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## Differences in sensory ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis nattereri* (Chiroptera: Vespertilionidae)

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**Abstract** Coexisting animal species frequently differ in resource use in at least one niche dimension and thus avoid competition. While a range of morphological differences that lead to differentiation in animals' mechanical access to food have been identified, the role of sensory differences in within-guild niche differentiation has received less attention. We tested the hypothesis that differences in sensory access to prey contribute to resource partitioning between potentially competing species using two sympatric, similar-sized, congeneric bat species as a model system. Nursery colonies of Natterer's bat (*Myotis nattereri*) and Bechstein's bat (*Myotis bechsteinii*) roost in bat boxes in the same orchard and forage in forests and orchards nearby. In observations and behavioural experiments with freshly captured *M. bechsteinii*, we showed that individuals are able to hunt using prey-generated sound alone. In contrast, *M. nattereri* rarely uses prey-generated sound, but instead is able to find prey by echolocation very close to vegetation. In accordance with these behavioural data, we showed that *M. bechsteinii* has significantly larger ears than *M. nattereri*, providing it with superior detection and localization abilities for relatively low-frequency prey rustling sounds. We hypothesized that these differences

in sensory ecology of the two syntopic, congeneric species would contribute to resource partitioning, so that *M. bechsteinii* would find more noisy prey taxa, possibly hidden in vegetation, by listening for prey sounds, while *M. nattereri* would have better access to still prey using echolocation or associative learning. Analysis of faecal samples collected on the same nights from bat boxes occupied by each species corroborated this prediction. The diets of the two species differed significantly, reflecting their different prey perception techniques and thereby supporting the hypothesis that differences in sensory ecology contribute to niche differentiation.

**Keywords** Sensory ecology · Prey detection · Niche differentiation · Chiroptera · Gleaning

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### Introduction

Coexisting animal species frequently differ in resource use in at least one niche dimension and thus avoid competition (Munday et al. 2001; Bagchi et al. 2003; Denoel et al. 2004; Siemers and Schnitzler 2004; Tschapka 2004). However, in many cases, it is difficult to establish whether a pattern of niche differentiation is the result of ongoing competition, the 'ghost of competition past' (Connell 1980) or merely the outcome of divergent, possibly allopatric, evolutionary histories (Pianka 1981; Pfennig and Murphy 2003). While the evolutionary and ecological factors leading to different resource uses are still controversial, there is some agreement that difference in resource use, once established, will lead to resource partitioning, which mediates coexistence of species and ultimately promotes biodiversity (e.g., Tilman 1982; Svenning 1999; Fox 2004). There are current advancements reconciling the neutral theory of biodiversity (Hubbell 2001) with predictions of niche-differentiation-based theories (Chave 2004; Tilman 2004).

A number of studies on closely related species have identified morphological differences that lead to differentiation in their mechanical access to food (for a good

summary, see Schluter 2000). Examples include the classic case of Darwin's finches with differently sized and shaped beaks (Schluter and Grant 1984; Schluter et al. 1985) and also bumble bee species with different proboscis lengths and, hence, access to flowers with different corolla lengths (Pyke 1982). Coexisting mustelids and felids have been recorded to have different canine lengths that separate the prey size they can catch (Dyan et al. 1989, 1990); in a community of savannah-dwelling bats, correlation was recorded between the maximum bite force of the bats and the hardness of their prey species' exoskeletons (Aguirre et al. 2002). Less attention has been paid to interspecific differences in the senses used by animals to detect food and their role in promoting resource partitioning within foraging guilds (e.g., Tuttle et al. 1985; Bernays and Wcislo 1994). If a given prey type is easily detectable by one predator species but not by another, this would lead to the same prey being differentially available even if the two predators foraged in the same microhabitat. Swift and Racey (2002) showed differences in the sensory cues used to detect prey and also in diet composition over summer between two sympatric bat species (*Myotis nattereri* and *Plecotus auritus*) from different vespertilionid genera. Siemers and Schnitzler (2004) found in a performance test that five sympatric, congeneric species of bats, including *M. nattereri*, differed in their ability to find prey by echolocation close to echo-cluttering background substrates. The species' detection abilities were strongly correlated with parameters of echolocation calls used when searching for prey. The latter study suggested that sensory ecology plays a role in within-guild niche differentiation between closely related bat species, but field evidence is still needed.

