Diet of two *Eptesicus* bat species in Moravia (Czech Republic)

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A b s t r a c t . Faecal pellets were collected under one maternity colony of each of *E. serotinus* (*E.s.*) and *E. nilssonii* (*E.n.*). The distance between the colonies was 83 km. In total, 325 pellets (13 samples) of *E.s.* and 150 pellets (6 samples) of *E.n.* were analysed. Nematoceran Diptera, mainly Chironomidae, were the most frequent food items in both species. Coleoptera, Lepidoptera, Heteroptera (Corixidae, Lygaeidae) and Hymenoptera (Formicoidea, Ichneumonidae) were common in *E.s.*, Lepidoptera, Heteroptera (Miridae), Aphidomorpha, Psyllomorpha and brachyceran Diptera were common in *E.n.* If the samples of the two species are adjusted to the same time (16 June – 15 August), the prevalence of Coleoptera and Hymenoptera in *E.s.* and Heteroptera and Lepidoptera in *E.n.* are highly significant (p < 0.001) while the prevalence of Brachycera in *E.s.* is less significant (p < 0.05) and the difference in consuming Nematocera insignificant. At that time of year, potential prey niche overlap between the two species (O_{jk}) fluctuated between 6 % and 80 % with an average of 69 %. Prey diversity (H'), evenness (J'), measure of niche breadth (B) and the representation of four major insect groups varied seasonally and in the two species independently of each other. Both species prefer aerial hawking and hunt for swarming insects if available. Comparison with data of other authors revealed regional differences in foraging and diet within each of the species studied.

Introduction

Eptesicus serotinus Schreber, 1774 and *Eptesicus nilssonii* (Keyserling et Blasius, 1839) are two closely related bat species largely sympatric in central Europe. In most cases, however, they are not syntopic. *E. serotinus* prefers lowlands and was recorded up to 900 m above sea level in summer, while *E. nilssonii* occurs predominantly in foothills of mountains and in mountainous regions in central Europe and was recorded up to 2300 m (nursery up to 1660 m) (S c h o b e r & G r i m m b e r g e r 1998). Both species roost usually in buildings but there is no record of the two species roosting in the same building or even in a building within the same human settlement. In 1993–1998 the diet, foraging behaviour, temporal and spatial activity and predation risk were studied in a southern Moravian population of *E. serotinus* (see Study Areas), but only a small part of the results of these studies have been published (G a j d o š í k et al. 1996, Z u k a l et al. 1997, P e t r ž e l k o v á & Z u k a l 2001). The diet, foraging behaviour and habitat use of *E. serotinus* have been studied mainly in Great Britain (P o u l t o n 1929, R o b i n s o n & S t e b b i n g s 1993, C a t t o et al. 1994, 1996, V a u g h a n 1997), the diet and foraging behaviour of *E. nilssonii* mainly in southern Sweden (R y d e l l 1986, 1989, 1991, 1993). Only one study has assessed both *E. serotinus* and *E. nilssonii* feeding ecology in

the same locality (A n d r e a s et al. 1998, A n d r e a s 2002). Bats were netted and then kept in cloth sacks to produce faecal pellets which were collected for later analysis. Hence the study did not consider bat colony roosts. The aim of the present study, on the contrary, is to analyse the diet of two maternity colonies (one of each *E. serotinus* and *E. nilssonii*) and to compare food structure, diversity and seasonal dynamics with respect to trophic niche overlap in the two species. The localities were selected as close as possible to one another.

