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The Journal of Animal Ecology, Vol. 54, No. 1. (Feb., 1985), pp. 217-225.

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FEEDING ECOLOGY OF *PIPISTRELLUS PIPISTRELLUS* (CHIROPTERA: VESPERTILIONIDAE) DURING PREGNANCY AND LACTATION. II. DIET

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SUMMARY

(1) The representation of different groups of insects in the diet of pipistrelle bats, as determined by faecal analysis, was compared with their representation in suction trap samples on the same eighteen nights during pregnancy and lactation.

(2) Pipistrelles fed mainly on Nematocera and Trichoptera and the composition of their diet reflected the availability of these insects over a wide range of abundance. There was no evidence that pipistrelles selected their diet on the basis of insect size.

(3) Ephemeroptera and Neuroptera were significantly over represented in the diet and Nematocera, Coleoptera and Lepidoptera were significantly under represented.

(4) No differences in diet were recorded between sexes nor between pregnant and lactating females.

INTRODUCTION

There are few detailed studies of prey selection by insectivorous bats (Anthony & Kunz 1977; Belwood & Fenton 1976) although insectivorous birds have been investigated in detail (e.g. Bryant 1973; Davies 1977a,b; Krebs *et al.* 1977; Turner 1982). These studies have shown that prey size and encounter rate are important factors influencing the degree to which the predator's diet differs from the available food. Other factors which sometimes affect diet are the sex of the predator (Newton 1967; Selander 1966, 1972), particularly when the sexes differ in size, and its reproductive state (Davies 1977a,b).

This paper examines the effect of these factors on prey selection by free-flying pipistrelle bats during pregnancy and lactation.

MATERIALS AND METHODS

Trapping areas

Insects and bats were trapped on eighteen nights during the summers of 1978 and 1979 in riparian woodland along the south bank of the river Don at Inverurie (57°13'N, 02°09'W) and the north bank of the River Dee at Banchory (57°03'N, 02°25'W).

Insect trapping

A Johnson-Taylor insect suction trap powered by a portable generator was operated from dusk until dawn in areas where bats foraged intensively (Johnson 1950; Taylor 1951; Johnson & Taylor 1955). The trap used a 30 cm intake fan supported about 1.7 m

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above the ground, and its catch was automatically divided into half-hourly samples. A total of 34 798 insects were caught (ranging from 135 to 4625 per night) and stored in 70% ethanol for later examination.

Analysis of trap samples

Insects were identified from trap samples by reference to keys (Mosely 1939; Kimmins 1950; Frazer 1959; South 1961; Colyer & Hammond 1968; Chinery 1973). The proportion of each insect family in the trap samples was determined. A few insects from each family were then crushed with dissecting needles and keys compiled from the fragments to assist in the identification of insects from the small pieces of insect exoskeleton recovered from bat faecal pellets.

Bat trapping

Bats were trapped in nylon mist nets on known flight paths. Each net was examined at 10 min intervals throughout the night. Trapped bats ($n = 112$) were placed separately in clean cloth bags, where they were retained until dawn and then released. Faeces voided by pipistrelles were removed from the cloth bags, dried and stored for later analysis.

Analysis of faecal pellets

All faeces from each bat caught were combined and examined under a binocular microscope. Recognizable fragments of chitin were extracted, and by matching these with fragments in the keys from the trap samples, 24 250 insects consumed by pipistrelles were identified.

Quantitative analyses of fragments were carried out as follows: for each family, one or two clearly recognizable diagnostic features were selected, such as the distinctive, humped thoraces of chironomid midges or the characteristic mouthparts of some families of caddis flies (Trichoptera). Legs and wings were not used, since they are often bitten off and dropped by bats before the insect is chewed (Poulton 1929; Phillips 1966; Coutts Fenton & Glen 1973). From the number of diagnostic features recovered, estimates were made of the least number of individuals of each family consumed by the bat. The number of humped chironomid thoraces recovered, for example, was equal to the minimum number of chironomids consumed. If a particular mouthpart, such as the maxillary palp in the case of Trichoptera, was used as a key feature, the least number of insects was estimated by dividing the number of these mouthparts recovered by two. In the case of moths, where identification was made mainly from scales, the number consumed by a bat was scored at one, unless the scales were definitely shown by comparison with whole specimens to come from more than one moth or unless other features, such as mouthparts, were also recovered.