Natterer's bat (*M. nattereri*) and Bechstein's bat (*Myotis bechsteinii*) are congeneric, similar-sized vespertilionid bat species (body mass of 4–13 g in *M. nattereri* and 6–13 g in *M. bechsteinii*; Baagoe 2001; Topal 2001) that are ecologically and morphologically similar, syntopic and potentially competing. Fossil evidence for the occurrence of both species in central Europe dates back to the early Pleistocene (summarized in Baagoe 2001; Topal 2001). Both species possess short, broad wings and low wing loading, as well as the ability to fly slowly and manoeuvrably and to hover (Norberg and Rayner 1987). Both forage close to vegetation and glean (i.e. catch directly from surfaces) a proportion of their diet (Taake 1992; Wolz 1993; Swift 1997; Swift and Racey 2002). Preferred foraging habitats for both species are woodland and orchard (Wolz 1986; Swift 1997; Siemers et al. 1999; Smith 2000; Kerth et al. 2001), and nightly activity patterns are similar (Wolz 1988; Siemers et al. 1999). Both *M. bechsteinii* and *M. nattereri* roost in groups of up to a few dozen individuals in tree holes, and both species readily accept bat boxes as artificial roosts (Kerth and König 1999; Siemers et al. 1999; Kerth et al. 2001). Both species use short, downwards, frequency-modulated echolocation calls of broad bandwidth (Staden 1995; Parsons and Jones 2000; Siemers and Schnitzler 2000, 2004; Siemers and Kerth 2005).

The main morphological difference between these two species is in ear length, which is 13–20 mm for *M. nattereri* and 19–29 mm for *M. bechsteinii* (Baagoe 2001; Topal 2001). In relation to their body size, Bechstein's bats have the longest ears among European *Myotis* species. Long ears are associated with foraging by listening to prey-generated sounds in species such as the European brown long-eared bat (*P. auritus*; Anderson and Racey 1991; Swift and Racey 2002) and the North American long-eared bat (*Myotis evotis*; Faure and Barclay 1992). Such so-called 'passively listening' bats use echolocation for spatial orientation, but locate arthropod prey by listening to the fluttering or rustling sounds they make. While previous studies (Siemers and Schnitzler 2000, 2004; Siemers 2001; Swift and Racey 2002) have shown that *M. nattereri* does not use this strategy, but uses echolocation and associative learning to find prey, there is some behavioural evidence suggesting that *M. bechsteinii* relies on listening for prey sounds (Staden 1995; Staden and Schnitzler 1995).

In our study, the presence of colonies of both *M. nattereri* and *M. bechsteinii* living in bat boxes in the same orchard and having access to the same foraging habitat allowed us to investigate their interaction. The aims of the study were to establish the degree of resource partitioning in these congeneric, syntopic bats and to relate differences in diet composition to their respective methods of prey perception. We hypothesized that: (1) based on ecomorphological (ear size) and behavioural evidence, the two species would show differences in their sensory ecologies; and (2) these differences would contribute to niche separation. We predicted that noisy (fluttering or walking) prey caught in contact with vegetation would dominate in the diet of *M. bechsteinii*, while *M. nattereri* would forage more on silent prey, much of which would be captured close to, but not in direct contact with, the substrate.

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## Methods

### Study site

Droppings were collected, and bats were caught for morphometric measurements and behavioural experiments from bat and bird boxes in an orchard close to Mössingen (Baden-Württemberg, Germany) in the foothills of the Swabian Alb (48°23'N, 9°01'E; licensed by Regierungspräsidium Tübingen Az.73-8/8852.21 and Az.56-6/8852.15). The area was situated between 470 and 700 m asl and was characterized by orchard belts, beech-dominated deciduous forests and monocultures of spruce (*Picea abies*); villages and roads lay interspersed. We regularly checked a total of 29 bat and bird boxes, most of which were used by both *M. nattereri* (Siemers et al. 1999; Siemers and Schnitzler 2000) and *M. bechsteinii*. Both colonies changed roosts every few days, and the two species sometimes used the same box consecutively. However, mixed groups of both species in the same box were never observed during 8 years of regular visits to the study area (Siemers, unpublished data).