Study Areas

The two areas are situated within Moravia, the smaller eastern part of the Czech Republic (Fig. 1). The maternity colony of *E. serotinus* was situated in the loft of a church at Brod nad Dyjí at the elevation of 175 m. The area is part of the Dyje-Svratka Graben with a flat to slightly undulated relief. A lowland character is displayed by the belts of floodplains and terraces along the main streams and three water reservoirs, over 3000 ha in total water surface. There is a small fishpond in the village, agrocoenoses with windbreaks and small woods prevail in its surroundings. The climate is warm, dry with a moderate winter (D e m e k & S t ř í d a 1971).
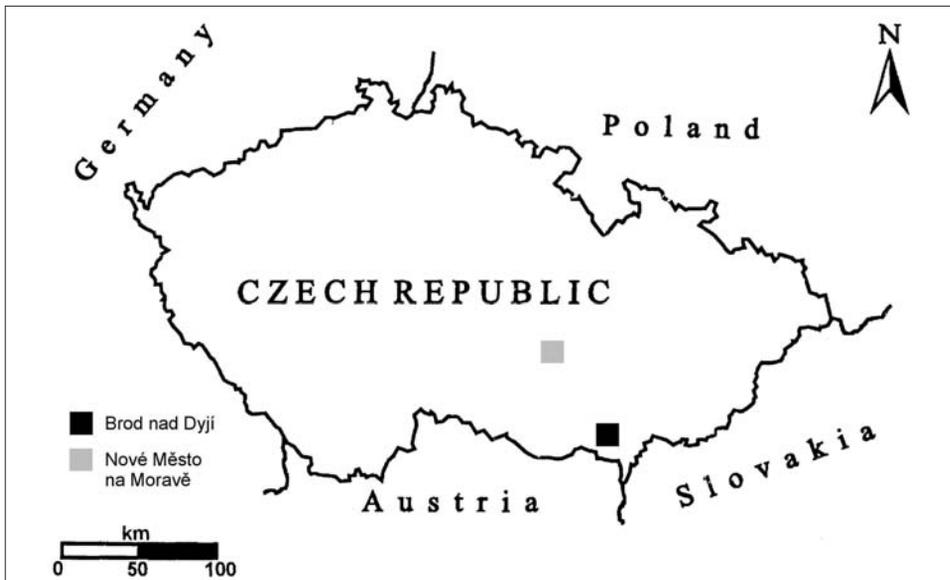
Fig. 1. Situation of the localities: Brod nad Dyjí with a breeding colony of *Eptesicus serotinus* (maximum 60 individuals) and Nové Město na Moravě with a breeding colony of *Eptesicus nilssonii* (maximum 42 individuals). For details see Study areas.

The maternity colony of *E. nilssonii* was situated in the loft of a family house at Nové Město na Moravě at the elevation of 594 m. The area is part of the Bohemian-Moravian Highlands and the subunit Žďárská vrchovina. Narrow ridges and deep but wide open valleys are typical of its relief. There are numerous fishponds, some of them at the outskirts of the small town in question. Agrocoenoses are less represented than within the first study area, coniferous and mixed forests prevail. The climate is moderately warm, moderately humid, of highland character (D e m e k & S t ř í d a 1971). The distance between the two maternity colonies is 83 km.

Material and Methods

Faecal pellets were collected by spreading polythene sheets on the attic floor, under the crevices with roosting bats. Sampling was performed in the morning after the bats returned to the roost, at about 10 day intervals from the first to the last occurrence of bats. Sampling dates were shifted in unfavourable weather between two sampling periods (heavy rain, etc.). From the pellets collected, 25 were chosen as a main and another 25 as a spare sample and each of the samples deposited in a separate plastic tube. In total 650 pellets of *E. serotinus* and 300 pellets of *E. nilssonii* were stored of which 325 pellets (13 samples) of *E. serotinus* and 150 pellets (6 samples) of *E. nilssonii* were analysed. Each pellet was soaked in 96 % ethanol for 24 h, then teased apart in glycerol with dissecting needles on a Petri dish underlayed with a millimetre paper and under a binocular microscope (M c A n e y & F a i r l e y 1989). The number of identifiable and unidentifiable items was determined and the percentage of their occurrence, frequency and relative volume estimated. Important items were mounted on slides in Liquido-Foure for further determination and 299 microphotographs were made (x 175-1225). Identification of insect fragments to family was achieved using entomological guide-books (C h i n e r y 1978, 1981), papers focussed on bat diets (K u n z & W h i t a k e r 1983, W h i t a k e r 1988, M c A n e y et al. 1991, W o l z 1993) and a reference collection of whole insects trapped in the vicinity of roosts. For technical reasons, the two maternity roosts were sampled in two different years, that of *E. serotinus* in 1997 and that of *E. nilssonii* in 1998. However, the two sampling seasons did not differ significantly in terms of climate, there were no unusual temperatures or rainfall (P e t r ž e l k o v á & Z u k a l 2001).

