Dietary composition, resource partitioning and trophic niche overlap in three forest foliage-gleaning bats in Central Europe

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A diverse syntopic bat community was studied in Central Europe. The study was primarily aimed at forest bats utilizing a foliage-gleaning foraging strategy (*Myotis nattereri*, *M. bechsteinii* and *Plecotus auritus*). The results indicated the foliage-gleaning foraging strategy and the effective resource partitioning. Once a certain diet item comprises an important food resource for one bat species, it is usually exploited much less by the other two bat species, and despite important seasonal dietary changes this pattern lasts throughout the entire season. Dietary composition varies more among the entire guild of forest foliage-gleaning bats than it does between these species and their morphological siblings or evolutionarily related species (e.g., *Plecotus auritus* vs. *P. austriacus* or *Barbastella barbastellus*, *Myotis nattereri* vs. *M. emarginatus*). The results are not fully consistent with the predictions of sensory ecology, which presume that bats with longer ears feed more frequently on prey that generates sound. The results do not support the hypothesis that rare bats exploit a narrower range of prey. The relatively rare *M. bechsteinii* has a wider trophic niche, whereas the more common *P. auritus* exploits a narrower range of prey. Comparison of dietary composition and morphological and echolocation parameters indicates that larger species feed on harder prey, species with longer ears are moth-eating specialists and species with a higher call intensity exploit small dipterans, probably in uncluttered habitats.

Key words: gleaning bats, foraging strategy, trophic niche overlap, *Myotis nattereri*, *Myotis bechsteinii*, *Plecotus auritus*

INTRODUCTION

It has been suggested that insectivorous bats, sometimes feed on whatever insects are available at a given time and place (Belwood and Fenton, 1976; Fenton and Morris, 1976) and study of syntopic community provides an excellent opportunity to test the hypothesis that insectivorous bats simply feed on the available insect taxa: if bats eat what is available, then all bats taken at the same time and place should essentially feed on the same foods (e.g., Whitaker, 2004). The current study is focused on three bat species of similar body size, dwelling in the same habitat and furthermore, applying the same foraging strategy. Aforementioned prediction of Whitaker (2004) leads to a guiding hypothesis that the studied species should have very similar diet compositions. On the other hand, it is alternatively hypothesised that animals living in the same habitat are usually distinguished by various niche

parameters that enable their coexistence (MacArthur and Pianka, 1966; Siemers and Schnitzler, 2004). Therefore, the question arises, how syntopic species share the available food resources. Different species should consequently diverge in their trophic niches despite their occurrence in the same habitat. The main aim of the study is to compare two alternative hypotheses being previously mentioned. Niche partitioning and coexistence ability together with regional species pool and distribution patterns determines species composition, richness and morphological assembly mechanisms in bat assemblages (e.g., Arita, 1997; Moreno *et al.*, 2006).

The diets of *Myotis nattereri* (Kuhl, 1817), *Plecotus auritus* (Linnaeus, 1758) and *Myotis bechsteinii* (Kuhl, 1817) were studied throughout most of Europe (Bauerová and Červený, 1986; Beck, 1991; Beck, 1995; Swift and Racey, 2002; Siemers and Swift, 2006; C. M. McAney and C. Morris, in litt.,

and many others). All three species are medium sized bats classified as foliage gleaners preferring broadleaved forests (Swift and Racey, 1983; de Jong, 1995; H. Schofield and C. Morris, in litt., etc.). Notable variation in the diets of all three species among different sites was recorded along with significant seasonal variability (Swift and Racey, 1983, 2002; Shiel *et al.*, 1991), showing the remarkable ecological flexibility of these bat species. It is therefore vital to study their ecology simultaneously in syntopic populations if we wish to identify actual trophic niche overlap or understand their resource partitioning and levels of competition. Such studies are nonetheless rare and we can only judge actual trophic niche overlap from a few papers (e.g., Shiel *et al.*, 1991; Taake, 1992; Swift and Racey, 2002; Siemers and Swift, 2006).

The mechanism of resource partitioning is believed to be at least partially based on different sensory ecology. *Plecotus auritus* and *M. bechsteinii* frequently hunt using prey-generated sounds, whereas *M. nattereri* rarely uses such sounds, but instead, is able to find prey by echolocation very close to vegetation (Anderson and Racey, 1991, 1993; Swift and Racey, 2002; Siemers and Schnitzler, 2004; Siemers and Swift, 2006). *Plecotus auritus* also uses visual cues to capture its prey (Eklöf and Jones, 2003). The ecological significance of chiropteran morphology and echolocation calls has been widely discussed by many authors (e.g., Findley and Wilson, 1982; Norberg and Rayner, 1987; Bogdanowicz *et al.*, 1999) along with its correspondence with foraging strategies. All three studied species possess broad and short wings (i.e. with a low aspect ratio), can hover or fly slowly and manoeuvrably and have relatively low wing loading. The main differences between these species are in ear length and body size. In comparison to the others, *M. nattereri* has much shorter ears and an echolocation loudness and *M. bechsteinii* has a larger body size (Norberg and Rayner, 1987; Schober and Grimmberger, 1997; Řehák, 1999; Siemers and Swift, 2006).

The aims of the study were: (1) to analyse the dietary composition of particular species and quantify trophic niche parameters; (2) to compare in detail the dietary composition of the species being studied simultaneously in sympatry and syntopy; (3) to quantify trophic niche overlap and illustrate resource partitioning among the studied species; (4) to compare dietary composition with echomorphological parameters of the studied bats.

