Acta Chiropterologica, 14(1): 81–92, 2012
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS
doi: 10.3161/150811012X654295

Prey selection and seasonal diet changes in the western barbastelle bat (*Barbastella barbastellus*)

MICHAL ANDREAS[1, 5], ANTONÍN REITER[2, 4], and PETR BENDA[3, 4]

[1]*The Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Květnové náměstí 391, CZ-252 43 Průhonice, Czech Republic*
[2]*South Moravian Museum Znojmo, Přemyslovců 6, CZ-669 45 Znojmo, Czech Republic*
[3]*Department of Zoology, National Museum (Natural History), Václavské náměstí 68, CZ-115 79 Praha 1, Czech Republic*
[4]*Department of Zoology, Charles University, Viničná 7, CZ-128 44 Praha 2, Czech Republic*
[5]*Corresponding author: E-mail: michal.andreas@seznam.cz*

The objective of the study was to describe the diet composition of western barbastelle bat (*Barbastella barbastellus*), its seasonal changes and main factors determining trophic niche of the species. Barbastelle bat feeds predominantly on moths and has the narrowest trophic niche within the entire studied bat community. A comparison of the food supply and the diet composition showed selectivity for larger species of moths. An increasing of absolute abundance of preferred larger moths within summer is accompanied with narrowing of bat's trophic niche. This pattern corresponds well with the conclusions of optimal foraging theory. Larger moths are preferred even in a period of their low relative abundance within a peak of abundance of smaller species. There are no abrupt seasonal changes in the bat's diet within season, but the narrow pool of available food supply seems to determine the trophic niche breadth within low prey diversity periods in early spring and late autumn. The exception is a late autumn period; most probably due to a change in food supply are preferred larger moths replaced in the diet by smaller individuals. Most of the moths' species cease to fly and chiefly only smaller moth species are flying and attracted by UV light. Larger moths still occur at studied area at that time, but they display minimal flying activities and they are detected using vegetation beating and sweeping. Furthermore, syntopic moth-eating foliage gleaner (*Plecotus auritus*) still feeds on larger moths at that time. This may indicate that the change in the diet of *B. barbastellus* is a consequence of poor or absent gleaning abilities of this species, which is not able to pick up the prey from the surface as *P. auritus*. Different hunting strategies are probably efficient trophic niche partitioning mechanisms reducing interspecific competition between these syntopic moth eating bats.

Key words: *Barbastella barbastellus*, diet, optimal foraging, prey selection, trophic niche

INTRODUCTION

Bats constitute species-rich communities and their diverse structure is heavily influenced by resource partitioning (Findley, 1976; Patterson *et al.*, 2003). However, different foraging strategies present the most pertinent variables for the structuring of chiropteran communities and, consequently, the allocation of each species to the main categories of foraging strategies is a prerequisite of any analysis of bat community structure. The state of this variable is closely related to the foraging niche of the bats, their echomorphology, sensory ecology and their habitat preferences or microhabit use (Neuweiler, 1984; Norberg and Rayner, 1987; Fenton, 1990; Bogdanowicz *et al.*, 1999; Safi and Siemers, 2010).

Foraging strategies of European bat species are relatively well-known from studies of the diet of many species (Beck, 1995; Vaughan, 1997), including more detailed studies concerning particular bat species (Bauerová, 1978; Rydell, 1989; Catto *et al.*, 1994, and many others) as well as studies concerning flying apparatus and echolocation (Norberg and Rayner, 1987; Bogdanowicz *et al.*, 1999). Insectivorous bats are usually classified according to their foraging (aerial hawkers, foliage gleaners, uncluttered versus cluttered places, etc. — Findley, 1993; Patterson *et al.*, 2003).

Yet, actual diet composition is also heavily influenced by actual food supply availability, its seasonal fluctuations and the tactics with which a particular bat species responds to these changes. Significant seasonal changes (e.g., Swift and Racey, 1983;

Shiel *et al.*, 1991; Catto *et al.*, 1994) in the diet composition of insectivorous bats may indicate flexible exploitation of available food resources, certain foraging opportunism and less selective feeding (Belwood and Fenton, 1976; Fenton and Morris, 1976; Swift *et al.*, 1985; Rydell, 1986; Hoare, 1991). Furthermore, there are not many specialised insectivorous bat species with narrow trophic niches (Fenton, 1982).

From this point of view, the western barbastelle, *Barbastella barbastellus* (Schreber, 1774), is quite unusual. Until recently, important seasonal changes in its diet had not been recorded, and the species was considered to be extremely specialised among Palaearctic bats (Sierro and Arlettaz, 1997). This pattern contrasted with the feeding behaviour of most insectivorous bats.

The western barbastelle is a medium-sized bat, occurring in Europe from southern England to the Caucasus, which preferentially inhabits forests (Schober and Grimmberger, 1997; Rydell and Bogdanowicz, 1997; Sierro, 1999) and feeds predominantly on moths (Beck, 1995; Rydell *et al.*, 1996; Sierro and Arlettaz, 1997). Sierro and Arlettaz (1997) studied the diet of *B. barbastellus* in association with food availability and moths were heavily selected; however, the authors believed that smaller moths (wingspan < 30 mm) were the prevailing prey category. On the other hand, DNA-based diet analysis proved a preference for larger moths (Zeale *et al.*, 2011). There is little information regarding the foraging behaviour and flight patterns of *B. barbastellus*, and the information available is partly contradictory. The current prevailing opinion that the species is an aerial hawker is based on a selection of casual observations (Zingg, 1994; Sierro and Arlettaz, 1997; Denzinger *et al.*, 2001) or on the opinions of skilled bat detector researchers (Ahlén, 1990). On the contrary, some authors studied the species in captivity and observed that the animals adroitly picked house flies off the ceiling and consumed them in flight (Poulton, 1929), and like many gleaning bats, it sometimes consumed its food in a hanging position (Ryberg, 1947). The closest relatives of *Barbastella* from the tribe Plecotini are foliage gleaners (Anderson and Racey, 1991, 1993). *Barbastella barbastellus* is predicted to fly rather slowly and to be highly manoeuvrable (Norberg and Rayner, 1987). The echolocation calls are different from the calls of typical aerial hawkers (Sierro and Arlettaz, 1997; Denzinger *et al.*, 2001) and they are 10 to 100 times lower in amplitude than those of other aerial-hawking bats. This stealth echolocation allows the barbastelle to exploit tympanate moths (Goerlitz *et al.*, 2010). Rydell *et al.* (1996) proposed a flexible foraging strategy, including aerial hawking and probably also surface gleaning.

Prey selectivity in bats, quite apparent in the case of *B. barbastellus*, is supposed to be linked with the echomorphological constraints of a particular species (Barclay, 1985) and with efforts to optimise the diet. Optimal foraging theory presumes that the predator does not consume prey simply according to its frequency, but rather takes into account its profitability, considering search time and handling time, energy costs, or the predation risks during hunting (Pyke *et al.*, 1977; Stephens and Krebs, 1986).

Optimising trends in the diet of insectivorous bats were observed in the case of *Rhinolophus ferrumequinum* (Jones, 1990), where bats selected larger moths and rejected unprofitable Diptera and ichneumonids, except when more profitable prey was scarce. Agosta *et al.* (2003) similarly found that *Eptesicus fuscus* foraged selectively for beetles and consumed a wider variety of prey when beetle abundance was low. A study of the diet of *Myotis myotis* in the Mediterranean region (Pereira *et al.*, 2002) suggested that, although carabids were most often consumed, crickets were preferred. It is not clear if this was due to beetles being more conspicuous or if the choice was based on energetics or taste.