Shannon-Wiener measure of diversity H', Levin's measure of niche breadth B, evenness measure of the Shannon-Wiener function J', and Pianka's measure of niche overlap O_{jk} were calculated according to K r e b s (1989). The significance of variation in diet within and between the species was tested using χ^2 to compare percentage frequencies and percentage volumes (observed against expected values), df = 32. Difference test between two proportions was used to test significance of percentage occurrence of the food items. The statistics were performed using STATISTICA for Windows, StatSoft, Inc. (2001), Tulsa, OK, USA.

Results

F o o d c o m p o s i t i o n

Nematoceran Diptera of the family Chironomidae dominated the sample of food items in both species (Table 1). From among insect orders, Coleoptera in *E. serotinus* and Lepidoptera in *E. nilssonii* were the second most important food component. Carabidae, Scarabaeidae and Chrysomeloidea were well represented among beetles eaten by *E. serotinus*. The next component was Lepidoptera in *E. serotinus* and Hemiptera of the family Miridae in *E. nilssonii*. Other prey items relatively well represented were Hemiptera Corixidae, Lygaeidae and Cixiidae and Hymenoptera Ichneumonidae and Formicoidea in *E. serotinus* and Hemiptera Aphidomorpha and Psyllomorpha and brachyceran Diptera of the superfamily Muscoidea in *E. nilssonii*. In addition to insects which can be considered a prey, ectoparasitic Siphonaptera were found in both species and Collembola in *E. serotinus* and Araneida in *E. nilssonii* respectively, probably gleaned from either the ground or vegetation.

Since the sample of *E. nilssonii* pellets could be obtained within a shorter time than that of *E. serotinus* pellets, the sample of the latter species was reduced (Table 2). This comparison

concerned the summer months June to August. Prey items were lumped into orders except hemipteran suborders Psyllomorpha, Aphidomorpha and Heteroptera and dipteran suborders Nematocera and Brachycera. Of the 12 prey items identified, 11 were found in *E. nilssonii* while only eight in *E. serotinus*. By both percentage frequency and percentage volume the most important prey items of *E. serotinus* are Nematocera, Coleoptera, Lepidoptera, Heteroptera and Hymenoptera. Although Nematocera are most frequent in the diet of *E. nilssonii* as well, their dominance is less pronounced and Lepidoptera are almost equally represented. Further prey items common in the diet of *E. nilssonii* are Heteroptera, Psyllomorpha, Brachycera, Aphidomorpha and Coleoptera. In the sample of each species, the representation of prey items is significaly different by both percentage frequency ($\chi^2 = 115.9$, df = 32, p< 0.001 and $\chi^2 = 541.5$, DF = 32, p < 0.001) and percentage volume ($\chi^2 = 138.6$, df = 32, p < 0.001 and $\chi^2 = 4157.8$, df = 32, p < 0.001). Concerning the differences in consuming insect orders or suborders by the two species, the prevalence of Coleoptera and Hymenoptera in *E. serotinus* and Heteroptera and Lepidoptera in *E. nilssonii* are highly

