990). Prey selection by the greater horseshoe bat (*Rhinolophus ferrum-equinum*): optimal foraging by echolocation? *J. Anim. Ecol.* **59**: 587–602.

Kolb, A. (1958). Nahrung und Nahrungsaufnahme bei Fledermäusen. *Z. Säugetierk.* **23**: 84–95.

Krull, D. (1992). *Jagdverhalten und Echoortung bei* Antrozous pallidus (*Chiroptera: Vespertilionidae*). PhD thesis: University of München, Germany.

Kunz, T. H. (1988). Methods of assessing the availability of prey to insectivorous bats. In *Ecological and behavioral methods for the study of bats*: 191–210. (Ed. Kunz, T. H.). Smithsonian Institution Press, Washington and London.

Kunz, T. H. & Martin, R. A. (1982). *Plecotus townsendii. Mammalian Spec.* No. **175**: 1–6.

Kunz, T. H. & Whitaker, J. O. Jr. (1983). An evaluation of fecal analysis for determining food habits of insectivorous bats. *Can. J. Zool.* **61**: 1317–1321.

MacArthur, R. & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* **101**: 377–385.

Neuweiler, G. (1984). Foraging, echolocation and audition in bats. *Naturwissenschaften* **71**: 446–455.

Neuweiler, G. (1990). Echoortende Fledermäuse. Jagdbiotope, Jagdstrategien und Anpassungen des Echohörens. *Biol. unserer Zeit* **20**: 169–176.

Nowak, R. M. (1991). *Walker's Mammals of the world* **1** (5th edn). Johns Hopkins University Press, Baltimore & London.

Pont, B. & Moulin, J. (1985). Etude du régime alimentaire de *Myotis myotis*. Méthodologie—premiers résultats. In *Actes du 9° colloque francophone de mammalogie, les chiroptères, Rouen* 1985: 23–33.

Rudolph, B. U. (1989). *Habitatwahl und Verbreitung des Mausohrs* (Myotis myotis) *in Nordbayern.* Unpubl. Master's thesis: University of Erlangen, Germany.

Ruedi, M., Arlettaz, R. & Maddalena, T. (1990). Distinction morphologique et biochimique de deux espèces jumelles de chauves-souris: *Myotis myotis* (Bork.) et *Myotis blythi* (Tomes) (Mammalia; Vespertilionidae). *Mammalia* **54**: 415–429.

Sample, B. E. & Whitmore, R. C. (1993). Food habits of the endangered Virginia big-eared bat in West Virginia. *J. Mammal.* **74**: 428–435.

Simmons, J. A., Fenton, M. B. & O'Farrell, M. J. (1979). Echolocation and pursuit of prey by bats. *Science* **203**: 16–21.

Strelkov, P. P. (1972). *Myotis blythi* (Tomes, 1857): distribution, geographical variability and differences from *Myotis myotis* (Borkhausen, 1797). *Acta theriol.* **17**: 355–380.

Swift, S. M. & Racey, P. A. (1983). Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. *J. Zool., Lond.* **200**: 249–259.

Swift, S. M., Racey, P. A. & Avery, M. J. (1985). Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. II. Diet. *J. Anim. Ecol.* **54**: 217–225.

Thiele, H. U. (1977). Carabid beetles in their environments. A study on habitat selection by adaptations in physiology and behaviour. *Zoophysiol. Ecol.* No. 10: 1–369.

Wittenberger, J. F. (1981). *Animal social behaviour.* Duxbury Press, Boston.