The main aim of our study was to describe the diet composition of *B. barbastellus*, its seasonal changes and driving factors or constraints influencing the trophic niche of this extremely specialised bat. We tested four predictions on the diet of barbastelle bats: (i) they eat mainly moths and there are no important seasonal changes in diet composition, (ii) the mid-season dynamics in trophic niche breadth is simultaneously accompanied by increasing abundance of preferred prey in keeping with the predictions of optimal foraging theory, (iii) bats select smaller moths, and (iv) the diet of aerially hawking barbastelle bats differs from the diet composition of syntopic moth-eating gleaners.

MATERIALS AND METHODS

Study Area

The study material was collected at the Ledové sluje caves (48°53’03”N, 15°50’40”E; 380 m a.s.l.) in the Podyjí National Park located in the south-east of the Czech Republic. This is a large system of pseudokarst caves and crevices at the slope of a river bank, creating a unique bat swarming site, where 19 bat species have been observed and sufficient samples of bats can be collected there (Reiter *et al.*, 2010). A major part of the study site is covered with natural forest vegetation (mostly Aceri-Carpinetum) complemented with patches of wet meadows and a river with riparian habitats. The other habitats in the vicinity (< 5 km) are natural beech forests, rivers and creek valleys, ponds, fields, reservoirs, and several villages.

Bats were netted in front of cave entrances once a month from March to November in 1994 and 1995, with the exception of April, when two nettings were conducted. Several additional samples were collected in 1996–1998. The bats were kept individually in cloth sacks, and their faecal pellets were collected for a later analysis under a dissecting microscope.

The spatial activity of bats was monitored using ultrasound detectors (Pettersson D 100, D 200 and D 980 — Petterson Elektronik AB, Uppsala, Sweden) on points (e.g., Furlonger *et al.*, 1987) in different habitats in the vicinity of the studied site from sunset to midnight from May to October in 1996 and 1997. The device was tuned from 18 to 110 kHz at every point for ten minutes and elapsed time to the detection of bats was recorded (e.g., McAney and Fairley, 1988; Zahn and Maier, 1997). This totalled 2,820 minutes. *Barbastella barbastellus* was detected for 17 minutes exclusively in forest habitats (Andreas, 2002).

Faecal pellets were softened using water and were then teased apart with a dissecting needle and with a pair of tweezers under a binocular microscope. The particular prey categories were identified using comparative slides, methodological works (McAney *et al.*, 1991), entomological keys, and a reference collection of insects. Moths were divided into two size categories (smaller moths with a wingspan < 30 mm and larger ones with a wingspan > 30 mm) according to size of the remnants (frenulum, antennae, leg fragments, etc.) in the faeces. Several moths' eggs were identified using a specialised key (Döring, 1955).

To express the results of diet analyses, we modified the formulas suggested by McAney *et al.* (1991) for percentage occurrence (%oc) and percentage frequency (%f). The unit for analysis was not one dropping, but the sample of the faecal pellets collected from one animal. Percentage volume (%vol) was assessed according to Obrtel and Holišová (1974). The results were expressed as a percentage of the number of samples of faecal pellets of individual bats in which particular prey category occurred, i.e. percentage occurrence (%oc). This is the number of occurrences of the category (number of samples of droppings collected from one individual containing it), divided by the number of samples analysed, multiplied by 100. The other way the results were expressed was percentage frequency (%f). The result for particular prey category was expressed as the number of occurrences of the category, divided by total occurrences for all categories, multiplied by 100. Percentage volume (%vol) was expressed as the sum of all relative volumes of a particular prey category in individual faecal samples in the studied set of faecal samples divided by the number of faecal samples in the analysed set of the samples. Percent occurrence describes the proportion of bats in the corresponding data set that fed on a particular prey category. Percentage frequency indicates the relative importance of the particular categories according to the frequencies in which they were consumed. Percentage volume describes the proportion of the volume represented by each consumed particular prey in the set of faecal samples analysed. The trophic niche breadth index, B, was calculated according to formula proposed by Levins (Krebs, 1989). Niche breadth is estimated by measuring the uniformity of distribution of individuals across the resource states. Suggested way to measure this: $B = 1/\Sigma p_j^2$ which can also be written as $B = Y^2/\Sigma Nj^2$ where B = Levins' measure of niche breadth, p_j = the proportion of individuals found in or using resource state j, or the fraction of items in the diet that are of food category j (estimated by N_j/Y) ($\Sigma p_j = 1.0$). N_j = the number of individuals found in or using resource state j; $Y = \Sigma N_j$ = the total number of individuals sampled.

The available food was sampled within selected habitats (forest edge, meadow, riparian habitat and different parts of the forest) using a UV light and a screen. The other methods applied to assess food availability were beating, sweeping, and adhesive traps. The relative proportions of individuals representing crucial prey items were assessed in the UV light samples as well as in samples collected using sweeping and beating. Sampling was carried out during the night when bats were netted in the vicinity (50–300 m) of Ledové sluje caves. The non-vertebrate community was divided into 25 taxonomic, ecological, and size groups (Table 1). The particular non-vertebrate group abundances were classified monthly using the semi-quantitative scale shown in Table 1 with the following categories: absent (0), rare (*), common (**), frequent (***) and mass (****). Diversity was expressed as the number of taxa with common, frequent, and mass abundances at the study area in the corresponding month. The value of relative abundance was represented by the number of asterisks in the corresponding month.

The abundance of moths recorded in the extensive lepidopteran study (9,048 moths captured on 184 nights) carried out from mid-April to mid-October 2004 (Šumpich, 2004) were also taken into account (Table 2). The moths were caught using a stationary trap equipped with a mercury lamp in the territory of a National Park 13 km south-east from studied site near village Hnanice. The number for corresponding month was counted as the number of captured moths divided by the number of trapping nights. The species were divided arbitrarily into two size groups: larger moths (wingspan >30 mm) and smaller moths (wingspan < 30 mm) using lepidopteran keys (Leraut, 2006; Macek *et al.*, 2007, 2008).

Statistical Methods

The difference between the two proportion methods was used to compute the significance level for the difference between the two proportions. We compared percentage occurrences. The p-level was computed based on the *t*-value for the respective comparison:

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

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

The Kruskall-Wallis test is a non-parametric alternative to one-way (between-groups) ANOVA. It is used to compare three or more samples, and it tests the null hypothesis that the different samples in the comparison were drawn from the same distribution or from distributions with the same median. Using this test, we analysed the dataset of B values of individual diet samples. The independent (grouping) variable was month. The Mann-Whitney *U*-test is a non-parametric alternative to the *t*-test for independent samples. Spearman rank r_s can be thought of as the regular Pearson product-moment correlation coefficient (Pearson *r*); that is, in terms of the proportion of variability accounted for, except that Spearman r_s is computed from ranks. Spearman r_s assumes that the variables under consideration were measured on at least an ordinal (rank order) scale; that is, the individual observations (cases) can be ranked into two ordered series. All these tests were computed using STATISTICA for Windows. For more details, see the software manual (StatSoft, 2001).