## Morphometrics

Bats were captured by hand in their bat boxes in order to take measurements. Bechstein's bats were measured in August 2002, at a time when juveniles were present in the colony, while Natterer's bats were measured in May 2004. *M. bechsteinii* was classified as adult or juvenile by epiphyseal fusion and fur colour (Stebbins 1968). All bats were sexed and weighed (precision 0.1 g; Ohaus LS 200), and forearm and ear lengths were measured from the base of the tragus to the ear tip (precision 1 mm; ruler). To compensate for the slight difference in body size between the two species when comparing ear sizes, we calculated ear size residuals from a regression of ear length on forearm length. We obtained data from 41 adult female *M. nattereri* and from 12 (7 female, 5 male) juvenile and 16 (13 female, 3 male) adult *M. bechsteinii*.

## Prey detection behaviour

Observations were restricted to *M. bechsteinii* in the present study, since previous studies have already shown (Siemers and Schnitzler 2000, 2004; Swift and Racey 2002) that *M. nattereri* locates prey essentially by echolocation close to substrates, continues to emit calls throughout attacks on arthropod prey and makes little or no use of prey-generated sounds as a cue.

We made our observations with six freshly captured Bechstein's bats in a flight tent with fine nylon gauze walls, a waterproof nylon roof and dimensions of 3.5×3.5 m ground area and 2.5 m central height. On most occasions, it was situated in the orchard where the bats were captured either by hand inside their day roosts or by statically held hand nets as they emerged to forage. In one experiment, two interconnected tents, erected at Tübingen University, were used. Experiments were carried out over four nights in 1998, 1999 and 2002 using two female *M. bechsteinii* each time (all adults, except for one juvenile in 1999). Experiments 1–4 were performed as follows:

1. A fine gauze cage (0.2 m base diameter×0.3 m height) containing approximately 15 moths (*Noctua pronuba* and some other large noctuid moths) was hung in the centre of the tent, surrounded by twigs and foliage from trees. The moths maintained a constant fluttering inside the cage. Two adult female *M. bechsteinii* were released into the tent, first separately and then together, and their reactions to the moths were observed and recorded (2002).
2. While the bats were active in the flight tent, live fluttering moths (mostly *N. pronuba*) were held against the grass on the tent floor (1999) or against the gauze wall of the tent (2002) by a pair of blunt forceps or by fingers.
3. Two flight tents were connected by a narrow adjoining doorway (1998). With two adult female bats hanging from the roof of one tent, a live fly (*Calliphora* sp.) was tethered in the other, where it made a clearly audible buzzing sound. The bats' reactions were recorded.

4. In the absence of any arthropod prey, one of us (B.M.S.) produced a vocal imitation of moth fluttering sounds in the centre of the tent (1999 and 2002). Any reaction from the bats was noted.

Part of the behaviour was videotaped (Orion Combi 600 LCD recorders) with charge-coupled device (CCD) video cameras (50 half-frames/s; Sanyo, VC 1950) under stroboscopic infrared illumination (custom-made; Department of Animal Physiology, University of Tübingen).

## Diet analysis

Matched samples of faecal pellets collected from colonies of each species on the same nights were analysed. The orchard was visited in the afternoon and the boxes were inspected, causing as little disturbance to the bats as possible; those occupied by each species were identified, and a clean piece of paper towel was placed on the floor. On the following morning, provided the same species was in the same box, the paper towel was removed, and the accumulated faecal pellets were dried and stored. In this way, matched pairs of samples were obtained for 11 nights over the summers of 2002 and 2003; this permitted a valid comparison of diets to be made between species without the need to investigate prey availability. The samples were later analysed by extracting and identifying chitinous arthropod fragments under a binocular microscope (Shiel et al. 1997). Ten faecal pellets were selected at random from each sample for analysis. The only exception was 1 June 2002, when only eight pellets were available from Bechstein's bats. Consequently, we chose eight pellets, instead of ten, from Natterer's bats for that night as well. Arthropod fragments were identified to order level and, wherever possible, to family level. Results were expressed as percentage frequency (i.e., the percentage of the total number of fragments identified, which were attributed to each arthropod group). We retrieved a total of 1,196 prey fragments from faecal pellets of *M. bechsteinii* and 1,223 from those of *M. nattereri*.

