

Diet composition and foraging activity of *Pipistrellus pygmaeus* in a floodplain forest

Tomáš Bartonička¹, Zdeněk Řehák¹ & Michal Andreas²

¹*Institute of Botany and Zoology, Masaryk University, Kotlářská 2, CZ–61137 Brno, Czech Republic; e-mail: bartonic@sci.muni.cz, rehak@sci.muni.cz*

²*The Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Květnové nám. 391, CZ–252 34 Průhonice, Czech Republic; e-mail: michal.andreas@seznam.cz*

Abstract: In 2000–2002 bat droppings were collected under the emerging crevice of a nursery colony of *Pipistrellus pygmaeus*. The locality was situated in a floodplain forest at the confluence of the Dyje and Morava rivers (S Moravia, Czech Republic). In total, 27 samples (20 pellets in one sample) of droppings were used to analyze prey remains. In the diet, 40 taxonomic groups of invertebrates were found. As expected, small dipteran insects were the main food item in which Nematocera dominated. Besides Chironomidae and Ceratopogonidae also a high percentage of nematoceran eggs were recorded. Surprisingly, a relatively high percentage of Brachycera was recorded. Further frequent prey items belonged to the orders of Trichoptera, Hymenoptera, Coleoptera and Sternorrhyncha. A heterodyne bat detector was used to follow foraging activity of *P. pygmaeus* on line transects in forest and water habitats in the vicinity of the colony. A significant decrease in foraging activity over water habitats and in forest sites during the late pregnancy (mid-May – early June) and an increase during the lactation and post-lactation periods (mid-June – early August) were found. Changes in the frequency of occurrence of Chironomidae, Neuroptera, Trichoptera, Aphidinea and Simuliidae were correlated with the bats' foraging activity.

Key words: prey; droppings; bats; foraging activity

Introduction

Prey of bats is most often studied by analyses of their pellets and only rarely by examination of stomach contents (e.g., Whitaker 1972; Bauerová 1978), or prey remains under temporary night roosts, where bats eat larger prey (e.g., Robinson 1990; Botvinkin et al. 1998). Previous studies have focused mostly on basic prey structure of particular bat species (Roer 1970; Bárta 1975; Bauerová & Červený 1986; Gregor & Bauerová 1987; Bauerová & Ruprecht 1989; Vaughan 1997; Pereira et al. 2002). There are few studies in which seasonal changes in prey structure were analysed (Labee & Voute 1983; Gajdošík & Gaisler 2004). Prey preferences of two or more species at the same sites were seldom studied (Swift & Racey 1983; Barlow 1997; Andreas et al. 2001). However, the widely accepted general conclusions concerning an overlap of prey niches and the competition for prey sources have emerged from such research.

Since 1990 two ecotypes of the common pipistrelle, *Pipistrellus pipistrellus* Schreber, 1774 (Ahlén 1990; Zingg 1990), and since 1993 two sibling species, *P. pipistrellus* and *P. pygmaeus* Leach, 1825, have been identified in Europe (Jones & van Parijs 1993; Barratt et al. 1995, 1997). Both pipistrelle species occur in the Czech Republic including our study area in SE Moravia (Gaisler et al. 2002), where they often exploit

the same foraging sites. Earlier studies concern the prey of *P. pipistrellus* sensu lato and not that of *P. pygmaeus* (Swift et al. 1985; Hoare 1991; Beck 1995). Barlow et al. (1999) attributed dissimilarity in prey composition to differences in skull parameters between *P. pipistrellus* sensu stricto and *P. pygmaeus* (Barlow et al. 1999). Nevertheless, these differences are small and varying composition of prey could be related to the competition pressure between the two cryptic species (Barlow 1997).

Due to their sympatric distribution in most of Europe (Mayer & Helversen 2001) and similar diet (Arnold et al. 2002), the competition might be reduced by altering timing or spatial distribution of the two species (Bartonička & Řehák 2004). In the Moravian lowlands, *P. pipistrellus* seems to be common in urban habitats and rare in floodplain forests, while *P. pygmaeus* prefers floodplain forests in the alluvial areas where its flight activity is very high (Bartonička & Řehák 2004). The fact that *P. pygmaeus* forages predominantly over habitats associated with water, whereas *P. pipistrellus* forages over a much wider range of habitats, has been confirmed by other authors (Vaughan et al. 1997; Oakeley & Jones 1998; Braun & Häussler 1999). Recent studies on habitat use, foraging activity and roost preferences of *P. pygmaeus* show some distinction between the central European populations and the populations in England, where more specific prey can be expected

in floodplain forest habitats than in surrounding agricultural areas (Davidson-Watts & Jones 2006; Nicholls & Racey 2006; Bartonička & Řehák 2007).

The aim of this study is to add new information about the ecology of *P. pygmaeus*, which is insufficiently known compared to that of *P. pipistrellus*. In particular, our goal is to contribute to the knowledge of the diet composition of a nursery colony of *P. pygmaeus* foraging in a floodplain forest and to reveal seasonal changes in diet regarding the changes in the bats' foraging activity.