TABLE 1. Estimated quantities of non-vertebrates recorded at the studied site Ledové Sluje caves in the following categories: absent (0), rare (*), common (**), frequent (***), and mass (****). ad. — imagoes

Food item	March	April	May	June	July	August	September	October	November
Lepidoptera (ad., smaller wingspan < 30 mm)	*	*	**	***	****	****	**	**	**
Lepidoptera (ad., larger wingspan > 30 mm)	**	**	**	***	****	****	***	**	**
Lepidoptera (larvae)	**	**	***	***	***	***	**	0	0
Dermaptera	***	***	**	**	**	**	**	***	***
Araneae	**	**	****	***	***	***	****	***	**
Tipulidae	**	**	****	***	**	**	**	**	**
Chironomidae	*	**	****	****	****	***	**	**	*
Brachycera	*	*	***	***	***	***	**	**	*
Diptera (other)	*	*	****	***	***	***	**	**	*
Curculionidae (medium — 5−10 mm)	*	**	***	****	***	**	**	*	*
Scarabaeidae	0	*	****	****	**	**	*	*	0
Carabidae (medium — 5–10 mm)	*	*	**	**	***	***	**	*	*
Carabidae (larger — > 10 mm)	**	***	***	***	**	**	***	**	*
Cerambycidae	*	**	***	****	****	***	**	*	0
Coleoptera (other, small — < 5 mm)	*	**	****	****	***	***	***	**	*
Trichoptera	0	0	*	***	***	****	****	***	*
Hymenoptera	0	*	**	***	****	***	**	*	*
Neuroptera	*	*	**	***	***	***	***	**	*
Auchenorrhyncha	*	*	**	***	***	***	**	**	*
Heteroptera	*	*	**	***	****	****	***	**	*
Sternorrhyncha	0	*	****	***	***	***	****	**	*
Ephemeroptera	0	0	*	**	**	**	**	*	0
Blattodea	0	0	*	**	***	***	**	*	0
Plecoptera	0	0	*	**	**	**	**	*	0
Orthoptera	0	*	**	***	***	****	****	**	0

RESULTS

Diet Composition and Its Seasonal Changes

A total of 1,604 faecal pellets were collected from 154 individuals, 43 females and 111 males. Important differences in the diet between males and females were not recorded. To our knowledge, such a large number of faecal pellets of *B. barbastellus* has never been analysed.

According to the literature, and also in agreement with our analysis of dietary composition, *B. barbastellus* is a highly specialised species, feeding predominantly on Lepidoptera adulti (89.1% vol), especially medium-sized and larger specimens. The other frequently found prey categories were Neuroptera (mostly Chrysopidae, much less Hemerobiidae and Sisyridae). Diptera (Tipulidae and Brachycera), Araneae, Lepidoptera larvae, Trichoptera, Blattodea, Coleoptera, Hymenoptera, Auchenorrhyncha, Plecoptera, and Orthoptera were also recorded in the diet (Fig. 1).

There were no abrupt or very remarkable seasonal changes (Fig. 2) in the diet composition until the late autumn (November), when most of the moths stopped their flying activity and flying moths available for aerial hawkers were predominantly *Operophtera brumata* (wingspan ≤ 30 mm). Due to smaller body size of the moths, the change was easily detectable in the diet composition (Fig. 2). We

TABLE 2. Results of lepidopterological study. Numbers of moths collected in stationary moth trap equipped with mercury lamp near village Hnanice (Šumpich, 2004)

Parameter	April	May	June	July	August	September	October
Sampled nights	16	31	30	31	31	30	15
Number of larger moths	116	170	433	572	908	726	322
Number of smaller moths	23	359	1456	2266	1500	182	15
Total number of moths in month	139	529	1889	2838	2408	908	337
Larger moths/night	7.25	5.48	14.43	18.45	29.29	24.20	21.47
Smaller moths/night	1.44	11.58	48.53	73.10	48.39	6.07	1.00
Proportion of larger moths (%)	83.45	32.14	22.92	20.16	37.71	79.96	95.55
Proportion of smaller moths (%)	16.55	67.86	77.08	79.84	62.29	20.04	4.45

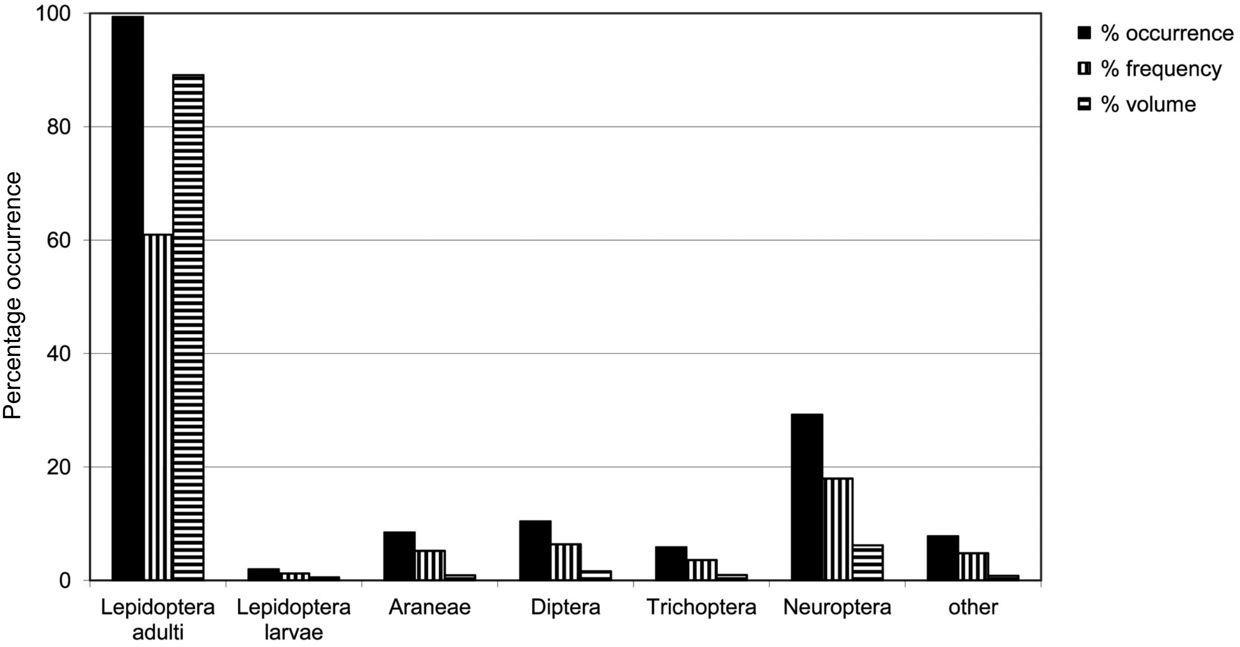

FIG. 1. Percentage occurrence (%oc), percentage frequency (%f), and percentage volume (%vol) of particular prey categories in the diet of *B. barbastellus*; the entire year is presented in this data set. (other = Coleoptera, Hymenoptera, Auchenorrhyncha, Blattodea, Plecoptera, Orthoptera)

do not know the species identity of the eaten moths for sure, as we did not prove this using DNA barcoding. However, due to body size and availability at the studied site, we suppose that it was *O. brumata*. The decrease in the amount of the larger moths in the bat diet between the combined September–October and November samples, as well as the increase in smaller moths, were