MATERIAL AND METHODS

Bat Netting

Bats were netted in front of cave entrances in 1994–1998 once a month from March to November with the exception of April, when two nettings were carried out. Bats were kept individually in cloth sacks and their faecal pellets were collected for later analysis under a stereomicroscope. In total 553 faecal pellets were collected from 149 individuals of *M. nattereri*, 450 pellets from 58 individuals of *M. bechsteinii*, and 4038 pellets from 578 individuals of *P. auritus*.

Dietary Analysis

Faecal pellets were softened using water, and teased apart with a dissecting needle and a pair of tweezers under a binocular microscope. Particular prey categories were identified using comparative slides, methodological studies (McAney *et al.*, 1991), entomological keys and a reference collection of insects. We distinguished some 23 taxonomic and ecological groups (Lepidoptera adults, Larvae, Dermaptera, Araneae, Brachycera, Tipulidae, Chironomidae, other Diptera, Coleoptera, Trichoptera, Orthoptera, Heteroptera, Neuroptera, Blattodea, Hymenoptera, Auchenorrhyncha, Chilopoda, Sternorrhyncha, Ephemeroptera, Plecoptera, Mecoptera, Raphidioptera, and Opilionida). We ignored several cases of fleas (Siphonaptera) and mites (Acarina) in our figures and analyses, since these are not, in fact, prey items, but most probably a result of grooming activity. These taxa were found rarely and their volume was negligible. Sawfly larvae (Symphyta) were identified in two cases in the diet of *M. nattereri*. Due to their similar morphology and way of life we coupled these two cases with the data for caterpillars (Lepidoptera larvae) to one category Larvae. Presented results are part of a wider study covering the entire bat community of the studied site described by Reiter *et al.* (2010) and some results of dietary analyses have already been presented (Andreas *et al.*, 2001, 2012; Andreas, 2002).

Expressing The Results and Statistical Analysis

To express the results of dietary analyses we modified the formulas suggested by McAney *et al.* (1991) for percentage occurrence (% oc) and percentage frequency (% f). The unit for analyses was not one pellet, but a sample of faecal pellets collected from one animal. Percentage volume (% vol) was calculated according to Obrtel and Holišová (1974). Percentage occurrence shows the proportion of bats in the corresponding data set that fed on a particular prey category. The percentage frequency indicates the relative importance of the particular categories according to the frequencies in which they are consumed. The percentage volume demonstrates the proportion of the volume represented by each particular prey in the set of faeces samples analysed.

The trophic niche breadth index, B, was calculated according to Levin's formula (Krebs, 1989). The diversity index H' was calculated according to Shannon-Wiener's formula (Krebs, 1989). The trophic niche overlap O_{jk} was expressed according to the formula reported by Pianka (1974). The equitability index J' was based on Shannon-Wiener's formula (Krebs, 1989).

The difference between two proportions was computed using STATISTICA for Windows, © StatSoft, Inc. The *P*-level

was calculated based on the *t*-value for respective comparison:

$$|t| = [(N1*N2)/(N1+N2)]^{2}*|p1-p2|/(p*q)^{2},$$

where p = (p1*N1+p2* N2)/(N1+N2) and q=1-p (StatSoft, 2001).

We used CCA (canonical correspondence analysis), a uni-modal method of direct ordination, to identify interrelations between the dietary composition of particular bat species and their echolocation and morphological characteristics. CCA is a uni-modal method of direct ordination that directly expresses the relation between dietary composition, invertebrate taxa in the bat diet and independent variables (echolocation and morphological characteristics — ter Braak and Šmilauer, 1998). Input data matrix (rows=samples; columns=volume of particular prey categories, echolocation and morphological characteristics) was composed of prey volume data of all samples after arcsin transformation. Calculations were performed using CANOCO for Windows (ter Braak and Šmilauer, 1998).

Study Site

Material was collected from the Ledové sluje caves (48°53'03"N, 15°50'40"E; 380 m a.s.l.) in the Podyjí National Park in the south-east of the Czech Republic. These comprise a large system of pseudokarst caves and crevices on a slope of a river bank, and form a unique bat swarming site, at which 20 bat species have been recorded to date (Reiter *et al.*, 2010). The community is dominated by indigenous species of the Central European forested landscape, whereas thermophilous species specific for the adjacent Pannonian-like lowlands are only an accessory faunal element (Reiter *et al.*, 2010). The majority of the study site is covered with natural forest vegetation (mostly Aceri-Carpinetum) complemented with patches of wet meadows and river plus riparian habitat (Chytrý, 1996). The other habitats in the vicinity (< 5 km) are natural beech forests, river and creek valleys, ponds, fields, a reservoir and several villages.

RESULTS

Dietary Composition

The most frequently consumed prey of *M. nattereri* were spiders (Araneae), true flies as a whole (Diptera), earwigs (Dermaptera) and moths (Lepidoptera adults). The other important food items were Larvae and true bugs (Heteroptera). Diurnal flies (Brachycera), especially the families Muscidae, Calliphoridae and Asilidae, were the most important among true flies (Diptera). Other recorded families of true flies (Diptera), such as Tipulidae, Chironomidae, Culicidae, Simuliidae or Cecidomyiidae, were of lesser importance.

The most important dietary components of *M. bechsteinii* were Orthoptera, especially Ensifera (e.g., *Meconema thalassinum*), and moths (Lepidoptera ad.), particularly medium-sized and larger species (wingspan > 30 mm). The other important items were Larvae, beetles (Coleoptera), particularly Carabidae, Scarabaeidae, Curculionidae, and true flies (Diptera), especially diurnal species (Brachycera), mainly Muscidae, Syrphidae, Rhagionidae and Asilidae. Neuropterans (Neuroptera), and in particular, Chrysopidae, were also frequently found, but their volume in the diet was relatively low.