Material and methods

Pellets were collected during vegetation seasons 2000–2002 at approximately two week intervals under the emerging crevice of a nursery colony dwelling in spaces beneath the roof of a game keeper's log-cabin. The site was situated in a floodplain forest at the confluence of the Dyje and Morava rivers (S Moravia, Czech Republic). Pellets, 20 per sample, were wetted on Petri dishes in the laboratory. After 20 minutes, each pellet was decomposed by a pair of tweezers under a binocular microscope. Particular prey remains were usually identified at a 28× magnification. We selected the body parts of arthropods relevant to their correct identification and evaluated their frequency in each pellet. Particular taxa were identified according to previous knowledge of bat prey (Andreas et al. 2001), after comparisons with a series of arthropod preparations, by means of guides (Döring 1955; Doskočil 1977; Chinery 1993a, b; Buchar et al. 1995; Reichholf-Riehmová 1996, 1997) and using a special handbook (McAney et al. 1991). Unidentifiable prey remains were archived as permanent preparations and later identified by specialists of each particular taxonomic group. Permanent preparations were made using Schwann's solution (Whitaker 1988; Wolz 1993a, b; Shiel et al. 1998).

Lepidoptera were identified by the presence of scales in the pellets. However, small numbers of moths' scales in a pellet were ignored, because they may remain in a bat's digestive system for a long period (Whitaker 1988). Nematoceran eggs were very well preserved in the droppings in comparison to other body remains; therefore their abundance in pellets was high. To avoid an overestimation of Nematocera, small numbers of eggs (less than 10) were ignored. Dipteran families Ceratopogonidae and Chironomidae could not be distinguished in the pellets and were therefore allocated to the more common, thus more likely group – Chironomidae (Fig. 3) (Sullivan et al. 1993). Similarly, Culicidae and Chaoboridae were consolidated into one group (Culicidae).

A heterodyne bat detector (Pettersson Elektronik D200) was used to follow foraging activity of *P. pygmaeus* on six line transects. Each monitoring event started 10 minutes after sunset and continued until the end of the first third of the respective night (McAney & Fairley 1988). The monitoring events lasted 10 minutes and covered a distance of ca 250 m. Transects, including their extreme points, were situated at distances of 70–420 m from the colony roost. Seasonal monitoring was determined only during the 2001 vegetation season, always one night before the date of pellet sampling (i.e. in ca two weeks intervals). Transects in two habitat types, water bodies (3) and forest sites (3), were regularly cycled during a night. The detector was tuned at 53 kHz (peak frequency of *P. pygmaeus* in this area, Bartonička & Řehák 2004). The level of flight activity was assessed as the relative number of individual minutes (positive minutes,

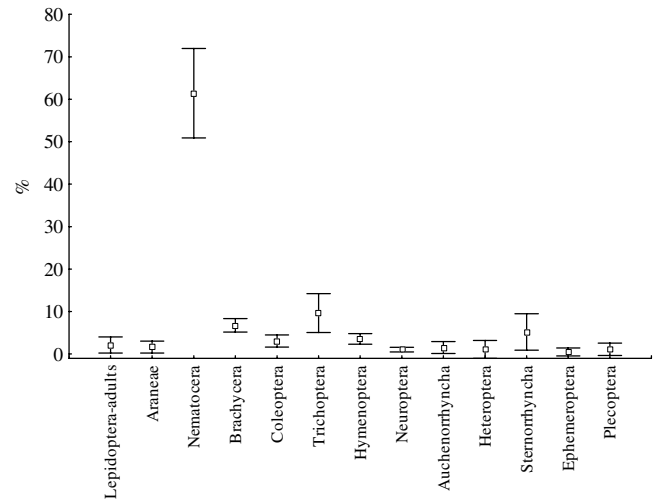


Fig. 1. Proportional representation of the most abundant prey groups found in the diet of *Pipistrellus pygmaeus*. Bars represent the means (\pm SD) of percentage items for 27 samples of droppings (20 pellets in one sample).

+ min) in which ultrasound signals were detected with respect to 60 minutes of monitoring (McAney & Fairley 1988; Zukal & Řehák 2006). The study period was divided into three parts with respect to bat reproduction, i.e., pregnancy (until June 15th), lactation (from June 16th up to July 13th), and post-lactation (after July 14th).

All groups of prey showed a normal distribution following arcsin transformation (Zar 1984). Two methods were used to quantify the relative dietary importance of prey items of the respective taxon in the pellets – percentage occurrence (relative presence of the taxon in all faecal pellets, McAney et al. 1991) and percentage items (the number of items of the respective taxon in percent of the total number of all items, Vaughan 1997). We compared the percentage occurrence of taxa in particular samples statistically using STATISTICA for Windows 7.0. For each period of the season, mean percentage of occurrence of every prey group was calculated. Analysis of variance (ANOVA) tests were used to assess seasonal differences in prey composition. Among the seasons the total number of analysed pellets differed (2000 – 13 samples, 2001 – 11 samples, 2002 – 3 samples). Seasonal differences within individual groups of prey were evaluated using F-tests and post-hoc T-tests. Bonferroni correction was used when the same data set was submitted to multiple tests. Logistic regression was used to evaluate some differences between the level of foraging activity and the percentage representation of a particular group of prey. In total, 27 samples of droppings were collected and 660 minutes of bat detecting were performed.