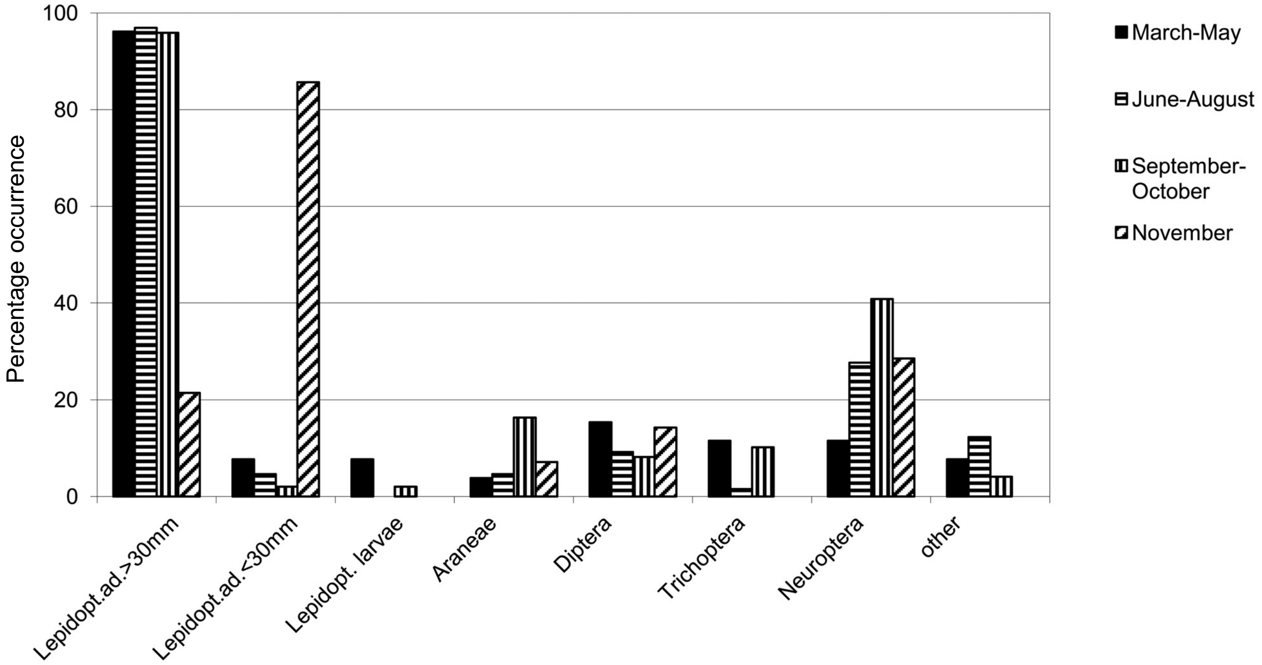

FIG. 2. Seasonal changes in the diet of *B. barbastellus* in particular seasons (March–May, June–August, September–October, November) expressed as percentage occurrence in the number of samples of faecal pellets of individual bats. Animals caught in particular months: *n* (March–May) = 26, *n* (June–August) = 65, *n* (September–October) = 49, *n* (November) = 14. (other = Coleoptera, Hymenoptera, Auchenorrhyncha, Blattodea, Plecoptera, Orthoptera). 30 mm denotes wingspan

significant (Differences between two proportions method: $t = 6.07$, $P < 0.001$ and $t = 6.82$, $P < 0.001$, respectively, *d.f.* = 61).

We studied the diet of *B. barbastellus* along with the syntopic *Plecotus auritus* (Linnaeus, 1758). Both species fed predominantly on medium-sized and larger moths until October, but then, during November, larger moths at the studied site broke their flight and *B. barbastellus* fed on the flying smaller moths available for aerial hawkers. This change in the diet of *B. barbastellus* was dissimilar to the continuous feeding of *P. auritus* on larger moths. Comparing the representation of the larger moths in the November diets of *B. barbastellus* (%oc = 21.43, $n = 14$) and *P. auritus* (%oc = 76.92, $n = 13$), we obtained significant differences (Differences between two proportions method, $t = 2.88$, *d.f.* = 25, $P < 0.01$). Larger moths still occurred at the study area in November, but they seldom flew and were detected using vegetation beating and sweeping, as well as in the diet of other gleaning bats.

We recorded a low diversity and abundance of the food supply during the cold part of each season, with diversity and abundance peaking in summer (Fig. 3 and Table 1). The absolute abundance of the preferred prey (larger moths) was highest in late summer and in early autumn (Table 2). The estimated proportion of larger moths in the community of flying insects, based on our semi-quantitative sampling, was the highest within both edges of the activity season, as dipterans prevailed in the mid-season but were less abundant at other times.

A quantitative lepidopteran study (Šumpich, 2004) provided us with data regarding the relative abundance of moths of particular size categories. Larger moths dominated over smaller ones at the edges of the season. In mid-season, there was a peak of smaller moths that significantly prevailed (Mann-Whitney *U*-test, June–August period, $U = 2{,}614.00$, *d.f.* = 1, $P < 0.001$) over the larger ones (Fig. 4 and Table 2). Similar results (summer peak of flying smaller moths) were obtained in the semi-quantitative sampling at the site where the bats were netted.

A completely different situation was observed in November, when only the semi-quantitative samplings at the study site were conducted, and most of the moth species ceased to fly. The larger species remained common at the study site (as seen using vegetation beating and sweeping), but rarely flew. We collected actively flying moths on the projection screen floodlit by UV lamp for two hours. Thirty-six moths were collected (32 smaller individuals, 4 larger). Using 20 sweeps ca. one meter long in the bushes and lower parts of trees we collected 12 moths (5 smaller individuals, 7 larger).

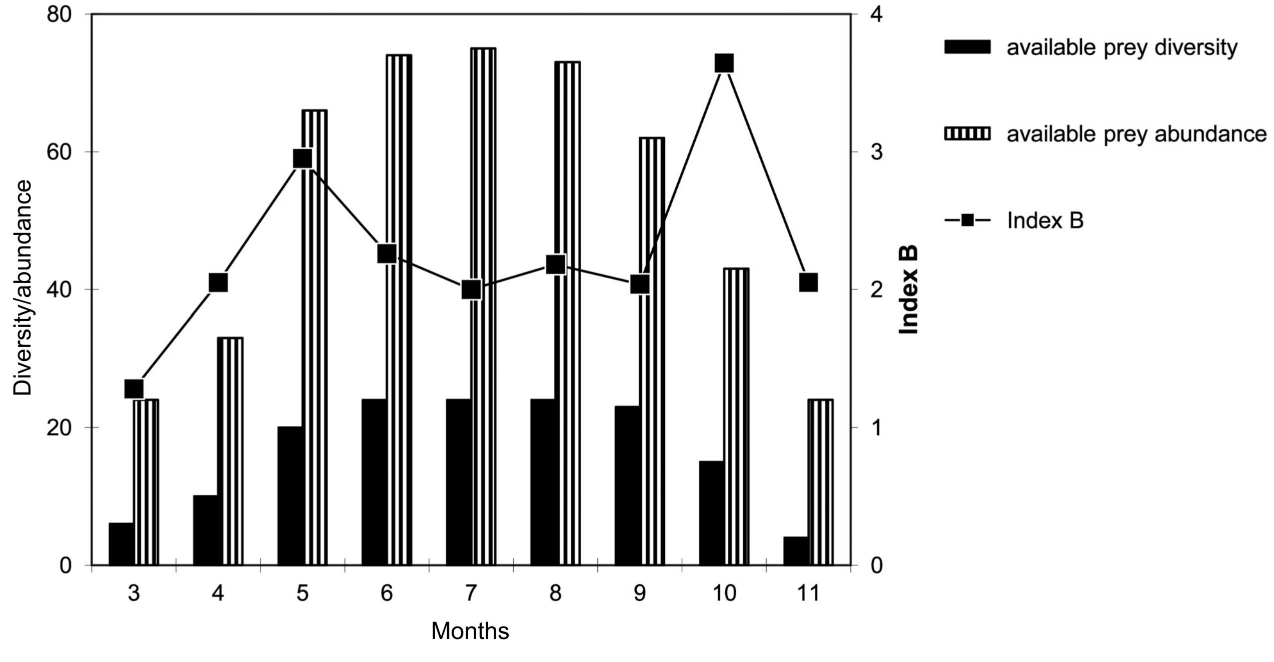

FIG. 3. Comparison of the prey availability and diet parameters of *B. barbastellus*. Seasonal changes in diversity and the relative abundance of available prey at the study site are indicated together with the seasonal changes in the bats' diets expressed by Levins' index of niche breadth (B)