Moths (Lepidoptera ad.) unequivocally dominated the diet of *P. auritus*. The prevailing size category was medium-sized individuals (wingspan ca.
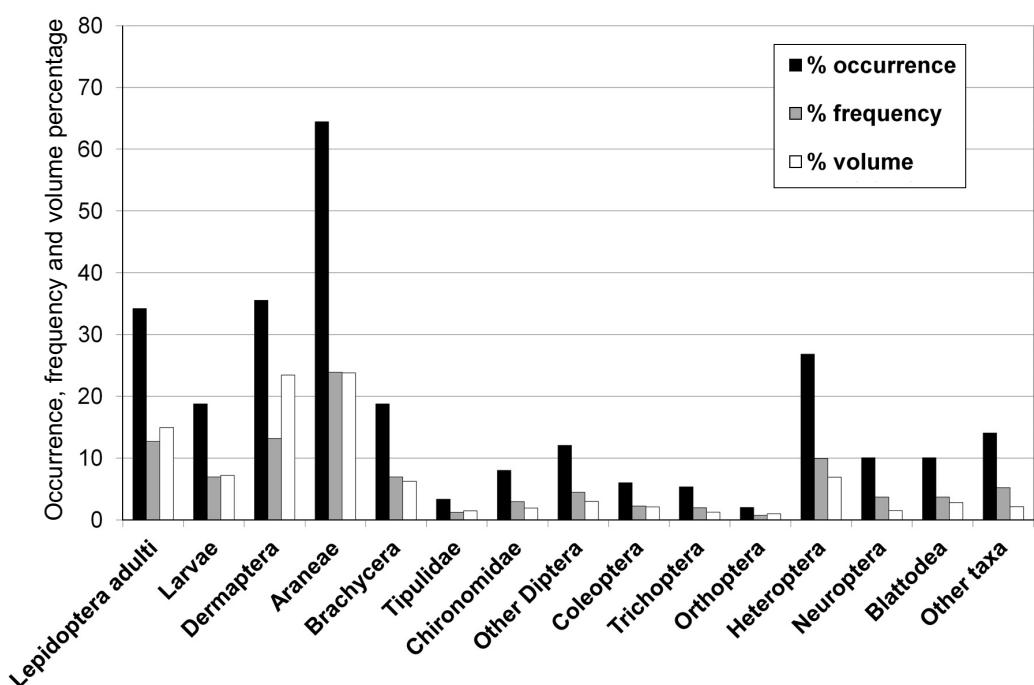

FIG. 1. Dietary composition of *M. nattereri* (whole season, 553 faecal pellets from 149 individuals). Other taxa: Hymenoptera, Auchenorrhyncha, Chilopoda, Sternorrhyncha, Plecoptera, Opilionoda
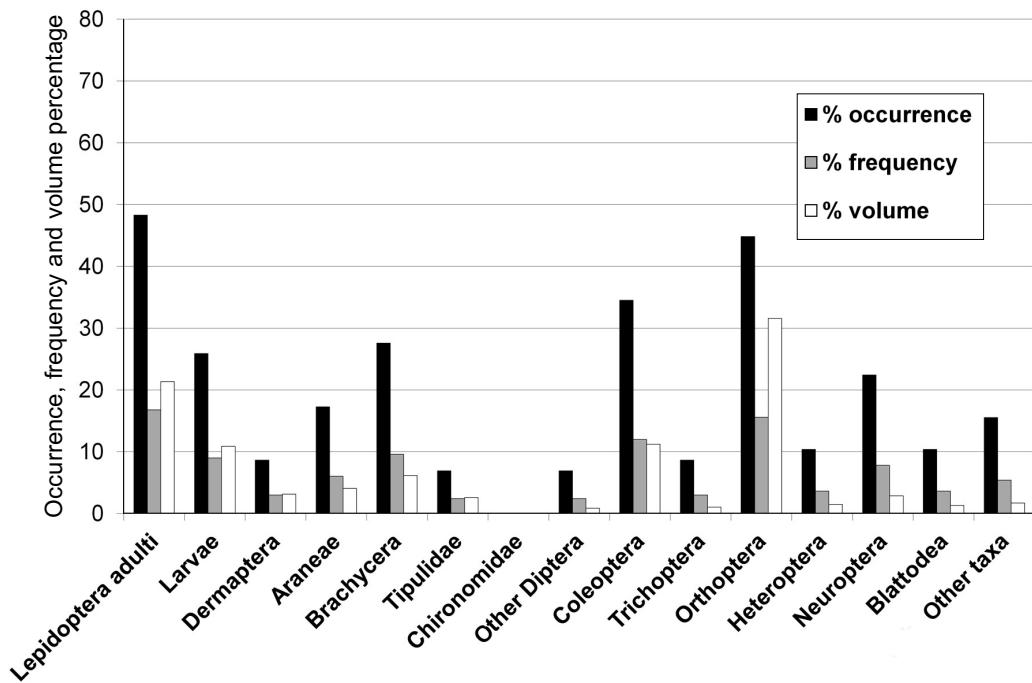
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FIG. 2. Dietary composition of *M. bechsteinii* (whole season, 450 faecal pellets from 58 individuals). Other taxa: Hymenoptera, Chilopoda, Raphidioptera