Results

Prey groups in the diet of P. pygmaeus

Altogether 40 taxonomic groups were recorded in the droppings (Table 1). In total, Diptera was the most abundant order in all seasons (Fig. 1). Of this order, the family Chironomidae (combined with Ceratopogonidae) was the most important Nematoceran group (Fig. 2). In addition to Diptera, Trichoptera, Hymenoptera and Sternorrhyncha were also found to be

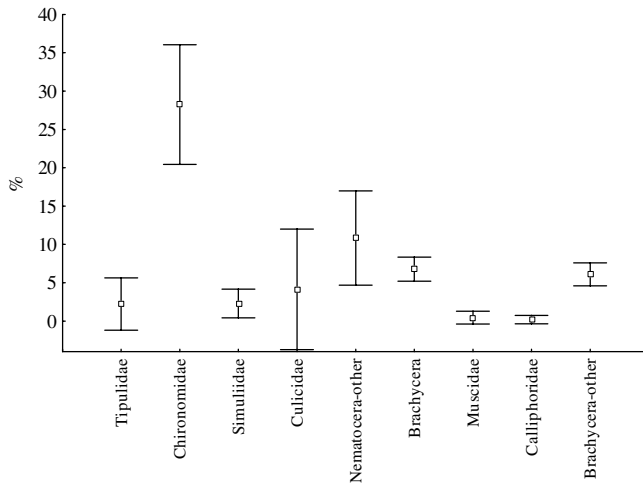


Fig. 2. Proportional representation of Diptera families. Each bar represents the mean (\pm SD) of percentage of occurrence for 27 samples (20 pellets in one sample) of droppings in three seasons pooled. Two items cover several groups (Nematocera-other = Psychodidae, Cecidomyiidae, Trichoceridae, Anisopodidae etc.; Brachycera-other = small flies such as Drosophilidae but also bigger species of other families).

plentiful. Other groups were only found in small numbers. Some “food” items could have been eaten by the bats while cleaning, grooming or during consumption of real prey (i.e. Oribatida). Oribatida were found in the droppings mainly from mid-May till mid-June, but their percentage did not exceed 9%. Other groups of Acarina (e.g. Ixodidae) were present in very low percentages, up to 0.5% over the entire study period. Body remains of the family Blattodea (*Ectobius* spp.) were found only once (1%), on 25th July 2001.

Seasonal changes in the prey

In total, no between-year differences (2000–2002) in the percentage of a particular prey group were recorded (ANOVA, $F = 5.78$, $P = 0.158$, $df = 48$), thus the data were pooled for further analyses. Significant differences were found among sampling dates ($F = 535.55$, $P = 0.034$, $n = 27$), as well as among the days of sampling ($F = 1041.76$, $P = 0.023$, $n = 27$). Significant seasonal fluctuation was found only in Nematocera (F -test, $F = 2.54$, $P = 0.048$, $n = 27$), Muscoidea ($F = 2.60$, $P = 0.046$, $n = 27$), Tipulidae ($F = 6.75$, $P = 0.001$, $n = 27$), Heteroptera ($F = 6.47$, $P = 0.001$, $n = 27$), Simuliidae ($F = 4.42$, $P = 0.001$) and Trichoptera ($F = 3.92$, $P = 0.001$) (Table 1).

Statistically significant differences in Nematocera occurrence was recorded between the beginning of May (the highest proportion) and the end of June (the lowest proportion) (t -test, $t = 7.01$, $P = 0.006$, $df = 3$, Bonferroni correction). Further seasonal changes in abundance of Nematocera were insignificant (Fig. 3). Significantly high percentages of superfamily Muscoidea were recorded at the beginning of August ($t = 2.74$, $P = 0.002$, $df = 2$, Bonferroni correction) and significantly decreasing towards the end of October ($t = 2.12$, $P = 0.007$, $df = 3$, Bonferroni correction). The

Table 1. The diet of *Pipistrellus pygmaeus* in three seasons.

Prey groups/year	2000	2001	2002
Order Araneida	*	*	*
Order Acari	*	*	*
Suborder Ixodida	*	*	–
Suborder Oribatida	*	*	*
Order Lepidoptera	*	*	*
Order Trichoptera	*	*	*
Order Hymenoptera	*	*	*
Superfamily Formicoidea	*	*	–
Family Ischnumonidae	*	–	*
Order Diptera	*	*	*
Suborder Nematocera	*	*	*
Family Tipulidae	*	*	*
Family Chironomidae	*	*	*
Family Ceratopogonidae	*	*	*
Family Simuliidae	*	*	*
Family Culicidae	*	*	*
Family Psychodidae	*	*	*
Family Cecidomyiidae	*	*	*
Family Chaoboridae	*	*	*
Nematocera – other	*	*	*
Suborder Brachycera	*	*	*
Family Muscidae	*	*	*
Family Anthomyiidae	*	*	*
Family Fanniidae	*	*	*
Family Drosophilidae	*	*	–
Family Calliphoridae	*	–	*
Brachycera – other	*	*	*
Order Coleoptera	*	*	*
Family Ipidae	–	–	*
Family Curculionidae	*	*	*
Family Carabidae	*	*	*
Order Neuroptera	*	*	*
Family Chrysopidae	*	*	*
Family Hemerobiidae	*	*	–
Order Heteroptera	*	*	*
Family Miridae	*	*	–
Family Lygaeidae	*	–	–
Family Corixidae	*	–	*
Order Plecoptera	*	*	*
Order Psocoptera	–	*	–
Order Blattodea	–	*	–
Order Hemiptera	*	*	*
Suborder Sternorrhyncha	*	*	*
Infraorder Psyllomorpha	–	*	–
Infraorder Aphidomorpha	*	*	*
Suborder Cicadomorpha	*	*	*
Family Cicadellidae	*	*	*
Family Cercopidae	*	*	*
Family Delphacidae	*	*	*
Order Ephemeroptera	*	*	*