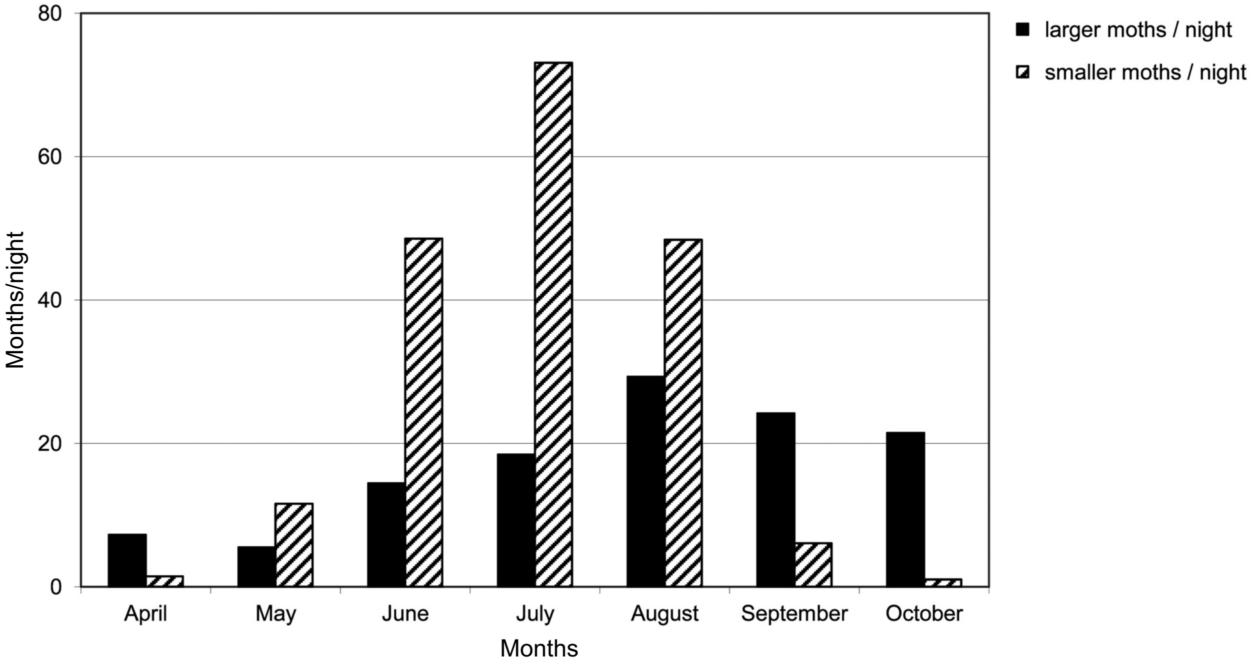

FIG. 4. Daily mean numbers of larger and smaller moths collected by a stationary moth trap (Šumpich, 2004) in each particular month. Note the predominance of smaller moths in the summer period

Seasonal Changes of Trophic Niche Breadth and Prey Selection

We studied changes in diet diversity, expressed as Levins' trophic niche breadth index B, and we observed conspicuous seasonal changes (Fig. 3). There was a low diversity in the food supply at the study site during the early spring and, consequently, very low values of B were recorded. All of these values increased in spring. During the summer, a decrease in the diet diversity was observed (index B). The trophic niche narrowed despite the continuing increase and summer peak of food supply diversity. As the summer is not only a period of high food supply diversity, but also a season of high larger moths' abundance (preferred prey item, see below), we could see that the predator seemed to be become more specialised when the preferred prey was abundant. To prove this premise (i. e. whether the summer decrease of B was significant), we tested the dataset of B values of individual diet samples to see whether the differences among the particular month values were an important factor of variability between the two peaks (May and October). We obtained significant differences (non-parametric Kruskal-Wallis ANOVA, independent (grouping) variable — month, $H = 24.99$, $d.f. = 5$, $P < 0.001$). Accordingly, a considerable negative correlation between all moth numbers (Table 2) and Levins' index of niche breath B (Spearman rank order correlation $r_s = -0.83$, $t_4 = -2.96$, $P < 0.05$) was found between May and October.

Seasonal changes in the trophic niche breadth of most of the other species at the studied site had the opposite pattern as they had the widest throphic niche breadth within the summer season. Only specialised species with a generally narrow trophic niche (besides *B. barbastellus* also *M. myotis*) displayed the lowest values of diet diversity within the summer (Fig. 5).

Comparing the diet composition and the available food, the prey size selection was the most significant within the summer months (June–August). We collected faecal samples from 65 animals during this period. Within these samples, only medium and larger individuals of moths were present in 62 of the samples, while small individuals were present in only two samples, and one sample contained both larger and smaller moths (%oc of larger moths = 96.9, %oc of smaller moths = 4.6). This significant superiority of larger moths in the diet (Differences between two proportions method, $t = 11.05$, $d.f. = 128$, $P < 0.001$) was even more striking if we considered the predominance of small moths in the food supply (Mann-Whitney *U*-test, $U = 2{,}614.00$, $d.f. = 1$, $P < 0.001$). The proportion of larger moths in the food supply was only 26.8% in summer (Table 2 and Fig. 4.). Accordingly,