30–40 mm). The other important dietary components were earwigs (Dermaptera) and diurnal flies (Brachycera), especially Muscidae, Syrphidae and Calliphoridae. Within some seasons of the year the nematoceran family Tipulidae also played an important role in the diet of this species. The other relatively important dietary components were spiders (Araneae) and neuropterans (Neuroptera).
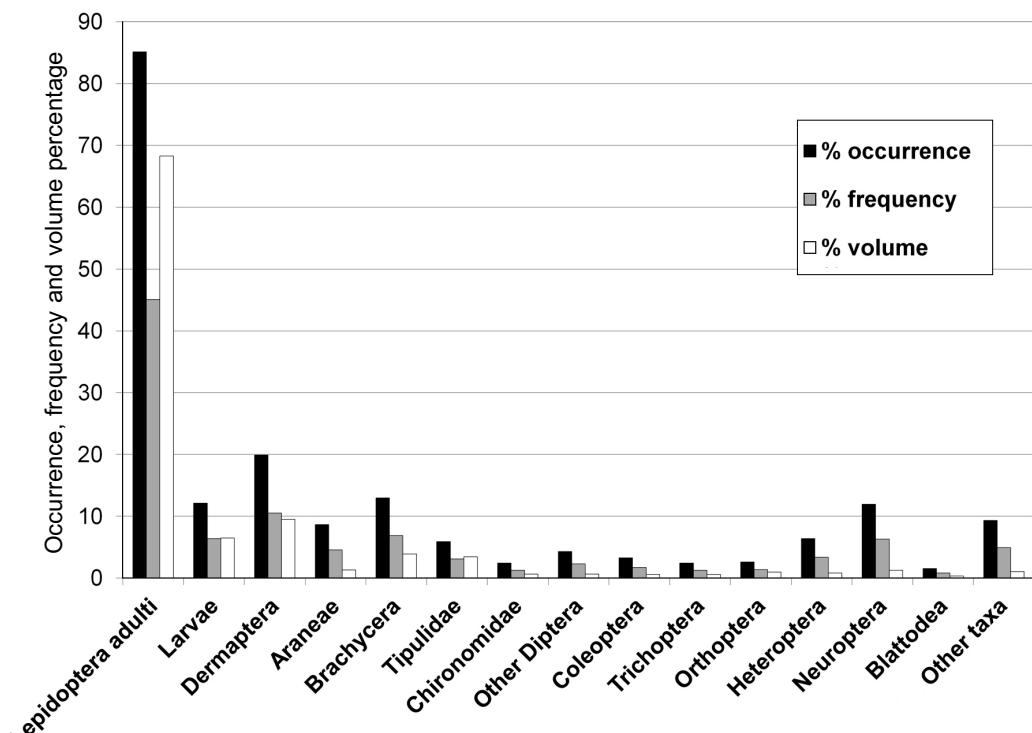

FIG. 3. Dietary composition of *P. auritus* (whole season, 4038 faecal pellets from 578 individuals). Other taxa: Hymenoptera, Auchenorrhyncha, Chilopoda, Sternorrhyncha, Ephemeroptera, Plecoptera, Mecoptera, Opilionoda

Trophic Niche Parameters and Resource Partitioning

The results show a degree of trophic niche displacement among the studied species. Once a certain dietary item comprises an important food resource for one bat species (% occurrence ca. 20% or more), it is exploited much less by the other two bat species and this pattern of mutual vicariation in important dietary items lasts for the entire season (Table 1). The exceptions are diurnal flies (Brachycera), which were consumed approximately equally by all three species, and earwigs (Dermaptera). This dietary component was a relatively important prey not only for *M. nattereri* but also for *P. auritus* (Table 1).

As far as trophic niche breadth (B), diet diversity (H') and equitability (J') are concerned, we recorded the lowest values in the case of *P. auritus*. The highest values of B, H' and J' among the studied species were found for *M. bechsteinii*.

Value of Pianka's trophic niche overlap index O_{jk} (Table 2) was highest between *M. bechsteinii* and *P. auritus* ($O_{jk} = 0.696$), mainly due to their higher consumption of moths (Lepidoptera ad.). Substantial overlap was also observed in the consumption of diurnal flies (Brachycera), Larvae and neuropterans (Neuroptera). *Myotis nattereri* and *P. auritus* ($O_{jk} = 0.605$) mainly shared moths (Lepidoptera ad.), Larvae, diurnal flies (Brachycera) and earwigs (Dermaptera). *Myotis nattereri* and *M. bechsteinii* ($O_{jk} = 0.612$) showed overlap in the consumption of moths (Lepidoptera ad.), Larvae and diurnal flies (Brachycera).

A diverse bat community and high bat numbers at the study site enabled syntopic collection of sufficient samples from several other species. In terms of trophic niche overlap, we found that within the whole bat community, the studied species showed no substantial overlap with the other forest gleaners (with the exception of the overlap between *M. bechsteinii* and *P. auritus*), although they are believed to use a relatively similar foraging strategy in the same habitat. We observed the greatest overlap in dietary composition with their morphological siblings (*M. nattereri* vs. *M. emarginatus*, *P. auritus* vs. *P. austriacus*) or with their close relatives in the tribe Plecotini (*P. auritus* vs. *B. barbastellus*).

Seasonal Changes in Dietary Composition

We observed seasonal changes in the dietary composition of the studied species (Table 3). Among the most important were an increase in the proportion of orthopterans (Orthoptera) in the diet of *M. bechsteinii* from spring to autumn, and the lower proportion of brachyceran Diptera and higher proportion of Tipulidae in the diet of all species in the spring. Higher proportion of Larvae in the diet of *M. nattereri* and *M. bechsteinii* in spring samples is worth mentioning too. Nevertheless, the main traits of dietary composition remained the same for the whole season and corresponded well with the traits shown in Fig. 4. Likewise, trophic niche partitioning and the degree of niche overlap in important prey