## Statistics

Because some data sets deviated significantly from normal distribution (Kolmogorov–Smirnov test using Lilliefors adaptation;  $p < 0.05$ ), we used non-parametric tests throughout. All statistics were computed using Systat 10 (SPSS).

## Results

### Morphometrics

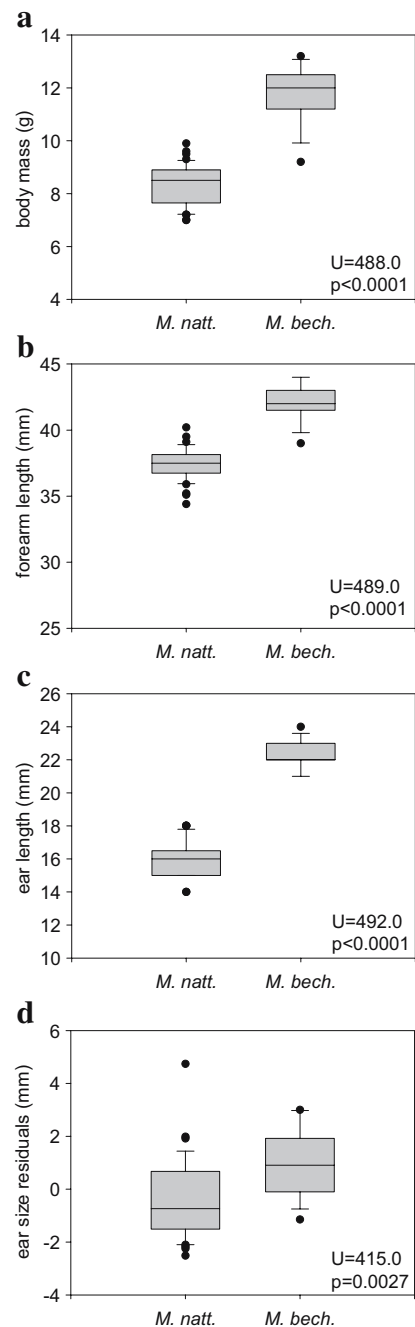
Juvenile Bechstein's bats were lighter, had shorter forearms and had relatively longer ears than adults [mass,  $11.5 \pm 1.3$  g for adults (mean±SD),  $9.8 \pm 0.7$  g for juveniles, Mann–Whitney  $U$  test,  $U = 137.0$ ,  $p = 0.0046$ ; forearm,  $41.9 \pm 1.3$  mm

for adults,  $41.0 \pm 0.9$  mm for juveniles,  $U=140.0$ ,  $p=0.0344$ ; ear size residuals,  $0.3 \pm 1.9$  mm for adults,  $1.7 \pm 1.5$  mm for juveniles,  $U=45.0$ ,  $p=0.0175$ ]. Within *M. bechsteinii*, there was no age dimorphism in absolute ear length ( $U=87.5$ ,  $p=0.6763$ ). Within the two age classes, there was no sexual dimorphism in any of the four morphometric parameters, the only exception being that adult *M. bechsteinii* males had lower masses than adult *M. bechsteinii* females (males,  $9.4 \pm 0.4$  g; females,  $11.8 \pm 1.0$  g;  $U=25.0$ ,  $p=0.0412$ ). In *M. nattereri*, we obtained measurements from adult females only. Therefore, we likewise used only data from adult *M. bechsteinii* females for an interspecific comparison of morphometric parameters, as presented in Fig. 1. This excluded any sex-related or age-related variation. Body mass and forearm length were both lower in *M. nattereri* than in *M. bechsteinii* (Fig. 1). Both absolute and relative ear lengths (ear size residuals from a regression on forearm lengths) were considerably larger in *M. bechsteinii* (Fig. 1). When all four parameters were compared using the entire data sets, including male and juvenile *M. bechsteinii*, differences were likewise significant (forearm,  $U=1140.0$ ,  $p<0.0001$ ; mass,  $U=1034$ ,  $p<0.0001$ ; ear lengths,  $U=1148.0$ ,  $p<0.0001$ ; ear size residuals,  $U=895.0$ ,  $p=0.0001$ ).