RESULTS

Size selection

Data from all nights and all bats were combined to test whether pipistrelles selected insects within a particular size range. Abundance in the faeces was plotted against abundance in the trap samples for twenty-three insect groups (Table 1). These twenty-three groups were then assigned to three size classes on the basis of their body lengths (the mid-points of the ranges given in Table 1 were used) and their deviations from the line of no selection were measured. The three size classes do not differ in their average

TABLE 1. The relative abundance of insect families in suction trap samples and in the faeces of *P. pipistrellus* Kuhl captured during the summers of 1978 and 1979*

Order	Family	Body length (mm)	% in trap samples	% in diet	
Diptera (sub-order Nematocera) (Longhorn flies)	Chironomidae (non-biting midges)	4-12	53.8	56.4	
	Ceratopogonidae (biting midges)	1-4	7.8	4.1	
	Psychodidae (owl midges)	2-5	3.6	2.1	
	Cecidomyiidae (gall-midges)	2-5	2.0	2.3	
	Mycetophilidae (fungus-gnats)	2-10	0.7	0.7	
	Tipulidae (crane-flies)	5-35	0.9	2.2	
	Scatopsidae	2-8	0.3	0.3	
	Culicidae (mosquitoes)	3-7	0.1	0.2	
	Other families	—	<0.1	<0.1	
	Other Diptera	Empididae	4-14	0.3	0.3
		Other families	—	0.2	0.1
Trichoptera (Caddis flies)	Glossosomatidae	3-8	23.5	23.4	
	Hydroptilidae	1-4	0.9	0.9	
	Molannidae	5-6	0.9	0.7	
	Sericostomatidae	5-9	0.4	0.6	
	Hydropsychidae	5-10	0.3	0.3	
	Limnephilidae	9-12	0.2	0.2	
	Other families	—	<0.1	<0.1	
Lepidoptera (Moths)	Noctuidae	6-28	0.7		
	Geometridae	6-16	0.5		
	Pyralidae	5-15	0.3	0.8	
	Other families	—	0.3		
Coleoptera (Beetles)	Scarabaeidae	7-25	0.8	0.1	
	Other families	—	<0.1	<0.1	
Ephemeroptera (Mayflies)	Baetidae	4-7	0.4	0.7	
	Caenidae	3-7	0.4	0.9	
	Ephemeridae	4-8	0.3	1.2	
	Ecdyonuridae	6-12	0.2	0.6	
Neuroptera (Lacewings)	Hemerobiidae (brown lacewings)	6-7	<0.1	0.6	
	Sialidae (Alder flies)	10-12	<0.1	0.1	

* Groups of insects whose incidence in both trap samples and diet was less than 0.1% have been omitted.

deviations from this line (Kruskal-Wallis one-way analysis of variance, $P > 0.1$) so it appears that pipistrelles do not select their prey on the basis of size over the range of sizes represented in this study. In all further analyses, insects were grouped into the following taxonomic categories: Nematocera; other Diptera; Trichoptera; Lepidoptera; Coleoptera; Ephemeroptera; Neuroptera.

Sex differences

The diets of male and female bats were compared with sign tests (Siegel 1956) within insect categories using each night as a separate comparison. None of these seven tests approached significance (all $P > 0.1$), indicating that there are no large differences in diet between sexes. In all subsequent analyses data from both sexes are combined.