TABLE 1. The dietary composition of particular species expressed as percentage occurrence and significance of recorded differences (differences between two proportions), * — $P < 0.05$, ** — $P < 0.01$, *** — $P < 0.001$. Results refer to the whole season. Other taxa: see Figs. 1–3

| Prey category/species	% oc			Differences		
	M. nattereri	*M. bechsteinii*	*M. nattereri*	*M. nattereri* vs *M. bechsteinii*	*M. bechsteinii* vs *P. auritus*	*P. auritus* vs *P. auritus*
Lepidoptera adults	34.2	48.3	85.1	n.s.	***	***
Larvae	18.8	25.9	12.1	n.s.	**	*
Dermaptera	35.6	8.6	19.9	***	*	***
Araneae	64.4	17.2	8.7	***	*	***
Brachycera	18.8	27.6	13.0	n.s.	**	n.s.
Tipulidae	3.4	6.9	5.9	n.s.	n.s.	n.s.
Chironomidae	8.1	0.0	2.4	*	n.s.	**
Other Diptera	12.1	6.9	4.3	n.s.	n.s.	***
Coleoptera	6.0	34.5	3.3	***	***	n.s
Trichoptera	5.4	8.6	2.4	n.s.	**	n.s.
Orthoptera	2.0	44.8	2.6	***	***	n.s.
Heteroptera	26.8	10.3	6.4	*	n.s.	***
Neuroptera	10.1	22.4	11.9	*	*	n.s.
Blattodea	10.1	10.3	1.6	n.s.	***	***
Other taxa	14.1	15.5	9.3	–	–	–
n and *d.f.*	*n* = 149	*n* = 58	*n* = 574	*d.f.* = 205	*d.f.* = 630	*d.f.* = 721
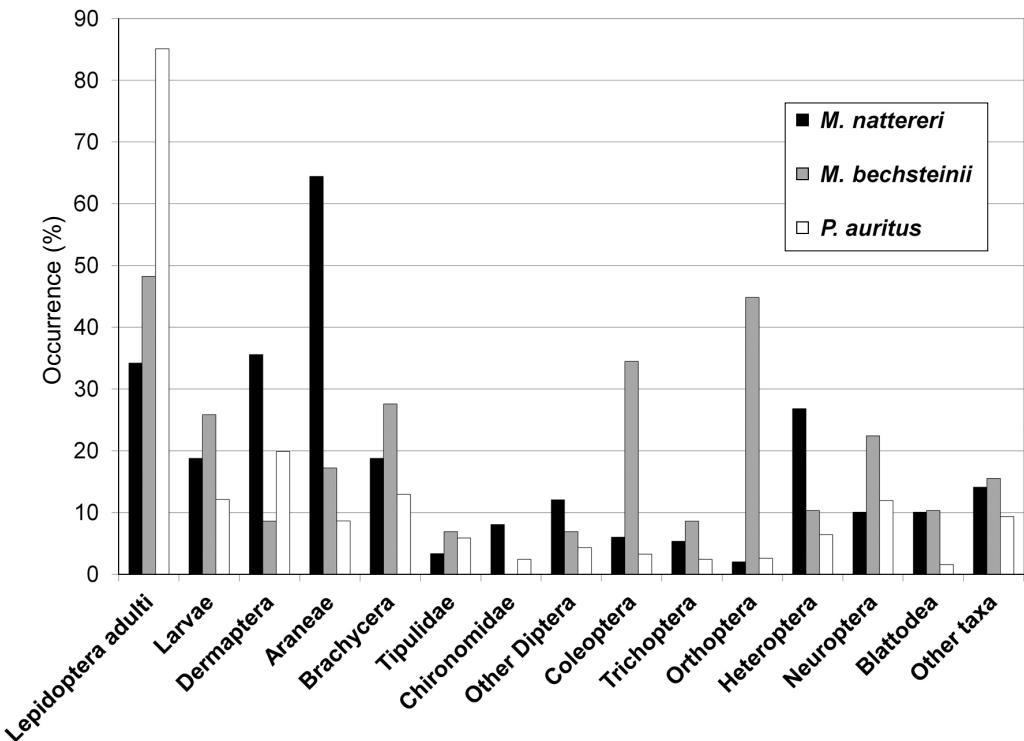
FIG. 4. Dietary composition of all three species expressed as percentage occurrence

categories remained stable, and with some exceptions those items important for one species were preyed upon much less frequently by the other two bat species.

We observed an interesting phenomenon within the seasonal changes in the proportion of Larvae in the diet of *P. auritus* and *M. bechsteinii*, resembling seasonal competitive exclusion in the hunting of this prey item. Larvae were consumed by both species between May and September. *Myotis bechsteinii* significantly ($P < 0.01$) reduced its utilization

of this food resource from July (% oc = 60, $n = 10$) to August (% oc = 10.4, $n = 29$). Inversely, *P. auritus* increased consumption of Larvae significantly ($P < 0.001$) from July (% oc = 0, $n = 79$) to August (% oc = 60.5, $n = 76$). The significance was tested using difference between two proportions method.

Morphological and Echolocation Parameters

We compared the dietary composition of all species at the study site for which 10 or more faeces samples were collected. A significant non-random character of the position of bat species according to their dietary composition on the gradients of morphological and echolocation characteristics (see Table 4) was indicated using CCA. Among the factors most significantly corresponding with the variation in dietary composition were the characteristics of body size, such as weight, forearm length and wind loading. Other important factors were the relative ear size (ear length/forearm length ratio) and the peak frequency of the echolocation call (Andreas, 2002). The three studied species significantly differ according to aforementioned morphological and echolocation characteristics ($P < 0.01$), but the extent of explained variability of the dataset on all canonical axes is very low (0.6%). CCA also
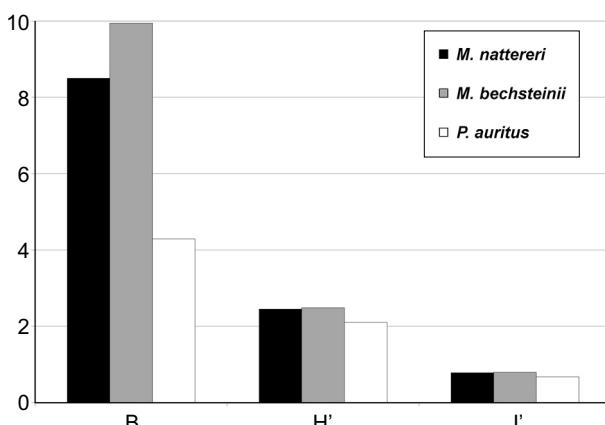