#### Prey detection behaviour

Experiments 1–4 yielded the following results and observations:

1. Both *M. bechsteinii* flew inside the tent for 10 min, passing the moth cage frequently. Both then approached the cage, made several close passes around it and, on a total of six occasions, hovered directly in front of it. On three occasions, a bat landed on the moth cage and crawled up. The bats were clearly able to detect the moths inside the cage, despite it being surrounded by twigs and foliage from trees.
2. When a moth held by forceps fluttered against the grass or the forceps itself, the bats flew towards the sound source, even when direct (echolocation) access was concealed by the experimenter's hand or body. The bats then landed and retrieved the prey (Video S1). When a moth held by forceps fluttered against the tent wall, one of the bats, which was resting on the same wall, immediately turned its head towards the sound. It then climbed down the wall, seized the moth in its mouth and ate it. In this way, it captured three moths in rapid succession.
3. One of the two resting bats took flight as soon as the fly began to buzz. It flew directly into the second tent, where it landed on and captured the fly. The dividing wall between the tents would definitively have precluded detection of the prey using echolocation.
4. On a total of four occasions, bats approached the person making the imitation moth fluttering sound and hovered directly in front of the person's mouth (Video S2). On two of these occasions, the bat touched the person's mouth with its wings or tail membrane.

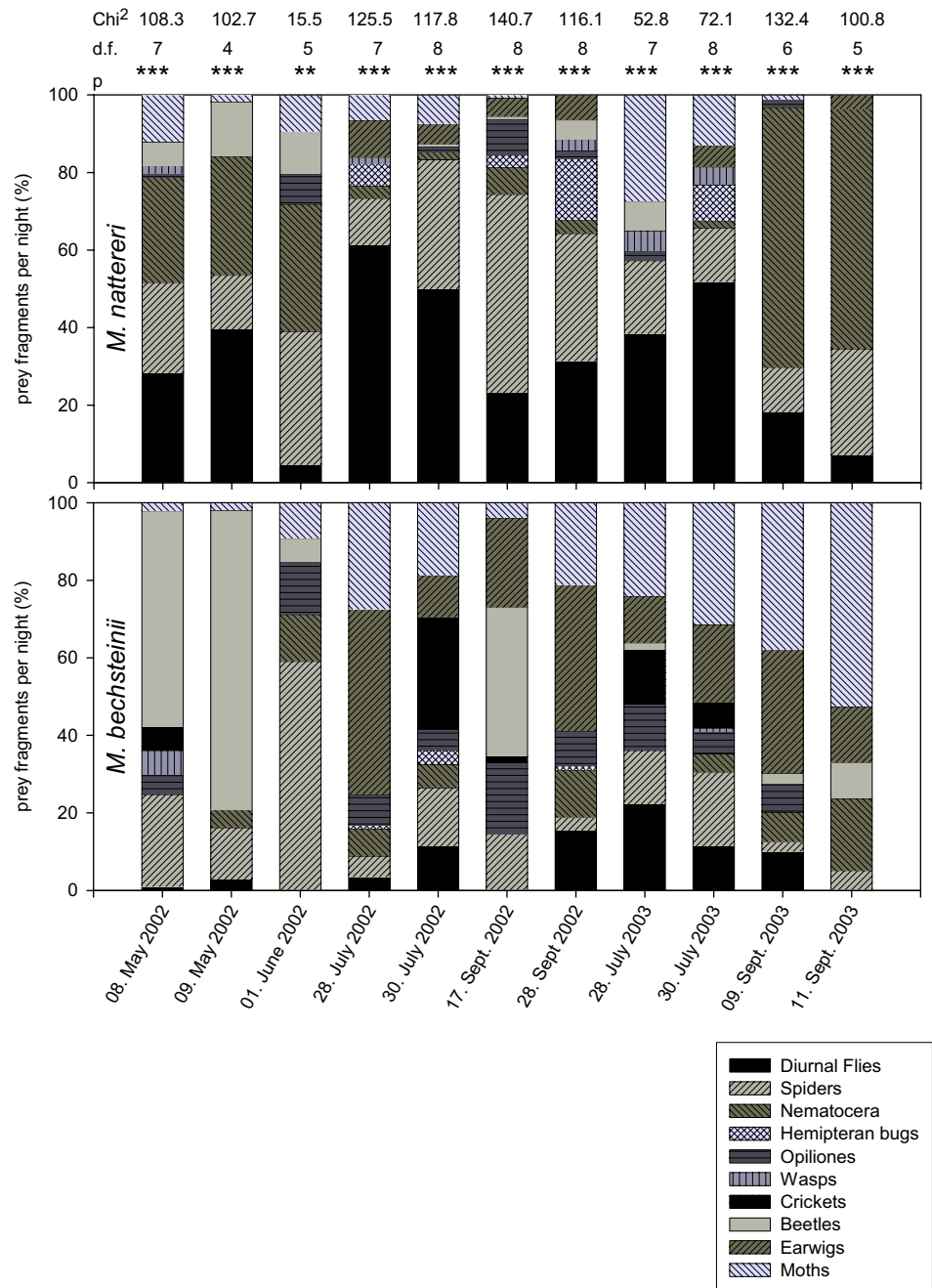