Variation in insect abundance within nights

The proportion of insects from each of the seven insect categories was ranked for both trap samples and faecal material for each night. For all eighteen nights the ranks were positively correlated (Spearman rank correlation coefficients; ranging from $r_s = 0.54$ to $r_s = 1.00$) and fifteen of these are significant at at least the 5% level (Table 2). These results indicate that the composition of the bats' diet reflects the availability of insects.

TABLE 2. Spearman rank correlation coefficients (r_s) for the relationship between percentage representation of seven insect categories in pipistrelle faeces and suction trap samples for eighteen nights

Day	r_s	P (two-tailed)
1	0.938	**
2	0.910	**
3	0.964	**
4	0.848	*
5	0.973	**
6	0.964	**
7	0.962	**
8	0.786	*
9	0.536	N.S.
10	0.973	**
11	0.902	**
12	0.884	**
13	1.000	**
14	0.848	*
15	0.714	N.S.
16	0.777	*
17	0.884	**
18	0.705	N.S.

* = $P < 0.05$; ** = $P < 0.01$; N.S. = $P > 0.05$.

Variation in insect abundance across nights

The percentage representation in the diet was plotted for each insect category, against its percentage representation in the traps (Fig. 1). The presence of points consistently below or above the line or no selection indicated whether any prey category was consistently under- or over-represented in the diet, respectively. The significance of deviation from the line of no selection was assessed using sign-tests (Siegel 1956). Possible variations in diet with female reproductive state were examined by comparing the deviations from the line of no selection (Fig. 1) during early pregnancy, late pregnancy, lactation and weaning. Such differences were not expected after it was established that there were no significant differences in diet between sexes, since it seems unlikely that male foraging would be affected by female reproductive state. Different bat reproductive states were not associated with differing degrees of representation in the diet for any insect category (Kruskal-Wallis one-way analysis of variance, all $P > 0.1$).

Trichoptera and Diptera other than Nematocera were present in the faeces in proportions not significantly different from their proportions in the trap samples (Table 3). This was particularly striking for Trichoptera whose representation in the trap samples varied between 2.7 and 56.5% over the eighteen nights of trapping. Coleoptera, Nematocera and Lepidoptera were significantly under-represented in the diet whereas Neuroptera and Ephemeroptera were significantly over-represented. Although for five out of seven of the insect groups, there is a significant difference between the representation of the insects in the faeces and in the trap samples (Table 3), the effects of these differences are small. Thus on fourteen nights out of eighteen, the percentage of Nematocera in the faeces was lower than that in the trap samples and the average difference between the two values (1.74%) was insignificantly small compared with the average representation in the trap samples (69.35%). Coleoptera were less common in the faeces than in the trap samples on fifteen out of eighteen nights. On average, the percentage representation in the faeces