* present in the diet, – absent

only statistically significant increase in number of superfamily Tipuloidea items was found at the beginning of June ($t = 9.80$, $P = 0.001$, $df = 2$, Bonferroni correction), however, at the beginning of September another, nearly significant increase, was also found ($t = -2.93$, $P = 0.008$, ns, Bonferroni correction). The percentage of Heteroptera items increased during July ($t = -9.39$, $P = 0.003$, $df = 3$, Bonferroni correction), but were well-balanced towards the end of season.

Foraging activity of bats and dynamics in their diet regarding reproduction status

Significant differences in the total foraging activity be-

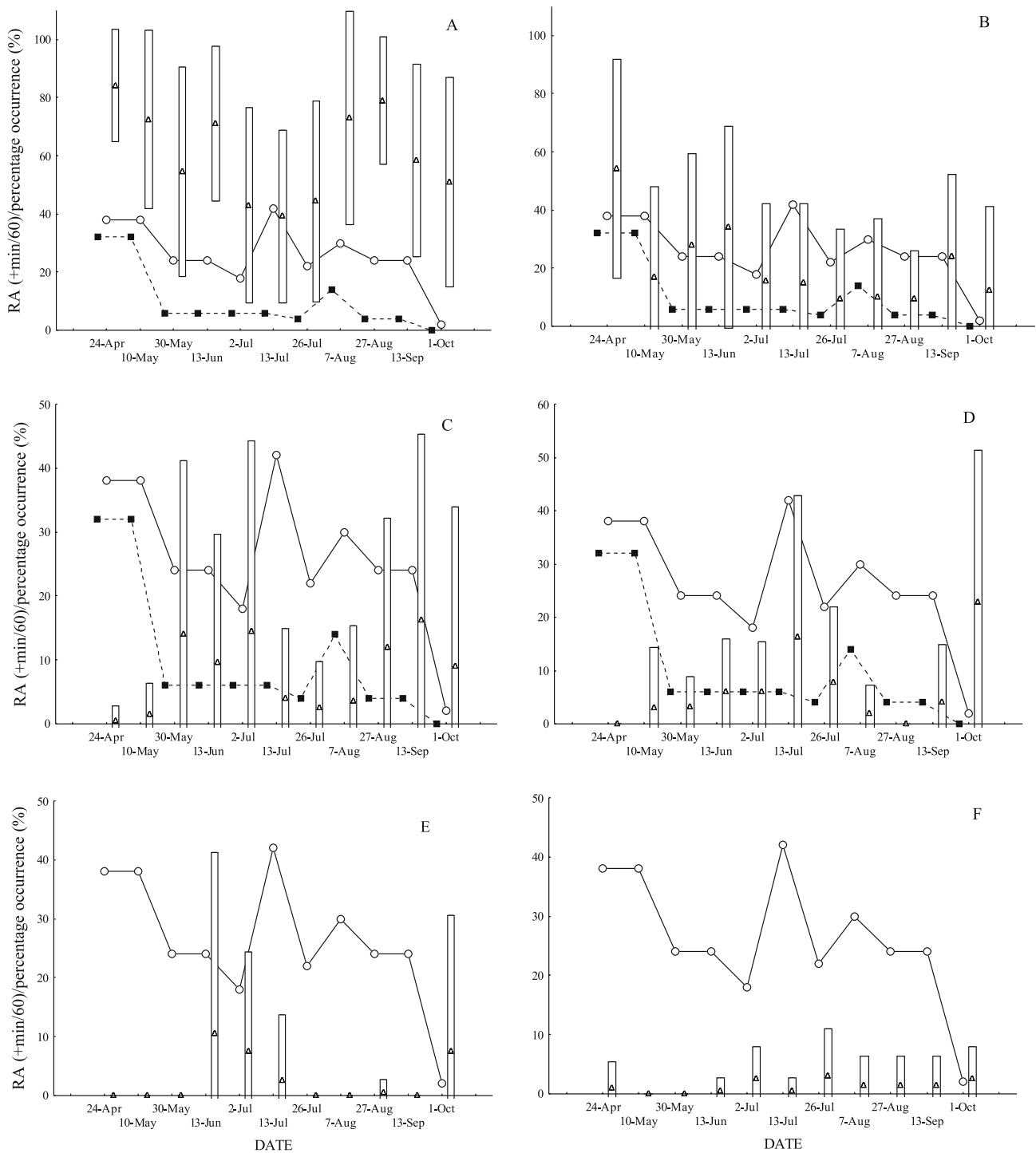


Fig. 3. Relative occurrence of categories (bars) in six the most frequent prey groups: A – Nematocera; B – Chironomidae; C – Trichoptera; D – Aphidinea; E – Simuliidae; F – Neuroptera. The curves represent relative activity in positive minutes/60 minutes of observation (RA), revealed by bat detector in foraging sites (dotted line – RA in forest; solid line – RA over water bodies).