**Fig. 1** *M. nattereri* differed from *M. bechsteinii* in **a** body mass, **b** forearm length, **c** ear length and **d** ear size residuals from a regression of ear length on forearm length. The grey box includes the 25th to 75th percentiles (median indicated by horizontal line); the whiskers give the 10th and 90th percentiles, respectively; and the dots depict data points outside these. In each panel, the Mann–Whitney  $U$  test and  $p$  value are given for interspecific comparison. Only data from adult female bats are included ( $n=41$  *M. nattereri* and  $n=13$  *M. bechsteinii*)

#### Diet analysis

In a night-by-night comparison, the diet composition of the two bat species differed significantly on all 11 nights for which we obtained matched faecal samples (Fig. 2). When prey categories were analysed separately, there was also a

**Fig. 2** Night-by-night comparison of the relative importance of different prey categories in the diets of *M. nattereri* (upper panel) and *M. bechsteinii* (lower panel) for 11 nights where matched samples could be obtained. The table above the two panels gives the results from chi-square tests comparing the diets between species separately for each night. The tests were computed on the raw data (absolute numbers of fragments retrieved), whereas the graph shows percentages of prey fragments per prey category and night for easier comparison. Prey categories that did not occur in the droppings of either of the two species on a given night were excluded from the chi-square test for that night (therefore, the degrees of freedom *df* differ between nights). Significance levels: \* $p < 0.05$ , \*\* $p < 0.001$ , \*\*\* $p < 0.0001$

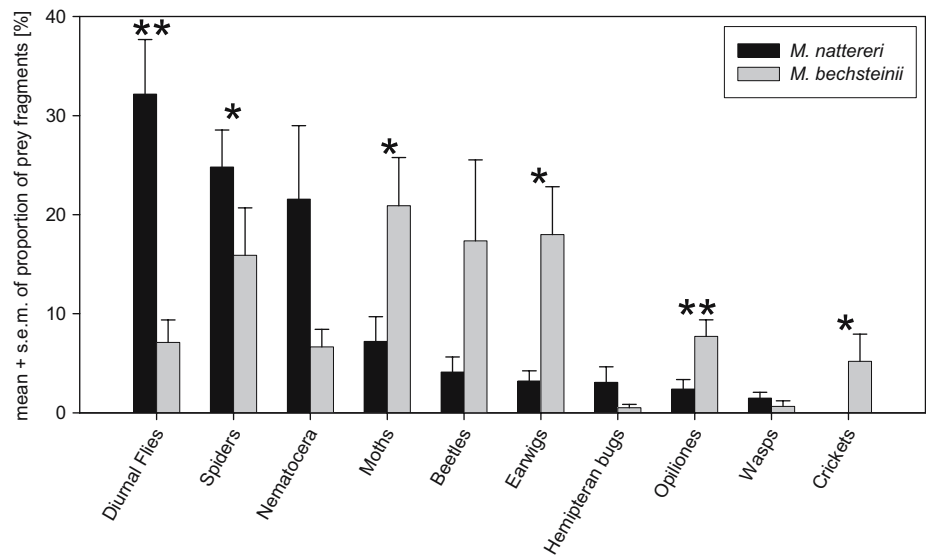


significant difference in the numbers of fragments from various arthropod categories identified from matched nightly samples for six of ten categories (Fig. 3). The diet of *M. bechsteinii* was dominated by moths (Lepidoptera), crickets (Orthoptera; Tettigoniidae), harvestmen (Opiliones) and earwigs (Dermaptera), while *M. nattereri* ate mainly diurnal flies (Diptera; Cyclorrhapha and Brachycera), spiders (Arachnida) and longhorn flies (Diptera; Nematocera).