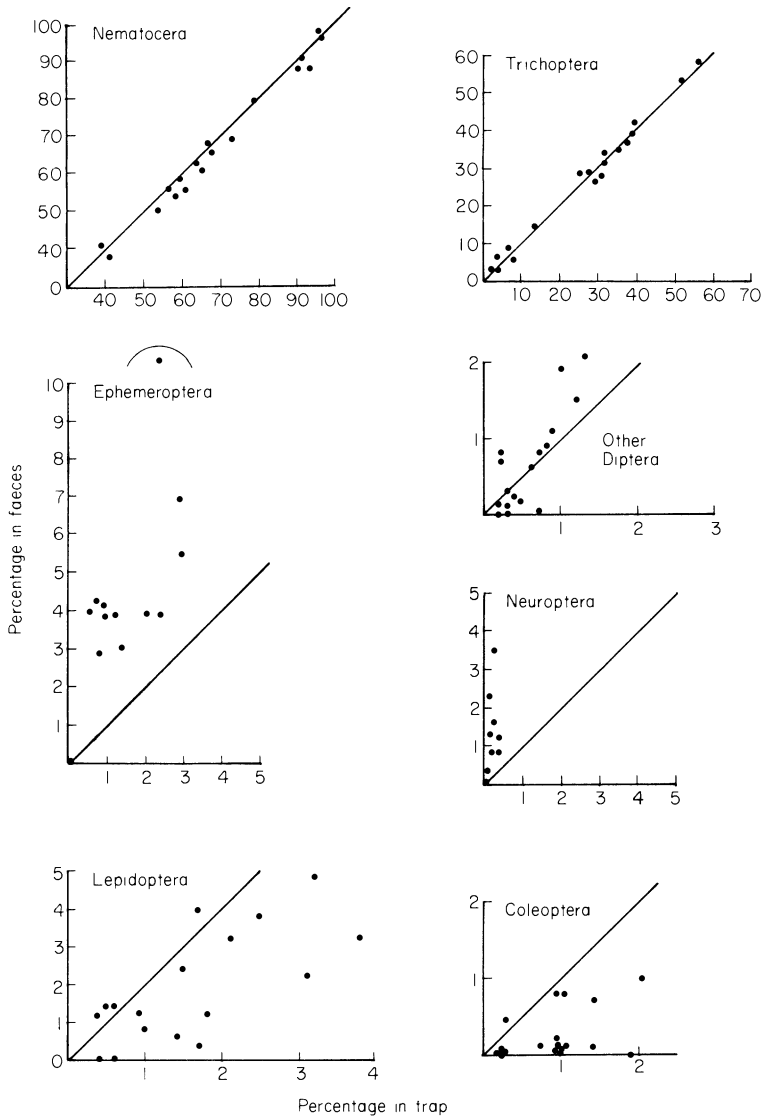


FIG. 1. The percentage representation of each of seven groups of insects in the faeces and in insect suction traps on individual nights during summer.

is 0.6% lower than in the trap samples. Although 0.6% is a large proportion of the average percentage representation of Coleoptera in the trap samples (0.8%), members of this order of insects were so rarely available that this made little difference to the overall diet. The same applies to Lepidoptera.

Variation in overall insect abundance

Whether variations in overall abundance of insects explained significant amounts of variation in representation in the diet for each insect category was examined by calculating correlation coefficients for the relationship between insect abundance and deviation from the line of no selection (Fig. 1). The total number of insects captured per night was

TABLE 3. The mean representation of seven insect groups in insect suction traps (% trapped insects \pm S.D.) and the mean deviation of their representation in pipistrelle faeces from their representation in the traps (\pm S.D.). Probability (*P*) refers to sign tests applied to establish whether each insect group was consistently commoner or rarer in the trap samples than in the faecal samples

	% trapped	% in faeces - % trapped	<i>P</i>
Nematocera	69.35 \pm 4.2	-1.74 \pm 0.51	*
Other Diptera	0.54 \pm 0.09	+0.058 \pm 0.092	N.S.
Trichoptera	26.30 \pm 3.9	+0.22 \pm 0.30	N.S.
Lepidoptera	1.51 \pm 0.26	-0.48 \pm 0.21	**
Coleoptera	0.83 \pm 0.14	-0.60 \pm 0.11	**
Ephemeroptera	1.27 \pm 0.27	+2.28 \pm 0.46	**
Neuroptera	0.078 \pm 0.026	+0.51 \pm 0.19	**
	n = 18	n = 18	

* *P* < 0.05; ** *P* < 0.01.