FIG. 5. Values of Levin's trophic niche breadth index B, diversity index H' and equitability index J'

TABLE 2. Values of Pianka's trophic niche overlap index O_{jk} within the framework of the whole bat community at the study site (whole season) (after Andreas, 2002). *B.ba.* — *Barbastella barbastellus*, *E.ni.* — *Eptesicus nilssoni*, *E.se.* — *E. serotinus*, *M.be.* — *Myotis bechsteinii*, *M.br.* — *M. brandti*, *M.da.* — *M. daubentonii*, *M.em.* — *M. emarginatus*, *M.my.* — *M. myotis*, *M.ms.* — *M. mystacinus*, *M.na.* — *M. nattereri*, *P.au.* — *Plecotus austriacus*, *P.at.* — *P. auritus*, *R.hi.* — *Rhinolophus hipposideros*

Species	*B.ba.*	*E.ni.*	*E.se.*	*M.be.*	*M.br.*	*M.da.*	*M.em.*	*M.my.*	*M.ms.*	*M.na.*	*P.au.*	*P.at.*	*R.hi.*
M. nattereri	0.39	0.46	0.35	0.61	0.56	0.38	0.79	0.13	0.61	–	0.35	0.61	0.27
M. bechsteinii	0.62	0.58	0.54	–	0.40	0.26	0.48	0.23	0.40	0.61	0.62	0.70	0.25
P. auritus	0.93	0.58	0.46	0.70	0.29	0.19	0.38	0.07	0.29	0.61	0.94	–	0.23
Analysed samples	156	34	56	58	118	183	34	42	53	149	41	578	10

showed that particular species significantly differ in the diet composition ($P < 0.01$) and species identity explains important part of dataset variability (48.8%) on all canonical axes. The diet significantly ($P < 0.01$) varied due to morphological and echolocation characteristics which explain the most important part of the variability of analysed diet dataset (50.6%). A larger body size seems to be linked to feeding on larger (Orthoptera) and/or harder prey (several groups of Coleoptera). Longer ears seem to be related to the consumption of larger moths. Low wing loading, higher peak frequency may enable effective foraging on silent motionless prey (Araneae). Higher echolocation loudness is probably associated with aerial hawking of swarming Chironomidae or other Diptera.

DISCUSSION

Dietary Composition

The results of dietary analyses from different parts of distribution ranges show considerable local and seasonal differences in dietary compositions in *M. nattereri* (Shiel *et al.*, 1991; Taake 1992; Swift, 1997; Swift and Racey, 2002), *M. bechsteinii* (Taake, 1992; Wolz, 1993; Siemers and Swift, 2006) and *P. auritus* (Heinicke and Krauss, 1978; Swift and Racey, 1983; Rydell, 1989; Barataud, 1990; Robinson, 1990; Shiel *et al.*, 1991; Taake, 1992; Beck, 1995) which suggests relatively high flexibility in resource utilization. It is also in good concordance with important seasonal changes observed at out studied site.
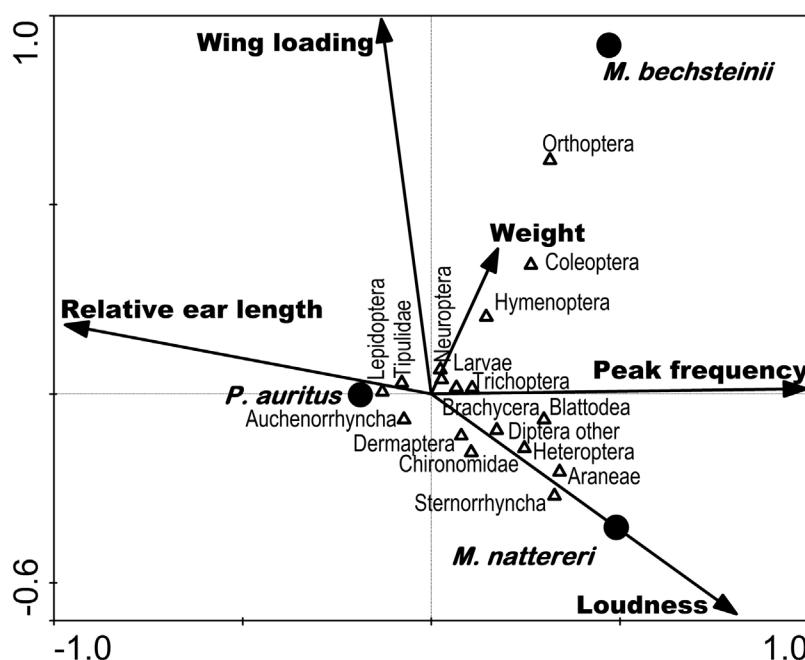

FIG. 6. Canonical correspondence analysis (CCA). Triplot of interrelations between prey categories, dietary composition of particular bat species and their echolocation and morphological characteristics (weight, peak frequency, relative ear length – i.e. ear length to forearm length LA/LAt, wing loading, echolocation loudness). Prey taxa with negligible representation (Raphidioptera, Ephemeroptera, Mecoptera and Chilopoda) were excluded from the graph to keep the figure uncluttered and well arranged. Different Coleoptera were grouped into one category for the same reason