Beetles (Coleoptera) were consumed to a considerable, and not statistically different, degree by both species. We therefore reanalysed the numbers of beetle fragments at family level. We found remains from four families, which we tentatively grouped either as cursorial, potentially loud

(Carabidae and Scarabaeidae) or vegetation-based, more stationary and likely to be silent (Chrysomelidae and Curculionidae). Of the four nights that yielded matched samples of beetle remains for both bat species, there was a significant difference in the occurrence of 'loud' vs 'silent' beetle families between bat diets on three of them (Table 1). *M. nattereri* showed a higher proportion of spider remains in the diet than *M. bechsteinii*. However, identification of spiders beyond class level relies heavily on soft body parts, such as genitalia (Werner Rose, personal communication), most of which do not survive passage through a bat's gut in recognizable form. We were therefore able to identify relatively few spiders as far as family, although our limited data indicated that both web-spinning (likely to be silent and

**Fig. 3** Comparison of *M. nattereri* and *M. bechsteinii* diets by prey category. The mean proportions (%) of each category in the species' diets are plotted ( $n=11$  nights) in order of decreasing importance of prey categories in the *M. nattereri* diet. The asterisks give significance levels from a Wilcoxon signed rank test computed on the raw data (absolute numbers of fragments retrieved per category; paired test design on the matched nights). For details on beetles and spiders, see text and Table 1. Significance levels: \* $p<0.05$ , \*\* $p<0.001$



hanging from threads) and cursorial (likely to be noisy) families occurred in the diets of both bat species.

## Discussion

This study has established that *M. bechsteinii* and *M. nattereri* partition food resources effectively, and it also proposes a mechanism for partition that depends on differences in sensory perception between the two species. While 'loud' prey producing low-frequency rustling or fluttering sounds can be heard and located within vegetation by *M. bechsteinii*, *M. nattereri* makes little use of prey-generated sounds, suggesting that 'loud' but hidden prey is effectively unavailable to it.

Our measurements on live bats show that *M. bechsteinii* has significantly larger ears than *M. nattereri*, even when corrected for body size. Long ears are associated with acute low-frequency hearing and the ability to hunt by listening to prey-produced sound in a number of bat species (Coles et al. 1989; Faure and Barclay 1992). Obrist et al. (1993) measured transfer functions in bat pinnae and showed that the large ears of 'passively listening' species provide high

gain and high directionality at relatively low frequency. Since frequencies that extend downwards into the human audio range contain most of the energy of insect rustling and fluttering sounds (Schmidt et al. 2000; Hubner and Wiegerebe 2003), the longer ears of *M. bechsteinii* therefore support our hypothesis that listening to prey sounds is a more important aspect of foraging in this species than in *M. nattereri*.

Our behavioural observations provided evidence that *M. bechsteinii* was able to detect prey under conditions that precluded the use of echolocation. These included conditions in which the prey was effectively hidden by structures between bat and prey (foliage, hand and tent roof) or by background clutter from substrate (Arlettaz et al. 2001; Siemers and Schnitzler 2004). Since visual cues were likewise concealed in several of these situations and odour was a very unlikely cue for prey detection in insectivorous bats over a distance (Faure and Barclay 1992; Siemers and Schnitzler 2000), the only consistently available cue was prey-produced sound. This clearly also applied to the human imitation of insect fluttering sound, which triggered prey capture behaviour. We conclude that prey-generated sound is both necessary and sufficient for prey detection in *M.*