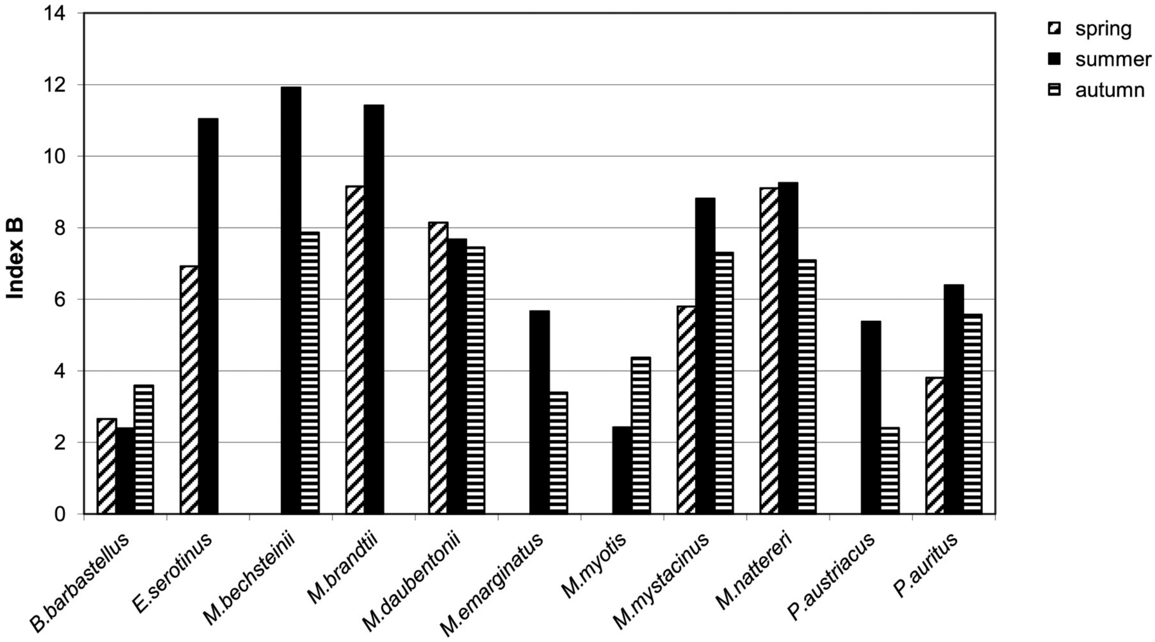

FIG. 5. Seasonal changes of Levins' trophic niche breadth index B. Numbers of bats: *B. barbastellus* (spring 26, summer 65, autumn 63), *E. serotinus* (9, 46, 0), *Myotis bechsteinii* (0, 42, 11), *M. brandtii* (9, 104, 0), *M. daubentonii* (41, 84, 57), *M. emarginatus* (0, 24, 10), *M. myotis* (0, 16, 26), *M. mystacinus* (16, 25, 12), *M. nattereri* (25, 42, 82); *Plecotus austriacus* (0, 23, 10), *P. auritus* (217, 158, 199)

several of the moth eggs that were found in the diet of *B. barbastellus* belonged to larger species.

DISCUSSION

Diet Composition and its Seasonal Changes

The observed diet compositions, as well as the small seasonal changes, are quite similar to the results of previous studies (Beck, 1995; Rydell *et al.*, 1996; Sierro and Arlettaz, 1997). Also, there were no major seasonal changes in the occurrence of particular prey taxa. There was, however, a significant seasonal shift in prey size categories in the most important prey item, i.e. moths in late autumn. There was small flexibility in the species, but the range of seasonal changes in the diet was quite low as compared to the diets of other species studied at the respective site (Andreas, 2002). This diet change supports the claim of Fenton and Morris (1976) that opportunistic feeding is not incompatible with selective feeding.

The aforementioned shift in the consumption of larger and smaller moths in November may indicate that this species is a true aerial hawker. *Barbastella barbastellus* generally preferred larger moths throughout the entire year, but as this size category ceased flight activity, *B. barbastellus* focused on the small flying moths. The driving factor for this change probably resulted from foraging abilities; if the preferred prey ceases to fly, true aerial hawkers must hunt other species. *Barbastella barbastellus* was subsequently forced to eat smaller moths which earlier had been nearly completely ignored, whereas non-flying larger moths were still consumed by *P. auritus*, a foliage gleaner (Anderson and Racey, 1991). Those findings support the current prevailing opinion that *B. barbastellus* is primarily an aerial hawker (Sierro and Arlettaz, 1997; Denzinger *et al.*, 2001) and cast doubt upon conclusions presuming gleaning (Poulton, 1929; Ryberg, 1947) from observations of *B. barbastellus* in captivity.

Accurate assessment of the food available to predators is one of the more perplexing problems facing animal ecologists. Even if it were possible to accurately assess insect abundance in a given habitat, such estimates may not actually represent the prey available to insectivorous bats. Also, many bat species feed in several different and often unknown habitats in the course of the night; consequently, they may encounter prey distant from where insect traps are deployed (Kunz, 1988). The observed seasonal changes of non-vertebrate diversity and abundance (a peak of both quantity and diversity during summer) at our study site was the same as the general pattern from non-vertebrate studies carried out in the vicinity of Podyjí National Park (Helešic and Kubíček, 1999) and corresponds well with the dynamics of most of the terrestrial temperate belt habitats and with general studies of insect phenology (Williams, 1939; Denno and Dingle, 1981). The moth size category ratio in the food supply in summer (the period when the selectivity of *B. barbastellus* was tested) corresponds well with the results of Sierro and Arlettaz (1997) in a study of the food supply of *B. barbastellus* in the Swiss Alps. Therefore, we consider our results of food supply sampling to be a reliable source of information concerning the main patterns of abundance and diversity of the non-vertebrate community at the studied site.

Seasonal Changes of Trophic Niche Breadth and Prey Selection

Trophic niche narrowing in *B. barbastellus* in mid-summer corresponds well with the theory that increasing food abundance leads to greater foraging specialisation (Pyke *et al*., 1977). The narrowing of the trophic niche in summer appears to depend mostly on the abundance of the preferred prey (Figs. 3 and 4) at our study site. This is similar to the results of Agosta *et al.* (2003). The highest diet diversity in spring and autumn is also similar to the results of Jones (1990). The low values in early spring and late autumn are probably a consequence of the narrow pool of potential prey.

The pattern of a narrowing of trophic niche in the middle of the season was also observed in *Myotis myotis*. Seasonal changes of the available food of *M. myotis* were studied in a wider region (Bauerová, 1978) and the abundance peak fell into the summer period when we observed a decrease of diet diversity. Diet diversity also decreased in the period of abundant food supply, as observed in a Mediterranean population of *M. myotis* (Pereira *et al*., 2002).

Generally, more specialised species in periods of abundant food supply narrows their trophic niche, whereas diet diversity of more generalist species has trends more similar to supply diversity (see Fig. 5). This inconsistency may be caused by differences between generalists and specialists. Regarding hunting difficulty, detectability and energy intake, the differences between, for example, tipulid, small moths and neuropterans can be negligible for generalists. They may differentiate those prey types using their echolocation apparatus, but they consume all these items simply as ‘one’ mixed group of slow-flying middle-sized soft-bodied prey. Other encountered taxa with these qualities can be easily incorporated into the diet without changing energy intake per unit time. The diversity of the diet of such a species consequently increases with the diversity of the food supply. On the other hand, more specialised species may asses the differences between hunted taxa more precisely, and due to more specialised echolocation or flying apparatus, the differences in hunting difficulty or detectability may be of greater consequence to their optimal foraging. Those species do not asses several taxa as a one mixed group and therefore do not incorporate many taxa in the diet. Their foraging is much more selective and the absence of mixed groups of prey enables a more precise comparison of the diet and food supply. The trends of specialisation in seasons of abundant preferred prey may be observed regardless of increasing food supply diversity. The considerable importance of perception on the diet composition and prey selection of bats has been reliably proven (e.g., Siemers and Swift, 2006). The next factor driving prey selectivity and consequently trophic niche breadth changes is probably also approach speed (Barclay, 1985). Narrowing of the trophic niche within a period of higher abundance of preferred prey has also been observed in the case of less specialised bats (e.g., Jones, 1990; Agosta *et al*., 2003). This may be caused by very distinct detectability of those prey taxa and related high energy rewards.

The issue of prey selection in bats is difficult to solve as it is not possible to sample the food supply availability in the same way as it is available to a particular bat species. Furthermore, we do not know exactly how bats perceive particular diet taxa, whether they are able to distinguish between some of them and what kind of prey of different taxa bats perceive as one diet type.