Table 1. Results of faecal analyses of *E. serotinus* (n = 13 samples, 325 pellets) and *E. nilssonii* (n = 6 samples, 150 pellets). Explanations: n(z) = number of pellets in which the item z was found; %oc(z) = percentage occurrence of the item z; %f(z) = percentage frequency of the item z; %vol(z-tot) = percentage volume of the item z from the total (tot) volume of all items (M c A n e y et al. 1991)

| Prey item	*Eptesicus serotinus*				*Eptesicus nilssonii*			
	n(z)	%oc(z)	%f(z)	%vol(z-tot)	n(z)	%oc(z)	%f(z)	%vol(z-tot)
Psyllidae	-	-	-	-	5	3,4	1,6	0,9
Triozidae	-	-	-	-	2	1,4	0,6	0,1
Psyllomorpha indet.	-	-	-	-	10	6,7	3,2	0,7
Aphidomorpha	-	-	-	-	15	10	4,9	0,6
Cixiidae	12	3,7	1,7	0,9	-	-	-	-
Miridae	-	-	-	-	64	42,7	20,8	26,6
Corixidae	62	19,1	8,7	2,8	-	-	-	-
Lygaeidae	27	8,3	3,8	0,7	-	-	-	-
Hemerobiidae	3	0,9	0,4	0,4	6	4	1,9	1,6
Carabidae	133	40,9	18,7	23,4	5	3,4	1,6	0,3
Scarabaeidae	29	8,9	4,1	3,4	8	5,4	2,6	1,1
Chrysomeloidea	14	4,3	2	0,9	-	-	-	-
Coleoptera indet.	1	0,3	0,1	0	-	-	-	-
Hydropsychidae	-	-	-	-	3	2	1	1
Lepidoptera	115	35,4	16,2	4,8	81	54	26,3	29,8
Chironomidae	241	74,2	33,9	57,2	86	57,3	27,9	34,7
Tipulidae	5	1,5	0,7	0,2	-	-	-	-
Anisopodidae	-	-	-	-	2	1,4	0,6	0,2
Tachinidae	-	-	-	-	1	0,7	0,3	0,1
Sarcophagidae	1	0,3	0,1	0	-	-	-	-
Calliphoridae	1	0,3	0,1	0	-	-	-	-
Chloropidae	1	0,3	0,1	0	-	-	-	-
Syrphidae	-	-	-	-	1	0,7	0,3	0
Muscidae	1	0,3	0,1	0	-	-	-	-
Muscoidea indet.	5	1,5	0,7	0,2	13	8,7	4,2	1,2
Diptera indet.	-	-	-	-	1	0,7	0,3	0
Ichneumonidae	23	7,1	3,2	0,9	-	-	-	-
Formicoidea	35	10,8	5	4	1	0,7	0,3	0,4
Apoidea	-	-	-	-	1	0,7	0,3	0,1
Hymenoptera indet.	-	-	-	-	1	0,7	0,3	0
Siphonaptera	1	0,3	0,1	0	1	0,7	0,3	0
Collembola	1	0,3	0,1	0	-	-	-	-
Araneida	-	-	-	-	1	0,7	0,3	0.7
Total	711	218,7	99,8	99,8	308	206	99,9	100,1

significant (p < 0.001), while the prevalence of Brachycera in *E. nilssonii* is less significant (p < 0.05) and the difference in consuming Nematocera insignificant.

Table 2. Comparison of quantitative representation of major prey items found in the pellets of *E. serotinus* and *E. nilssonii* within the same time of year, 16 June – 15 August (n = 6 samples, 150 pellets in each of the species). Explanations as in Table 1.

Prey item	*Eptesicus serotinus*				*Eptesicus nilssonii*			
	n(z)	%oc(z)	%f(z)	%vol(z-tot)	n(z)	%oc(z)	%f(z)	%vol(z-tot)
Psyllomorpha	-	-	-	-	16	10,7	5,3	1,7
Aphidomorpha	-	-	-	-	15	10	4,9	0,6
Heteroptera	40	26,7	11,7	3,8	64	42,7	21,1	26,6
Homoptera	12	8	3,5	1,5	-	-	-	-
Neuroptera	1	0,7	0,3	0,7	6	4	2	1,6
Coleoptera	85	56,7	24,9	34,9	13	8,7	4,3	1,3
Trichoptera	-	-	-	-	3	2	1	1
Lepidoptera	73	48,7	21,4	6,8	81	54	26,6	29,8
Nematocera	90	60	26,4	43	86	57,3	28,3	34,7
Brachycera	2	1,3	0,6	0,1	16	10,7	5,3	1,5
Hymenoptera	38	25,3	11,1	9,1	3	2	1	0,5
Araneida	-	-	-	-	1	0,7	0,3	0,7
Total	341	227,4	99,9	99,9	304	202,8	100,1	100,1