tween sampling dates (ANOVA, $F = 60.01$, $P = 0.001$, $df = 9$) were found. There was a significant decrease in foraging activity over water habitats and in forest sites during late pregnancy (between May 14th and June 3rd, water: $t = 10.59$, $P = 0.032$, $df = 4$; forest: $t = 8.51$, $P = 0.022$, $df = 3$) and an increase in both habitats during the lactation and post-lactation periods (from June 13th up to August 2th, $t = 13.35$, $P = 0.038$, $df =$

5). An increase of foraging activity in forest sites also occurred during late lactation between June 23th and July 13th ($t = 16.15$, $P = 0.018$, $df = 3$).

Logistic regression indicated some differences exist between the level of foraging activity and percentage occurrence of prey groups. Nematocera (linear regression, $F = 16.59$, $P = 0.001$, $R^2 = 0.27$), Chironomidae ($F = 4.02$, $P = 0.046$, $R^2 = 0.13$) and Aphidinea ($F = 8.53$,

$P = 0.004$, $R^2 = 0.19$) were positively correlated with changes in foraging activity over water habitats, while Neuroptera ($F = 4.26$, $P = 0.04$, $R^2 = 0.14$) and Simuliidae ($F = 7.16$, $P = 0.008$, $R^2 = 0.18$) were positively correlated with foraging activity in forest sites (Fig. 3). On the other hand, Trichoptera correlated negatively with foraging activity over water habitats ($F = 4.91$, $P = 0.028$, $R^2 = 0.15$).

Discussion

Prey groups in the diet of P. pygmaeus

This study found that the diets of *P. pygmaeus* was comprised of 40 taxonomic groups of invertebrates, as opposed to the 22 families of insects described by Barlow (1997). Surprisingly she did not find any other taxa in addition to insects. Both studies found a high percentage of Diptera, families Chironomidae and Ceratopogonidae, although distribution patterns differ with respect to location. Arnold et al. (2002) found these same families to be the most common prey items in Central Europe. However, Arnold et al. (2002) revealed a higher occurrence of Ceratopogonidae and Chironomidae (30%) while Barlow (1997) lower, only about 6%. Frequency of the occurrence of non-nematoceran Diptera was found to be of 7.3% on average in our samples and, e. g. frequency of Muscidae varied from 1 to 3% and most of their fragments derived from relatively big flies with body length of 6–12 mm, which made the biggest prey of *P. pygmaeus* (cf. Barlow 1997). Since *P. pygmaeus* usually hunts by aerial hawking (Norberg & Rayner 1987), the flies probably could not be collected when sitting on the foliage. Peng et al. (1992), however, showed that several species of Muscidae had crepuscular activity thus could be caught by bats flying in open space. Barlow (1997) also found body fragments of Muscidae (in ca 3%). This reopens the question of foliage gleaning by pipistrelle bats. Most Brachycera remains were not identified more accurately due to the absence of identification signs on the remains. This fact implies that after catching a bigger insect, the bat must separate its hard parts, such as antennas, mandibles, legs, head capsules and wing cases, to eat only the soft parts, particularly the abdomens. In bat species bigger than pipistrelles, which are able to chew up big prey, the identification of remains in their pellets is usually more accurate (Shiel et al. 1991, Andreas 1994, Shield et al. 1998). Insect orders Trichoptera (9.4%), Sternorrhyncha (mainly Aphidinea) (3.6%) and Coleoptera (3.5%), represented by families such as Ipididae, Curculionidae and Carabidae, were all found in relative small numbers. Barlow (1997) found very similar percentage items of beetles in the prey of *P. pygmaeus*, whereas Arnold et al. (2002) detected only 0.5% of samples with the remains of Coleoptera. Some authors found a very high frequency of Hymenoptera (14.8%). We identified Hymenoptera species only in approximately 3% of samples, which is comparable to Barlow (1997) who found them in about 2% of the sample. The opportunistic behaviour of *P. pygmaeus* is indicated by the very

high percentage items of the rare groups Empiridae and Staphilinidae, on 30 May 2001 and 22 August 2002, respectively.

In our prey analyses we also found some species of other arthropod groups such as the parasitic acarids (Acarina) including ticks (Ixodidea), as well as oribatids (Oribatida). Oribatids were probably consumed with epigeic insects living on the ground or when the oribatids moved on the bat's bodies while in close proximity to the soil during daily activities. Ticks similarly to bugs (genus *Cimex*) should not be classified as the prey of bats since they usually are swallowed during the grooming (Andreas et al. 2001).

Seasonal changes in the diet and foraging activity

To understand the trophic potential of particular foraging sites, it is important to be familiar with seasonal changes in the abundance of the bat's dominant prey. Unfortunately, most studies focussed only on particular model taxa, not on the whole prey zoocenosis. Nakano & Murakami (2001) surveyed trophic interactions between forest sites and water bodies. They assumed that in a deciduous forest and stream ecotone aquatic insect emergence peaked in spring, when terrestrial invertebrate biomass was low. In the forest, terrestrial prey biomass during the leafing period was much greater, peaking in mid summer (August), than during the leaflessness period in spring. Nevertheless, our results show high foraging activity of *P. pygmaeus* in forest habitats only in spring (April – May) when important prey groups are subject to presence of water. However, aquatic prey flux to the forest was greatest in spring. High spring activity of bats in the forest could be related to low foliage density, increasing prey availability and flight ability of pipistrelles.