Among moths, larger individuals were preferred by *B. barbastellus*. A high level of selectivity could be explained by the slow to moderate flight (Sierro and Arlettaz, 1997) that enables the species to differentiate the prey categories. The low-amplitude ‘stealth’ calls (Goerlitz *et al*., 2010) of *B. barbastellus* are particularly inconspicuous to the tympanate prey and may provide the species with a considerable competitive advantage. We suppose that high hunting effectiveness (producing a relative trophic welfare) enables the species to selectively hunt larger prey, which is similar to the observations of Fenton and Morris (1976) or the opinion of Jones (1990). The corresponding but inverse situation was observed by Hoare (1991), who recorded unselective feeding and linked it with relative food supply scarcity within the time of study material collection. Relatively opportunistic behaviour and diet composition corresponding with the food supply was also observed by Belwood and Fenton (1976).

Concerning prey size categories in the food supply, Sierro and Arlettaz (1997) also observed small moths as more abundant (69%) than larger ones (31%). These authors supposed that *B. barbastellus* fed on more abundant smaller moths on the basis of two findings of leg fragments of smaller moths (wingspan ca. 25–30 mm) and on the summer predominance of yellow scales of *Eilema complana* (authors gave ca. 30 mm wingspan) in the bat's diet. They found this fact to correspond with the higher abundance of smaller moths in the food supply. Those conclusions contradict our findings. We recorded proportions of small and large moths in the food supply during the summer season similar to Sierro and Arlettaz (1997), but the prey size category selection we found was different. These contradictions could be explained by an insufficient number of fragments of moths with identified size (only two specimens) in the study of Sierro and Arlettaz (1997) and a misclassification of the abundant and probably frequently fed-on moth, *E. complana*, which they included in the smaller species, despite the fact that the wingspan mentioned in literature ranges from 30 to 35 mm (Leraut, 2006). Species possessing similar wingspans were included among the medium-sized and larger species in our study. We found that the larger-sized moths in our large study sample (several dozen ingested moths) and the presence of several eggs belonging to larger species to be a credible basis for our statement that *B. barbastellus* prefers medium-sized and larger moths as prey. The latest findings concerning the diet composition of *B. barbastellus* based on DNA analysis (Zeale *et al.*, 2011) also confirm the great prevalence of larger moths in the diet. There seem to be two principal reasons for the selection of larger prey: 1) it is easily detectable, and therefore the searching time is reduced and hunting is more efficient (e.g., Siemers and Güttinger, 2006) and 2) the energy intake per time unit is higher if larger prey are hunted because the energy intake increases with prey size more progressively than with handling time (e.g., Jones, 1990).

ACKNOWLEDGEMENTS

The authors wish to thank everyone that helped with data collection, namely: Lenka Barčiová, Eva Cepáková, Kateřina Čapounová, Vladimír Hanák, Anna Hoffmannová, Josef Hotový, Ivan Horáček, Martin Pokorný, Zdeněk Řehák, Karolína Šůlová, Dita Weinfurtová and Jan Zukal. We want to thank The Podyjí National Park Administration for organisational assistance. D. Král, K. Hůrka and J. Farkač kindly helped with the determination of insects. D. Storch and E. Vávrová helped with the statistical analyses. A. Honěk provided the literature concerning insect phenology and J. Šumpich provided primary data regarding moth abundance; we thank them all. The authors also thank D. Storch, I. Horáček, J. O. Whitaker, Jr., and one anonymous referee for valuable comments on the manuscript. The research was supported by grants from the Czech Ministry of Environment (# MSM6293359101) and the Czech Ministry of Culture (# DE07P04OMG006 and MK00002327201). The authors declare that they have no conflicts of interest.

LITERATURE CITED

AGOSTA, S. J., D. MORTON, and K. M. KUHN. 2003. Feeding ecology of the bat *Eptesicus fuscus*: 'preferred' prey abundance as one factor influencing prey selection and diet breadth. Journal of Zoology (London), 260: 169–177.

AHLÉN, I. 1990. Identification of bats in flight. Swedish Society for Conservation of Nature & The Swedish Youth Association for Environmental Studies and Conservation, Stockholm, 50 pp.

ANDERSON, M. E., and P. A. RACEY. 1991. Feeding behaviour of captive brown long-eared bats, *Plecotus auritus*. Animal Behaviour, 42: 489–493.

ANDERSON, M. E., and P. A. RACEY. 1993. Discrimination between fluttering and non-fluttering moths by brown long-eared bats, *Plecotus auritus*. Animal Behaviour, 46: 1151–1155.

ANDREAS, M. 2002. Feeding ecology of a bat community. Ph.D. Thesis, Czech Agriculture University, Prague, 163 pp. [In Czech].

BARCLAY, R. M. R. 1985. Long- versus short-range foraging strategies of hoary (*Lasiurus cinereus*) and silver-haired (*Lasionycteris noctivagans*) bats and the consequences for prey selection. Canadian Journal of Zoology, 63: 2507–2515.

BAUEROVÁ, Z. 1978. Contribution to the trophic ecology of *Myotis myotis*. Folia Zoologica, 27: 305–316

BECK, A. 1995. Fecal analyses of European bat species. Myotis, 32–33: 109–119.

BELWOOD, J. J., and M. B. FENTON. 1976. Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology, 54: 1674–1678.

BOGDANOWICZ, W., M. B. FENTON, and K. DALESZCZYK. 1999. The relationship between echolocation calls, morphology and diet in insectivorous bats. Journal of Zoology (London), 247: 381–393.

CATTO, C. M. C., A. M. HUTSON, and P. A. RACEY. 1994. The diet of *Eptesicus serotinus* in southern England. Folia Zoologica, 43: 307–314.

DENNO, R. F., and H. DINGLE. 1981. Insect life history patterns: habitat and geographic variation. Springer-Verlag, New York, 225 pp.

DENZINGER, A., B. M. SIEMERS, A. SCHAUB, and H.-U. SCHNITZLER. 2001. Echolocation by the barbastelle bat, *Barbastella barbastellus*. Journal of Comparative Physiology, 187A: 521–528.

DÖRING, E. 1955. Zur Morphologie der Schmetterlingseier. Akademie-Verlag, Berlin, 154 + lxi pp.

FENTON, M. B. 1982. Echolocation, insect hearing, and feeding ecology of insectivorous bats. Pp. 261–285, *in* Ecology of bats (T. H. KUNZ, ed.). Plenum Press, New York, 425 pp.

FENTON, M. B. 1990. The foraging behaviour and ecology of animal-eating bats. Canadian Journal of Zoology, 68: 411–422.

FENTON, M. B., and G. K. MORRIS. 1976. Opportunistic feeding by desert bats (*Myotis* spp.). Canadian Journal of Zoology, 54: 526–530.

FINDLEY, J. S. 1976. The structure of bat communities. The American Naturalist, 110: 129–139.

FINDLEY, J. S. 1993. Bats: a community perspective. Cambridge University Press, Cambridge, 167 pp.

FURLONGER, C. L., H. J. DEWAR, and M. B. FENTON. 1987. Habitat use by foraging insectivorous bats. Canadian Journal of Zoology, 65: 284–288.

GOERLITZ, H. R., H. M. TER HOFSTEDE, M. R. K. ZEALE, and G. JONES. 2010. An aerial-hawking bat uses stealth echolocation to counter moth hearing. Current Biology, 20: 1568–1572.

HELEŠIC, J., and F. KUBÍČEK. 1999. Hydrobiology of the Dyje River in the National Park Podyjí, Czech Republic. Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Biologia, 102: 1–138.

HOARE, L. R. 1991. The diet of *Pipistrellus pipistrellus* during the pre-hibernal period. Journal of Zoology (London), 225: 665–670.