Seasonal variation

Seasonal changes in prey diversity, evenness and in the measure of niche breadth are well represented in *E. serotinus*, the breeding colony of which occupied its shelter from May till September (Fig. 2). A gradual increase of diversity from the beginning of the season till early August is evident, with only one exception in mid June (night 169). After a small drop, prey diversity increased again attaining its maximum value (H' = 3.071) in mid September (night 255). The values of prey evenness, not represented in the graph, roughly followed that of diversity having been the lowest at the beginning (J' = 0.257) and the highest in the last two
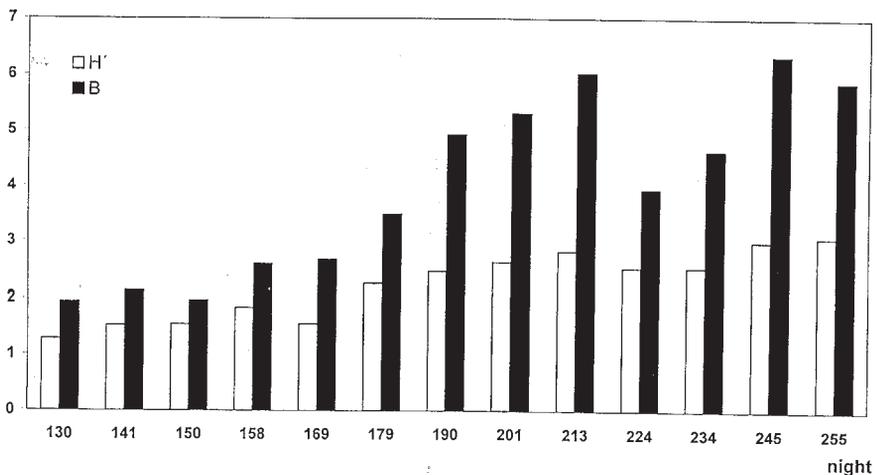
Fig. 2. Seasonal changes in prey diversity and prey niche breadth of *E. serotinus*. Explanations: H' = Shannon-Wiener measure of diversity; B = Levin's measure of niche breadth (K r e b s 1989); night = serial number of a night starting from 1st January.

samples from September (J' = 0.6). Similarly prey niche breadth was at its narrowest value at the beginning (B = 1.943), increased steeply from mid June to early August (nights 169 to 213), and attained its maximum breadth at the beginning of September (B = 6.338). The breeding colony of *E. nilssonii* occupied its shelter from 16 June to 15 August only (cf. Table 2), thus seasonal changes in its prey could only be assessed within this short time span (Fig. 3). All three values were at their minima in the first June sample (H' = 1.213, J' = 0.229, B = 1.834). Prey diversity and evenness attained their maximum values in late June (H' = 2.68, J' = 0.543), the same value of evenness was found in early July (night 190) together with the maximum niche breadth (B = 5.013). Following fluctuation of the three values does not show any trend.

Seasonal changes in the representation of four major insect groups preyed on by *E. serotinus* is shown in Fig. 4. The prevalence of Nematocera, represented mainly by Chironomidae, was significant at the beginning of the season from May to mid June (p < 0.001). At the same time, percentage frequency and percentage volume of Lepidoptera