During the post-lactation period (late July – mid-August) a small increase in foraging activity of bats was found inside the forest, possibly due to the increase in intra-specific competition over water habitats, when adult females can use foraging sites more distant from their colony roost and relinquish the trophic sites close to the roost and early fledged young (Adams 1997). Increased foraging in the forest may also account for the higher percentage of Hymenoptera (mainly Ichneumonidae and Formicoidea) and Neuroptera (Chrysopidae, Hemerobiidae) found in the post-lactation period as compared to the lactation period. Species of these groups are bound to forest rather than water habitats.

In contrast, aquatic prey biomass during the leaflessness period was much greater than during the leafing period. However, aquatic prey flux to the forest was not correlated with the biomass of aquatic prey over water bodies. Throughout all sampling periods, Nematocera was the most abundant taxon recorded in the droppings. The bimodal pattern of their occurrence during the season and the percentage of items positively correlated with the foraging activity of *P. pygmaeus*. Members of the Chironomidae group (Chironomidae and Ceratopogonidae) were the most abundant and best available prey mainly in spring (late April

– mid-June). The highest percentage of Chironomidae items in pellets positively correlated with the time of their first swarming (Chvála et al. 1980; Arnold et al. 2002). Changes in percentage of Chironomidae items during the vegetation season were recorded also by Barlow (1997) but they were not specified. Another nematoceran family, Simuliidae, was recorded in pipistrelles' prey by Beck (1995). Simuliidae have worldwide distribution but 60% of all species occur in Europe (Jelička & Knoz 2006). Two types of Simuliid species are found in the study area; species with one peak of adults' swarming per season (e.g. *Eusimulium securiforme* swarms in late October; *Boophthora erythrocephala* usually in mid-June) and species that have two or more generations per year (e.g. *Simulium noelleri*, *Boophthora sericata*) (Knoz 1965, Knoz & Šašinková 1969). The time of swarming in common species of Simuliidae correlates with two peaks found in the pellets (May – July, September – October) (Chvála et al. 1980). Black-mites could play an important role as bat prey mainly in autumn, in the floodplain forest, when the bats' foraging activity usually decreases (Bartonička & Řehák 2004). *Pipistrellus pygmaeus* prefers small insects in its food, especially small Nematocera, although prey sized 4–12 mm have also been found in food remains. In addition to Nematocera, brachyceran Diptera were also recorded in this species' prey. High frequency of Brachycera in the diet indicates that pipistrelles either glean them from the foliage or that some Brachycera fly during the night or at least at dusk. The findings of Oribatida in the pellets suggest that *P. pygmaeus* can rarely glean the ground or low grown vegetation. To clarify the relationship between foraging habitats and taxa found by analyses of pellets it is necessary to sample the prey supply of particular foraging sites. Simultaneous sampling of potential prey and analysis of droppings can show significant abundance of particular taxa in nature and facilitate precise identification of taxa in bats' diet.

Acknowledgements

We are very grateful to J. Gaisler, M. Nicholls and reviewers for valuable comments on the manuscript. The study was supported by the grants of Grant Agency of the Czech Republic No. 206/06/0954 and the grants of Ministry of Education, Young and Sports of the Czech Republic No. MSM0021622416 and MSM 6293359101.