JONES, G. 1990. Prey selection by the greater horseshoe bat (*Rhinolophus ferrumequinum*): optimal foraging by echolocation? Journal of Animal Ecology, 59: 587–602.

KREBS, C. J. 1989. Ecological methodology. Harper Collins Publishers, New York, 654 pp.

KUNZ, T. H. 1988. Methods of assessing the availability of prey to insectivorous bats. Pp. 191–210, *in* Ecological and behavioral methods for the study of bats (T. H. KUNZ, ed.). Smithsonian Institution Press, Washington, D.C., 533 pp.

LERAUT, P. 2006. Moths of Europe 1. NAP Editions, Verriéres le Buisson, 387 pp.

MACEK, J., J. DVOŘÁK, L. TRAXLER, and V. ČERVENKA. 2007. Butterflies and caterpillars of Central Europe. I. Night moths. Academia, Prague, 371 pp. [In Czech].

MACEK, J., J. DVOŘÁK, L. TRAXLER, and V. ČERVENKA. 2008. Butterflies and caterpillars of Central Europe. II. Night moths — Noctuidae. Academia, Prague, 490 pp. [In Czech].

MCANEY, C. M., and J. S. FAIRLEY. 1988. Activity patterns of lesser horseshoe bat *Rhinolophus hipposideros* at summer roost. Journal of Zoology (London), 216: 325–338.

MCANEY, C. M., C. B. SHIEL, C. SULLIVAN, and J. S. FAIRLEY. 1991. The analysis of bat droppings. The Mammal Society, London, 48 pp.

NEUWEILER, G. 1984. Foraging, echolocation and audition in bats. Naturwissenschaften, 71: 446–455.

NORBERG, U. M., and J. M. V. RAYNER. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society, 316B: 335–427.

OBRTEL, R., and V. HOLIŠOVÁ. 1974. Trophic niches of *Apodemus flavicollis* and *Clethrionomys glareolus* in a lowland forest. Acta Scientarum Naturalium Academiae Scientiarum Bohemicae Brno, 8: 1–37.

PATTERSON, B. D., M. R. WILLIG, and R. D. STEVENS. 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. Pp. 536–579, *in* Bat ecology (T. H. KUNZ and M. B. FENTON, eds.). University of Chicago Press, Chicago, 779 pp.

PEREIRA, M. J. R., H. REBELO, A. RAINHO, and J. M. PALMEIRIM. 2002. Prey selection by *Myotis myotis* (Vespertilionidae) in a Mediterranean region. Acta Chiropterologica, 4: 183–193.

POULTON, E. B. 1929. British insectivorous bats and its prey. Proceedings of the Zoological Society of London, 19: 227–303.

PYKE, G. H., H. R. PULLIAM, and E. L. CHARNOV. 1977. Optimal foraging: selective review of theory and tests. The Quarterly Review of Biology, 52: 137–154.

REITER, A., P. BENDA, A. HOFFMANNOVÁ, and M. ANDREAS. 2010. Project: swarming bats in Ledové sluje. Pp. 127–138, *in* A tribute to bats (I. HORÁČEK and M. UHRIN, eds.). The Publishing House Lesnická práce, s.r.o., Kostelec nad Černými lesy, 400 pp.

RYBERG, O. 1947. Studies on bats and bat parasites. Bokförlaget Svensk Natur, Stockholm, 330 pp.

RYDELL, J. 1986. Foraging and diet of the northern bat *Eptesicus nilssoni* in Sweden. Holarctic Ecology, 9: 272–276.

RYDELL, J. 1989. Food habits of northern (*Eptesicus nilssoni*) and brown long-eared (*Plecotus auritus*) bats in Sweden. Holarctic Ecology, 12: 16–20.

RYDELL, J., and W. BOGDANOWICZ. 1997. Barbastella barbastellus. Mammalian Species, 557: 1–8.

RYDELL, J., G. NATUSCHKE, A. THEILER, and P. E. ZINGG. 1996. Food habits of the barbastelle bat *Barbastella barbastellus*. Ecography, 19: 62–66.

SAFI, K., and B. M. SIEMERS. 2010. Implications of sensory ecology for species coexistence: biased perception links predator diversity to prey size distribution. Evolutionary Ecology, 24: 703–713.

SCHOBER, W., and E. GRIMMBERGER. 1997. The bats of Europe and North America. THF Publications Inc., Neptune City, NJ, USA, 239 pp.

SHIEL, C. B., C. M. MCANEY, and J. S. FAIRLEY. 1991. Analysis of the diet of Natterer's bat *Myotis nattereri* and the common long-eared bat *Plecotus auritus* in the West of Ireland. Journal of Zoology (London), 223: 299–305.

SIEMERS, B. M., and R. GÜTTINGER. 2006. Prey conspicuousness can explain apparent prey selectivity. Current Biology, 16: 157–159.

SIEMERS, B. M., and S. M. SWIFT. 2006. Differences in sensory ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis nattereri* (Chiroptera: Vespertilionidae). Behavioral Ecology and Sociobiology, 59: 373–380.

SIERRO, A. 1999. Habitat selection by barbastelle bats (*Barbastella barbastellus*) in the Swiss Alps (Valais). Journal of Zoology (London), 248: 429–432.

SIERRO, A., and R. ARLETTAZ. 1997. Barbastelle bats (*Barbastella* spp.) specialize in the predation of moths: implications for foraging tactics and conservation. Acta Oecologica, 18: 91–106.

STATSOFT. 2001. Statistica for Windows (Computer program manual). StatSoft, Inc., Tulsa, USA.

STEPHENS, D. W., and J. R. KREBS. 1986. Foraging theory. Princeton University Press, Princeton, 247 pp.

SWIFT, S. M., and P. A. RACEY. 1983. Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. Journal of Zoology (London), 200: 249–259.

SWIFT, S. M., P. A. RACEY, and M. I. AVERY. 1985. Feeding ecology of *Pipipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. II. Diet. Journal of Animal Ecology, 54: 217–225.

Šumpich, J. 2004. Results of butterfly communities monitoring (Lepidoptera: Hepialoidea, Zygaenoidea: Limacodidae, Cossoidea, Lasiocampoidea, Bombycoidea, Drepanoidea, Geometroidea, Noctuidea) in 2004 within the frame of project of establishing national biodiversity monitoring network in the Czech Republic (VaV/610/4/01). Part B: Report concerning monitored site near Hnanice. Research report for Agency for Nature Conservation and Landscape Protection of the Czech Republic, Prague, 16 pp. [In Czech].

Vaughan, N. 1997. The diets of British bats (Chiroptera). Mammal Review, 27: 77–94.

Williams, C. B. 1939. An analysis of four year captures of insects in a light trap. Part I. General survey; sex proportion; phenology and time of flight. Transactions of the Royal Entomological Society of London, 89: 79–132.

Zahn, A., and S. Maier. 1997. Jagdaktivität von Fledermäusen an Bächen und Teichen. Zeitschrift für Säugetierkunde, 62: 1–11.

Zeale, M. R. K., R. K. Butlin, G. L. A. Barker, D. S. Lees, and G. Jones. 2011. Taxon specific PCR for DNA barcoding arthropod prey in bat faeces. Molecular Ecology Resources, 11: 236–244.

Zingg, P. E. 1994. Neue Vorkommen der Mopsfledermaus (*Barbastella barbastellus* Schreber, 1774) im Berner Oberland. Mitteilungen des Naturwissenschaftliche Gesellschaft Thun, 12: 121–132.

Received 02 June 2011, accepted 23 November 2011