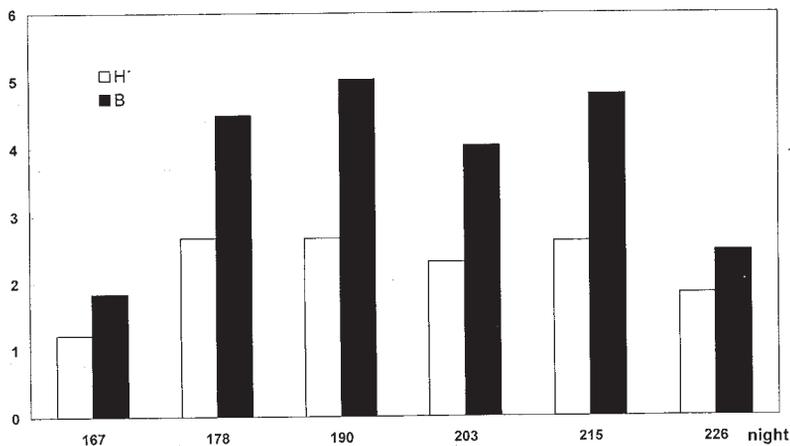**Fig. 3.** Seasonal changes in prey diversity and prey niche breadth of *E. nilssonii*. Explanations as in Fig. 2.
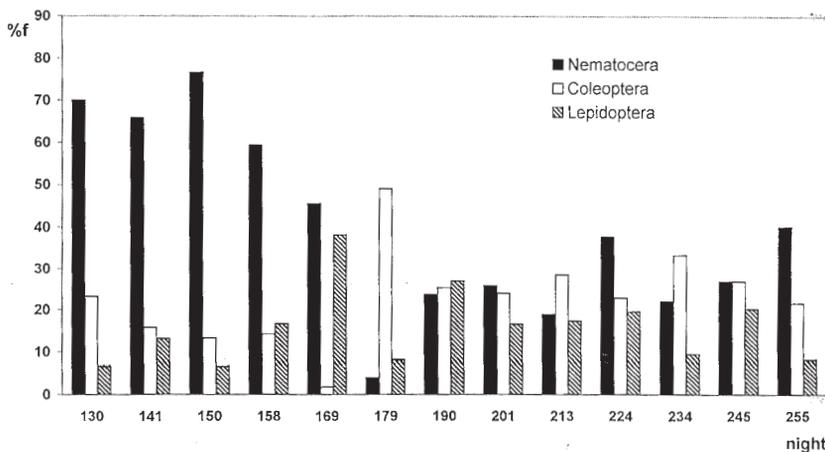

Fig. 4. Seasonal changes in frequency of the most important prey items of *E. serotinus*. Explanations: %f = percentage frequency; night = serial number of a night starting from 1st January.

increased and on 18 June (night 169) these values did not differ significantly from that of Nematocera. The next sample of 28 June (night 179) was characterized by high prevalence of Coleoptera, mainly Carabidae (p < 0.001). The representation of four major prey items in July, August and September was more or less balanced except the dominance of Coleoptera in the first August sample (p < 0.01) and the dominance of Nematocera in the samples of 12 August and 12 September (p < 0.001). Coleoptera and Heteroptera (Corixidae, Lygaeidae) prevailed at the end of August (p < 0.01). The decrease in representation of Lepidoptera from July to September is obvious but statistically insignificant. In *E. nilssonii*, the fluctuation in percentage frequency of major prey groups, as recorded within much shorter time than in *E. serotinus*, was rather irregular (Fig. 5). Lepidoptera were most abundant in the first and Nematocera (Chironomidae) in the last sample (p < 0.001), the two insect groups dominated all three samples from late July and first half of August (nights 203-226). Heteroptera (Miridae) were most frequent in late June (p < 0.001) and were well represented in all samples since that time, while Coleoptera were the least consumed prey throughout the season.
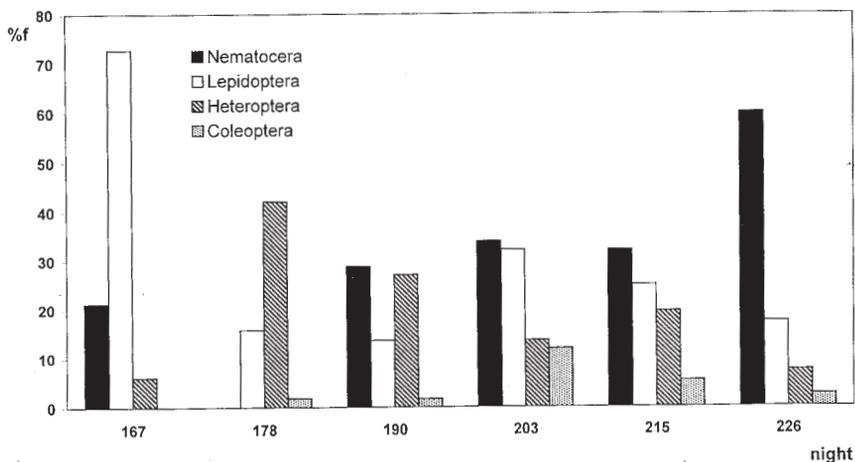