References

- Adams R.A. 1997. Onset of volancy and foraging patterns of juvenile little brown bats, *Myotis lucifugus*. *J. Mammal.* **78**: 239–246.
- Ahlén I. 1990. Identification of Bats in Flight. Swedish Society for Conservation of Nature & The Swedish Youth Association for Environmental Studies and Conservation, 50 pp.
- Andreas M., Reiter A., Benda P. & Zupal J. 2001. Research of the diet ecology of bat community in Ledové sluje in National park Podyjí. *Thayensia* **4**: 5–18.
- Arnold A., Häussler U. & Braun M. 2002. Comparative study of the diets of two pipistrelle species (*Pipistrellus pygmaeus/mediterraneus* and *P. pipistrellus*) in Southwest Germany. *Bat Res. News* **43**: 72.
- Arnold A., Häussler U. & Braun M. 2003. Feeding ecology of common and soprano pipistrelles (*Pipistrellus pipistrellus* and *P. pygmaeus*) in Heidelberg communal forest (SW-Germany). *Carolinea* **61**: 177–183.
- Barlow K. 1997. The diets of two phonic types of the bat *Pipistrellus pipistrellus* in Britain. *J. Zool. Lond.* **243**: 597–609.
- Barlow K., Jones G. & Barratt E.M. 1997. Can skull morphology be used to predict ecological relationships between bat species? A test of two cryptic species of pipistrelle. *Proc. R. Soc. Lond. B* **264**: 1695–1700.
- Barratt E.M., Bruford M.W., Burland T.M., Jones G., Racey P.A. & Wayne R. 1995. Characterization of mitochondrial DNA variability within the microchiropteran genus *Pipistrellus*: approaches and applications. *Symp. Zool. Soc. Lond.* **67**: 377–386.
- Barratt E.M., Deaville R., Burland T.M. & Bruford M.W. 1997. DNA answers the call of pipistrelle bat species. *Nature* **387**: 138–139.
- Bárta Z. 1975. Diet of brown big-eared bat (*Plecotus auritus* L.). *Lynx n.s.* **17**: 5–6.
- Bartonička T. & Řehák Z. 2004. Flight activity and habitat use of *Pipistrellus pygmaeus* in a floodplain forest. *Mammalia* **68**: 365–375.
- Bartonička T. & Řehák Z. 2007. Influence of the microclimate of bat boxes on their occupation by the soprano pipistrelle *Pipistrellus pygmaeus*: possible cause of roost switching. *Acta Chiropterologica*, 9(2), in press.
- Bauerová Z. 1978. Contribution to the trophic ecology of *Myotis myotis*. *Folia Zool.* **27**: 305–316.
- Bauerová Z. & Červený J. 1986. Towards an understanding of the trophic ecology of *Myotis nattereri*. *Folia Zool.* **35**: 55–61.
- Bauerová Z. & Ruprecht A.L. 1989. Contribution to the knowledge of the trophic ecology of parti-coloured bat, *Vespertilio murinus*. *Folia Zool.* **38**: 227–232.
- Beck A. 1995. Fecal analyses of European bat species. *Myotis* **32–33**: 109–119.
- Botvinkin A.D., Šilenkova Ju.V. & Šilenkov V.G. 1998. Sravnenie pitaniya burogo ushana (*Plecotus auritus* L.) v kontrastnykh mestoobytniyach Vostočnoj Sibiri. *Plecotus et al.* **1**: 27–34.
- Braun M. & Häussler U. 1999. Funde der Zwergfledermaus-Zwillingsart *Pipistrellus pygmaeus* (Leach, 1825) in Nordbaden. *Carolinea* **57**: 111–120.
- Buchar J., Ducháč V., Hůrka K. & Lellák J. 1995. Klíč k určování bezobratlých [Handbook of invertebrates]. Scientia, Prague, 285+LXIV pp.
- Davidson-Watts I. & Jones G. 2006. Differences in foraging behaviour between *Pipistrellus pipistrellus* Schreber, 1774 and *Pipistrellus pygmaeus* Leach, 1825. *J. Zool. Lond.* **268**: 55–62.
- Döring E. 1955. Zur Morphologie der Schmetterlingseier. Akademie-Verlag, Berlin, 154+LXI pp.
- Doskočil J. 1977. Klíč zvířeny ČSSR V, Diptera [Handbook of fauna ČSSR V, Diptera]. Academia, Prague, 373 pp.
- Gaisler J., Řehák Z. & Bartonička T. 2002. Mammalia: Chiroptera, pp. 139–149. In: Řehák Z., Gaisler J. & Chytil J. (eds), Vertebrates of the Pálava Biosphere Reserve of UNESCO. *Folia Fac. Sci. Nat. Univ. Masaryk. Brun. Biol.* **106**.
- Gajdošík M. & Gaisler J. 2004. Diet of two *Eptesicus* bat species in Moravia (Czech Republic). *Folia Zool.* **53**: 7–16.
- Gregor F. & Bauerová Z., 1987. The role of Diptera in the diet of Natterer's bat, *Myotis nattereri*. *Folia Zool.* **36**: 13–19.
- Hoare L.R. 1991. The diet of *Pipistrellus pipistrellus* during the prehibernal period. *J. Zool. Lond.* **225**: 665–670.
- Chinery M. 1993a. Insects of Britain and Western Europe. Harper Collins Publishers, London, 320 pp.
- Chinery M. 1993b. Insects of Britain and Northern Europe. Harper Collins Publishers, London-Glasgow-New York-Sydney-Auckland-Toronto-Johannesburg, 320 pp.
- Chvála M., Hůrka K., Chalupský J., Knoz J., Minář J. & Országh I. 1980. Krevsající mouchy a střechci – Diptera [Blood-sucking flies and botflies – Diptera]. *Fauna ČSSR*, Vol. 22, Academia, Prague, 538 pp.