TABLE 3. The dietary composition of particular species expressed as percentage occurrence (% oc) in spring (March, April, May), summer (June, July, August) and autumn (September, October, November)

Species	Season	Analysed sample	Lepidoptera adults	Larvae	Dermaptera	Araneae	Brachycera	Tipulidae	Chirono-midae	Other Diptera	Coleoptera	Tricho-ptera	Ortho-ptera	Hetero-ptera	Neuro-ptera	Blatodea	Other taxa
M. nattereri	Spring	25	44.0	40.0	28.0	52.0	0.0	16.0	16.0	28.0	8.0	8.0	0.0	8.0	8.0	4.0	20.0
	Summer	71	31.0	9.9	29.6	66.2	29.6	1.4	9.9	7.7	8.5	8.5	2.8	36.6	16.9	12.7	15.5
	Autumn	53	34.0	20.8	47.2	67.9	13.2	0.0	1.9	11.3	1.9	0.0	1.9	22.6	1.9	9.4	9.4
M. bechsteinii	Spring	5	0.0	80.0	0.0	20.0	0.0	40.0	0.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0	0.0
	Summer	42	59.5	23.8	9.5	16.7	31.0	4.8	0.0	9.5	42.9	7.1	42.9	9.5	28.6	9.5	14.3
	Autumn	11	27.3	9.1	9.1	18.2	27.3	0.0	0.0	0.0	9.1	18.2	72.7	18.2	9.1	18.2	27.3
M. auritus	Spring	217	83.4	4.6	20.3	10.1	2.8	12.4	5.5	3.2	5.1	0.5	0.0	0.9	6.0	0.0	5.1
	Summer	158	88.0	29.1	1.3	3.8	19.6	1.9	1.3	6.3	3.8	3.2	1.9	8.2	22.2	3.2	12.7
	Autumn	199	84.4	7.0	34.7	11.1	19.1	2.0	0.0	4.0	1.0	4.0	6.0	11.1	10.1	2.0	11.6

Due to considerable number of studies concerning the diets of the studied species, a detailed discussion regarding differences in proportions of particular prey categories is not meaningful. Some discrepancies can be explained by the different habitats prevailing at the study sites. We studied the diet of *M. nattereri* in a forested site, similarly to Taake (1992) and we obtained quite similar results. Shiel *et al.* (1991) and Swift (1997) collected their materials in less forested sites with pastures in Ireland and Scotland and they consequently reported lower proportions of spiders (Araneae) and earwigs (Dermaptera) and the higher representation of Diptera.

In terms of foraging behaviour, the high proportions of spiders, earwigs, Larvae and mostly diurnal brachycerans indicate gleaning from the foliage surface and/or hunting very close to the foliage in all three species. This fact is consistent with previously mentioned dietary studies, predictions of sensory ecology (Siemers and Schnitzler, 2004; Siemers and Swift, 2006) and behavioural observations (Anderson and Racey, 1991). Wolz (1993) also observed a high proportion of plant fragments including mosses (*Eurhynchium* and *Isothecium*), indicating ground gleaning in *M. bechsteinii*. *Myotis nattereri* is known to exploit freshly mown meadows and uses ground gleaning in such habitats (Arlettaz, 1996).

Trophic Niche Parameters and Resource Partitioning

Given that we studied species of similar size applying the same foraging strategy and living in the same habitat in the same place and time, the observed patterns of dietary composition show that bats partition food resources relatively effectively. This is consistent with the results of Swift and Racey (2002) and Siemers and Swift (2006) or general predictions based on opinions of MacArthur and Pianka (1966). Presumptions that bats feed on whatever insects available (e.g., Belwood and Fenton, 1976; Fenton and Morris, 1976) and all bats taken at the same time and place should essentially feed on the same foods (Whitaker, 2004) seem to be somewhat simplifying when compared with aforementioned works and also with results of this study. Dietary composition varied more distinctly among the studied species applying the same foraging strategy and occupying the same habitat than it differed between the studied species and their siblings. Effective resource partitioning in bat species seemingly occupying the same, or very similar, niche shows that detailed knowledge of diet composition is an important piece of information to comprehend

TABLE 4. Echolocation and morphological parameters for calculation of CCA. LAt[1] (forearm length), W[1] (body mass), in analysis were used individually measured forearm lengths and body masses of bats, in table we present arithmetic mean of these values, *n* (number of bats used for calculation of arithmetic mean LAt and W), LA[2] (ear length), LA/LAt (relative ear length to forearm length), PF[3] (peak frequency), HF[3] (highest frequency), IL[3] (interval length), RR[3] (repetition rate), TQ[3] (tonal quality according to echolocation sensitivity gradient, 1 = CF, 2 = FM, 3 = qcf-FM, 4 = FM-qcf, 5 = fm-QCF), LDN[3] (echolocation loudness, 0 = very quiet, 1 = medium loud, 2 = very loud), Loudness[4] (expressed as audibility in open space in m), M[5] (body mass), WS[5] (wingspan), S[5] (wing area), A[5] (aspect ratio), WL[5] (wing loading), Tl[5] (tip lenght ratio), Ts[5] (tip area ratio), I[5] (tip shape index)