Fig. 5. Seasonal changes in frequency of the most important prey items of *E. nilssonii*. Explanations as in Fig. 4.

Discussion

Diet of *Eptesicus serotinus*

In total, 13 insect orders have been found in the diet of this bat when the data of various authors and from various countries are combined. Usually, however, insects of six to seven orders can be identified from faecal pellets collected in summer roosts or from netted individuals within a particular territory. In England and Switzerland, Coleoptera, Lepidoptera, Diptera, Trichoptera, Hemiptera and Hymenoptera were the most frequently encountered groups while Neuroptera and Ephemeroptera appeared only occasionally (Robinson & Stebbings 1993, Catto et al. 1994, Beck 1995, Gerber et al. 1996). Scarabaeidae and Carabidae mostly dominated the sample of Coleoptera, Chironomidae and Tipulidae were frequent among Diptera. *Aphodius* spp. (Scarabaeidae) was very common in the diet of *E. serotinus* in southern England and its frequency of occurrence increased from July to September. In May and June, in contrast, *Amphimallon* and

Melolontha spp. were frequently eaten. These differences reflect seasonal changes in the occurrence of prey species. In addition to insect orders mentioned above, Orthoptera (Ensifera), Ephemeroptera, Dermaptera, Blattodea and Dictyoptera were identified in the diet of *E. serotinus* in Ukraine (S o l o g o r & P e t r u s e n k o 1973, S o l o g o r 1980). Our results confirm that Coleoptera are important in the species diet. However, Coleoptera were less represented in our material than in most other samples including those from animals netted at a locality only 48 km distant within the same territory of southern Moravia (A n d r e a s et al. 1998, A n d r e a s 2002). Unusually high representation of Chironomidae in our sample probably reflects the existence of large water reservoirs and a fishpond in the proximity of the locality. As shown by G e r b e r et al. (1996) who analysed faeces from 11 colonies of *E. serotinus* in Switzerland, the diet of the species is different in geographically distinct regions and there is no universal specialisation in any particular group of prey. Our data are in accordance with other authors' observations that significant difference exists in insect prey consumed during each month. Contrary to C a t t o et al. (1994) who found the greatest prey diversity in June, we observed increasing values of prey diversity from spring to summer with maxima in August and September. Our data support the assumption that *E. serotinus* is basically an aerial hunter preferring open uncluttered habitats. Occasional gleaning of food from the ground or other surface, however, cannot be excluded (cf. S c h o b e r & G r i m m b e r g e r 1998).