- Jones G. & van Parijs S.M. 1993. Bimodal echolocation in pipistrelle bats: are cryptic species present? *Proc. R. Soc. Lond. B* **251**: 119–125.
- Knoz J. 1965. Identification of Czechoslovakian Black-Flies (Diptera, Simuliidae). *Folia Fac. Sci. Nat. Univ. Purkyn. Brun. Biol.* **2**, 53 pp.
- Jedlička L. & Knoz J. 2006. Simuliidae. In: Jedlička L., Kúdela M. & Stloukalová V. (eds), Checklist of Diptera of the Czech Republic and Slovakia, Electronic version 1, CD ROM edition, Comenius University, Bratislava. Available also online at <http://zoology.fns.uniba.sk/diptera/Titul.htm> (retrieved 15.12.2007)
- Knoz J. & Šašínková V. 1969. Zur Kenntnis der Kriebelmücken (Simuliidae, Diptera) im Dyje-Gebiet in Morava. *Folia Fac. Sci. Nat. Univ. Purkyn. Brun. Biol.* **25**: 13–44.
- Labee A.H. & Voute A.M. 1983. Voedselkeuze vaneen kolonie laadvliegers *Eptesicus serotinus*. *Lutra* **26**: 12–19.
- Mayer F. & von Helversen O. 2001. Sympatric distribution of two cryptic bat species across Europe. *Biol. J. Linn. Soc.* **74**: 365–374.
- McAney M. & Fairley J.S. 1988. Activity patterns of lesser horseshoe bat *Rhinolophus hipposideros* at summer roost. *J. Zool. Lond.* **216**: 325–338.
- McAney C.M., Shiel C.B., Sullivan C.B. & Fairley J.S. 1991. Analysis of bat droppings. The Mammal Society, London, 48 pp.
- Nakano S. & Murakami M. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *PNAS* **98**: 166–170.
- Nicholls B. & Racey P.A. 2006. Contrasting homerange size and spatial partitioning in cryptic and sympatric pipistrelle bats. *Behav. Ecol. Sociobiol.* **61**: 131–142.
- Norberg U.M. & Rayner J.M. 1987. Ecological morphology and flight in bats: wing adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. Lond. B* **316**: 335–427.
- Oakeley S.F. & Jones G. 1998. Habitat around maternity roost of the 55 kHz phonic type of pipistrelle bats (*Pipistrellus pipistrellus*). *J. Zool. Lond.* **245**: 222–228.
- Pereira M.J.R., Rebelo H., Rainho A. & Palmeirim J.M. 2002. Prey selection by *Myotis myotis* (Vespertilionidae) in a Mediterranean region. *Acta Chiropter.* **4**: 183–193.
- Reichholf-Riehmová H. 1996. Motýli [Butterflies]. Ikar, Prague, 287 pp.
- Reichholf-Riehmová H. 1997. Hmyz a pavoukovci [Insect and arachnids]. Ikar, Prague, 287 pp.
- Robinson M.F. 1990. Prey selection by the brown long-eared bat (*Plecotus auritus*). *Myotis* **28**: 5–18.
- Roer H. 1970. Probleme der Ernährung und des Jagdverhaltens insektenfressender Fledermäuse. *Myotis* **8**: 3–8.
- Rozkošný R. & Vaňhara J. (eds) 1998. Diptera of the Pálava Biosphere Reserve of UNESCO. *Folia Fac. Sci. Nat. Univ. Masaryk. Brun. Biol.* **99**, 219 pp.
- Shiel C.B., Duvergé P.L., Smiddy P. & Fairley J.S. 1998. Analysis of the diet of Leisler's bat (*Nyctalus leisleri*) in Ireland with some comparative analyses from England and Germany. *J. Zool. Lond.* **246**: 417–425.
- Shiel C.B., McAney C.M. & Fairley J.S. 1991. Analysis of the diet of Natterer's bat *Myotis nattereri* and the common long-eared bat *Plecotus auritus* in the West of Ireland. *J. Zool. Lond.* **223**: 299–305.
- Sullivan C.M., Shiel C.B., McAney C.M. & Fairley J.S. 1993. Analysis of the diets of Leisler's *Nyctalus leisleri*, Daubenton's *Myotis daubentoni*, and pipistrelle *Pipistrellus pipistrellus* bats in Ireland. *J. Zool. Lond.* **231**: 656–663.
- Swift S.M. & Racey P.A. 1983. Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. *J. Zool. Lond.* **200**: 249–259.
- Swift S.M., Racey P.A. & Avery M.I. 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. II. Diet. *J. Anim. Ecol.* **54**: 217–225.
- Vaughan N. 1997. The diets of British bats (Chiroptera). *Mammal Rev.* **27**: 77–94.
- Vaughan N., Jones G. & Harris S. 1997. Habitat use by bats (Chiroptera) assessed by means of broad-band acoustic method. *J. Appl. Ecol.* **34**: 716–730.
- Whitaker J.O., Jr. 1972. Food habits of bats from Indiana. *Can. J. Zool.* **50**: 877–883.
- Whitaker J.O., Jr. 1988. Foods habits analysis of insectivorous bats, pp. 171–189. In: Kunz T. H. (ed.), *Ecological and behavioral methods for the study of bats*, Smithsonian Institution Press, Washington, D. C., 533 pp.
- Wolz I. 1993a. Untersuchungen zur Nachweisbarkeit von Beute-tierfragmenten im Kot von *Myotis bechsteini* (Kuhl, 1818). *Myotis* **31**: 5–25.
- Wolz I. 1993b. Das Beutespektrum der Bechsteinfledermaus *Myotis bechsteini* (Kuhl, 1818) ermittelt aus Kotanalysen. *Myotis* **31**: 27–68.
- Zar J.H. 1984. *Biostatistical analysis*. Simon and Schuster, Englewood Cliffs, New Jersey, USA, 718 pp.
- Zingg P.E. 1990. Akustische Artidentifikation von Fledermäusen (Mammalia: Chiroptera) in der Schweiz. *Rev. Suisse Zool.* **97**: 263–294.
- Zukal J. & Řehák Z. 2006. Flight activity and habitat preference of bats in the karstic area by using bat detectors. *Folia Zool.* **55**: 273–281.

Received March 13, 2007

Accepted June 15, 2007