Parameter	*M. nattereri*	*M. bechsteinii*	*P. auritus*
LAt[1] (in mm)	40.56	42.97	39.51
W[1] (in g)	7.89	9.28	7.90
n	1962	217	3680
LA[2] (in mm)		17	24.517
LA/LAt[2]	0.42	0.57	0.94
PF[3] (in kHz)	47.5	47.5	35
LF	35	35	25
HF[3] (in kHz)	80	80	80
PL	2	2.25	2
IL[3] (in ms)	80	82.5	50
RR[3]	14	12.5	21
TQ[3]	2	2	2
LDN[3]	1	0	0
Loudness[4]	20	5	5
M[5] (in g)		7	10.19
WS[5] (in cm)	26.8	25.6	26.7
S[5] (in cm²)	113	110	124
A[5]	6.40	6	5.70
WL[5] (in Nm⁻²)	6.10	9	6.10
Tl[5]	1.31	1.02	1.19
Ts[5]	0.76	0.83	0.70
I[5]	1.38	4.37	1.43

[1] — mean value measured at study site
[2] — mean value according to Anděra and Horáček (1982)
[3] — according to Řehák (1999)
[4] — according to Z. Řehák (in litt., personal estimate)
[5] — according to Norberg and Rayner (1987)

assembling processes, which are fundamental to an understanding of species diversity in local communities. Previous studies mostly followed an ecomorphological approach to assess how bat assemblages are assembled in local habitats within a single landscape (e.g., Arita, 1997; Moreno *et al.*, 2006).

Some of our results were inconsistent with the presumptions made by Siemers and Swift (2006). These authors hypothesized that effective food resource partitioning depends on differences in sensory perception between *M. bechsteinii* and *M. nattereri*. The former, with its longer ears, is expected to use passive listening and locate insects using prey-generated sounds more than the latter. The authors recorded different proportions of 'noisy'

and 'still' dietary components. *Myotis bechsteinii* fed more frequently on moths (Lepidoptera ad.), earwigs (Dermaptera), harvestmen (Opilionida), beetles (Coleoptera) and crickets (Orthoptera; Tetigoniidae), whereas diurnal flies (Brachycera), spiders (Araneae) and long horn flies (Nematocera) were more frequent in the diet of *M. nattereri*. In contrast to Siemers and Swift (2006), we recorded similar proportions of diurnal flies (Brachycera) in the diets of both species and higher proportions of moths (Lepidoptera ad.) and earwigs (Dermaptera) in the diet of *M. nattereri* than in *M. bechsteinii*. Similarly to their results we found higher proportions of spiders (Araneae) and long horn flies (Nematocera) in the diet of *M. nattereri* and lower proportions of beetles (Coleoptera) and orthopterans (Orthoptera). The results of Taake (1992) also seem to be partially contradictory with the premise that species with longer ears feed more frequently on 'noisy' prey (Swift and Racey, 2002; Siemers and Swift, 2006), as 'noisy' beetles (Coleoptera) were consumed in similar amounts by all three species and 'still' diurnal flies were present in similar proportions in the diet of the long-eared *M. bechsteinii* and short-eared *M. nattereri*.

The fact that dietary composition varied more distinctly among species applying the same foraging strategy and occupying the same habitat than it differed between the studied species and their siblings has evolutionary consequences; it seems in particular that it is easier to reduce competition by moving to another habitat and hunting the same or similar prey using the same strategy there, than to switch to another prey and/or to start applying a different strategy in the same habitat, as the latter would require the evolution of specific adaptations.

Vaughan (1997) speculated that rare bats may exploit a narrower range of prey. Safi and Kerth (2004) performed a relatively profound analysis of the relation between bats' dietary niche breadth and their endangerment status and found that bat species that are food specialists are generally no more vulnerable than species consuming a wide range of prey taxa. Our results are also inconsistent with the prediction of Vaughan (1997), as relatively the rarest *M. bechsteinii* had a wider trophic niche, whereas relatively the most common *P. auritus* exploited a narrower range of prey.

Seasonal Changes in Dietary Composition

Seasonal changes in dietary composition more or less correspond to observed changes in prey

availability observed at the studied site (see Andreas *et al*., 2012) and have no remarkable effect on competition pattern or trophic niche overlap. The large change in the amounts of Larvae in the diets of *M. bechsteinii* and *P. auritus* between July and August can be explained in several ways. These species may vary in microhabitat preferences, and the peak Larvae population may occur at different times in their preferred microhabitats. Some microhabitat spatial displacement which resulted in differences on dietary composition was observed by Arlettaz (1999) in *Myotis myotis* and *M. blythii*. Another explanation may be the effect of interspecific competition between the species. *Myotis bechsteinii* may be the stronger competitor, such that *P. auritus* only starts to hunt Larvae when *M. bechsteinii* vacates this niche to feed on more profitable orthopterans (Orthoptera). The opposite is also feasible i.e. the competitively stronger *P. auritus* ousts *M. bechsteinii* from the niche and forces it to hunt other prey — orthopterans.

Morphological and Echolocation Parameters

In terms of the interrelations between dietary composition and echolocation and morphological parameters, Bogdanowicz *et al*. (1999) noticed that incorporation of moths in the diet increased gradually as size decreased. In our study, moths were found at a medium frequency in the diet of the largest *M. bechsteinii*, whereas the two other bats, which were similar in body size, showed significant differences in moth consumption. The consumption of harder prey (Coleoptera) by larger species is consistent with our results for the whole community (Andreas, 2002). The higher peak frequency of *M. nattereri* and its higher call intensity (Skiba, 2003) may be associated with feeding on small dipterans in uncluttered habitats.

Concluding Remarks

The study showed an important role of foliage gleaning in the foraging of studied species. Seasonal changes in the diet showed certain flexibility of studied species in food resources utilization. Studied species effectively partition their food resources. Differences in the diets of studied species and consequent trophic niche partitioning and guild structure are significantly determined by differences in their echolocation and morphological characteristics.

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