Diet of *E p t e s i c u s   n i l s s o n i i*

Most data on this species' diet are from southern Sweden where Diptera, Lepidoptera, Trichoptera, Ephemeroptera, Neuroptera and Coleoptera were identified from faecal pellets (R y d e l l 1986, 1989). In Switzerland, Diptera, Lepidoptera, Neuroptera and Hemiptera were the most frequently encountered groups of prey (B e c k 1995). Nematoceran Diptera, mainly Chironomidae and, to a lesser extent, Tipulidae dominated all samples studied by these authors. In contrast, Lepidoptera and Neuroptera were found to be main prey components in the sample from southern Moravia studied by A n d r e a s (2002). The representation of insect groups is rather diverse in our material with more common Nematocera (Chironomidae, no Tipulidae), Lepidoptera and Heteroptera and less common Psyllomorpha, Aphidomorpha, Brachycera, Coleoptera, Neuroptera, Trichoptera, Hymenoptera and Araneida. Although most of the prey items were certainly captured in aerial hawking, the presence of daily brachyceran Diptera and of Araneida in faecal pellets suggests a small share of foliage gleaning in the foraging strategy of this species. As shown by R y d e l l (1986, 1989, 1993), habitats where foraging occurs are diverse: bats hunt in farmland and forest and over water. Our results are in accordance with this statement and we can also corroborate the observation of foraging *E. nilssonii* along rows of street-lights (R y d e l l 1991, G a j d o š í k 2003).

C o m p a r i s o n

Although the diet of the two species differs significantly in many respects, there are also striking similarities as pointed out by C a t t o et al. (1994). For example, both species hunt for swarming insects above or near to waters (B e c k 1995). Several authors supposed that *E. nilssonii* prefers smaller prey than *E. serotinus* as could be deduced from the generally greater representation of relatively large beetles in the diet of the latter. According to R y d e l l (1986), however, *E. nilssonii* consumes insects of 3–30 mm body length thus taking prey of a
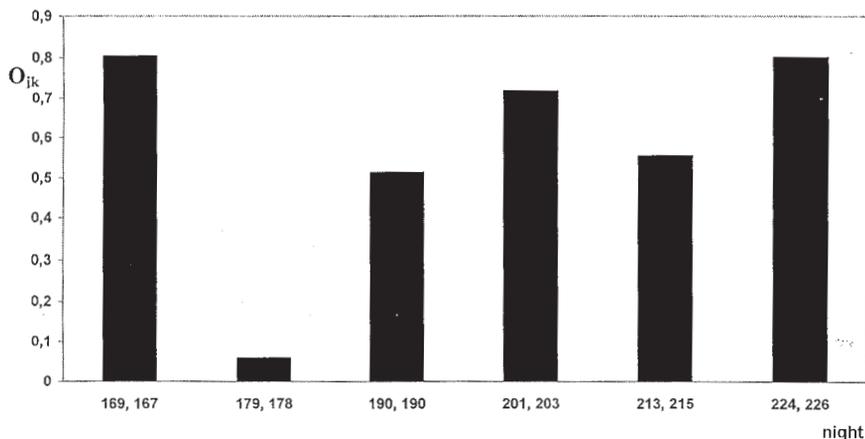
Fig. 6. Seasonal values of potential prey niche overlap between *E. serotinus* and *E. nilssonii*. Explanations: O_{jk} = Pianka's measure of niche overlap (K r e b s 1989); night = serial number of a night starting from 1st January (first number concerns *E. serotinus*, second number concerns *E. nilssonii*).

broad size. Unfortunately, hitherto data are insufficient to test interspecific differences in prey size. In our material, potential overlap of prey niche between the two species (K r e b s 1989) was rather high (O_{jk} = 0.73) but the diet of *E. serotinus* was documented by a larger sample from a longer time span. If the sample of this species is adjusted to the same time as that of *E. nilssonii*, i.e. from 16 June to 15 August, the resulting value of O_{jk} = 0.687. Seasonal fluctuation of O_{jk} was rather high but, except in late June, the overlap was > 50 % (Fig. 6). Interestingly, significant differences between the two species were found by analysing faecal pellets of individuals netted in one and the same locality (A n d r e a s 2002). As pointed out by the author, in *E. nilssonii* composition of the diet implyed foraging in forest habitats while food items of *E. serotinus* implyed foraging in more open country. The differences are greater than between the two colonies studied by us, namely because of little representation of insects swarming above water in Andreas' sample. This may have been due to lesser representation of stagnant waters in proximity of the locality studied by Andreas, in comparison with the two localities dealt with in the present paper. To conclude the diet of the two bat species appears to be similar yet reflecting differences in foraging habitats.

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