**Table 1** Beetle fragments retrieved from the two species' droppings

Night	Bat species	Number of fragments of Carabidae/Scarabaeidae <sup>a</sup>	Number of fragments of Chrysomelidae/Curculionidae <sup>b</sup>	Fisher exact test $p$ value
8 May 2002	<i>M. bechsteinii</i>	50	4	<0.0001
	<i>M. nattereri</i>	0	6	
9 May 2002	<i>M. bechsteinii</i>	71	1	<0.0001
	<i>M. nattereri</i>	0	16	
17 September 2002	<i>M. bechsteinii</i>	50	0	0.0196
	<i>M. nattereri</i>	0	1	
29 July 2003	<i>M. bechsteinii</i>	0	2	1.0 (ns)
	<i>M. nattereri</i>	0	9	

<sup>a</sup>Carabidae and Scarabaeidae are cursorial, mainly epigeic insects that can be considered to be potentially acoustically conspicuous ('loud')

<sup>b</sup>Chrysomelidae and Curculionidae are more vegetation-based, more stationary and therefore less conspicuous ('silent')

*bechsteinii*. This is supported by an earlier study (Staden 1995), which found that Bechstein's bats frequently locate prey by listening to prey sound. In contrast, *M. nattereri* locates prey mainly by echolocation in the air (Siemers and Schnitzler 2000, 2004). Taken together, available ecomorphological and behavioural evidence give rise to our hypothesis that a different sensory ecology would result in different prey availabilities for the two species, even when foraging in the same microhabitat. As predicted, the diets of the two bat species differed on all nights of comparison. The most important prey categories for *M. bechsteinii* in the study area were moths, earwigs and ground beetles, all of which were noisy and likely to have been gleaned within vegetation, while *M. nattereri* fed mainly on silent prey (cyclorrhaphan flies, spiders and crane flies) that could have been caught in the air close to vegetation or gleaned from plant surfaces. Natterer's bats glean by trawling through vegetation using the tail membrane as a net (Swift and Racey 2002) and also use associative learning (Siemers 2001), in which they learn to attack productive prey patches. This method enables them to find silent, resting arthropods on echo-cluttering vegetation surfaces. While such prey might not be accessible for *M. bechsteinii*, the latter species will effectively be able to detect and locate noisy arthropods, which it then captures in directed attacks.

Spiders were an important prey group for both bat species, and further research is needed into the latter's relative abilities to find and capture the former. We would predict a quantitative analysis to show that *M. bechsteinii* finds more cursorial spiders that produce noise when walking on, for example, leaf litter, while *M. nattereri* preys more extensively on web-building spiders that present themselves as noiseless but accessible for echolocation a few centimetres from vegetation. The case of the beetles that we determined to family level further corroborated our hypothesis, in that *M. bechsteinii* ate predominantly cursorial, terrestrial and potentially noisy beetles, while *M. nattereri* foraged on vegetation-based, potentially silent beetles. While the sample size was small and further research is needed, it is highly unlikely that the difference was due to the slightly larger *M. bechsteinii* simply being able to attack and handle bigger beetles. In an earlier study in Scotland (Swift and Racey 2002), Natterer's bats captured a considerable number of robust chafers (*Serica brunnea*; body length 10–11 mm) of similar size to the scarabaeid and carabid beetles eaten by Bechstein's bats in the present study. In the Scottish study, however, the chafers were caught by the Natterer's bats as they took flight from short grass; they would therefore have been detectable by echolocation. The considerably higher proportion of moths in the diet of *M. bechsteinii* than in that of *M. nattereri* deserves special attention. Tympanate moth species are able to detect the echolocation calls of bats and avoid capture (Fullard and Thomas 1981; Jones and Rydell 2003), so bats that can hunt by listening and can use low-amplitude echolocation calls for spatial orientation only are able to include more moths in their diet (Swift and Racey 1983; Shiel et al. 1991; Faure and Barclay 1992). In accordance with their respective methods of prey detection, the 'passively listen-

ing' *M. bechsteinii* in the present study ate far more moths (21% of its diet over 11 nights) than did *M. nattereri* (7% over 11 nights).

In summary, our morphometric, behavioural and diet data suggest that the two congeneric, ecologically similar, syntopic bat species have different sensory bases of prey detection and different access to prey even in the same habitat, and therefore show a considerable degree of food niche differentiation. We conclude that differences in sensory ecology might play an important role in the structuring of niche space not only between, but also within, ecological guilds.

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