TABLE 4. Spearman rank correlation coefficients between deviation from expected representation in the diet (i.e. deviation from the line of no selection, Fig. 1) and total numbers of insects caught, total numbers of insects of the same order which were caught, and percentage of total insects caught belonging to that order, for seven insect orders

	Total insects, numbers	Own order, numbers	Own order, % of total
Nematocera	0.04	0.01	0.146
Other Diptera	-0.16	0.32	0.30
Trichoptera	0.07	0.001	-0.135
Lepidoptera	-0.16	0.23	-0.57*
Coleoptera	-0.46	-0.64**	-0.74**
Ephemeroptera	0.16	0.65**	0.623**
Neuroptera	0.1	0.66**	0.89**

* *P* < 0.05; ** *P* < 0.01.

used as a measure of abundance. No corrections were made for variations in the duration of night, since most insect and bat activity occurs at dusk and dawn (Lewis & Taylor 1965; Swift 1980), separated by a variable period of low activity. Thus total insect captures per night provides a better indication of insect abundance experienced by the bats than total insects captured per hours of trapping.

There were no significant relationships between total insect abundance and deviation from the line of no selection (Table 4). However, for three insect groups there were significant relationships between their own abundance and their deviation from the line of no selection. As the abundance or percentage abundance of Coleoptera, Ephemeroptera or Neuroptera changed, so did the amount by which they deviated from the line of no selection. For example, as Coleoptera became more common, the amount by which their representation in the faeces falls short of their representation in the trap sample increased.

DISCUSSION

The most striking aspect of the present study is that male and female pipistrelles, throughout the summer, feed unselectively on the available flying insects. Although for five out of seven insect groups there were significant differences between the percentage representation in the faeces and the percentage representation in the trap samples, at the insect abundances and proportions recorded in this study, the deviations from a wholly

unselective diet were very small (Table 3). However, because, for four insect orders, the deviation from a wholly unselective diet increased significantly with the percentage representation of those orders (Table 4), it is possible that under some conditions pipistrelles feed selectively. For example, Neuroptera were generally uncommon in our insect samples. Their highest representation in the trap samples was 0.3%, yet when present (ten out of eighteen nights) they were selected by the bats so that their representation in the faeces was as high as 3.2%. This degree of selectivity was insufficient to make a large difference to the overall pattern of unselective feeding since Neuroptera usually formed a small proportion of the pipistrelle diet. On average, the representation of Neuroptera in the faeces was seven and a half times that in the trap samples. This suggests, by extrapolation, that if Neuroptera formed 14% of the available insects then pipistrelles might feed exclusively on them.

Nevertheless, under the conditions of the present study pipistrelles fed unselectively and large changes in the percentage representations of the two commonest insect orders in the suction traps (Nematocera and Trichoptera, Fig. 1) are mirrored in the bats' diet. These results are difficult to explain in terms of current optimal foraging theory. We do not know the profitabilities of the different prey types since it is not possible to measure handling times in the field. However, the very close fit between the representation of insect groups in the trap samples and in the faeces is an unexpected result since overall abundance of insects varied by a factor of 34 \times . This contrasts with studies of insectivorous birds cited earlier. Why might unselective feeding be an optimal feeding strategy for small insectivorous bats? We think two factors might be important. It is possible that selection of prey by echolocation (Griffin 1958; Griffin, Webster & Michael 1960) may not allow the rapid discrimination between prey items necessary for selective feeding. At high insect densities, when selective feeding would be most likely to occur (Charnov 1976; Pulliam 1974), pipistrelles can average ten feeding attempts per minute (Racey & Swift 1985) and sometimes achieve attempt rates of up to 20 min⁻¹ (M. I. Avery personal observation). Under these circumstances even very short discrimination times could favour unselective feeding. Houston, Krebs & Ericksen (1980) found that when discrimination time was experimentally increased, great tits would remain unselective feeders at presentation rates when they would normally be selective. The details of the speed of prey discrimination in insectivorous bats is not known.

Unselective feeding would also be favoured if handling times for all prey were very short or if handling and searching for prey could occur simultaneously. Both of these situations may apply to small insectivorous bats such as pipistrelles. Rates of echolocation pulses recorded during searching are resumed immediately after the short increase in repetition rate associated with insect captures so that handling of previous prey may continue during the next search phase. Two observations support this. First, pipistrelles entering roosts after foraging often have many smaller fragments of insects in their mouths (personal observation), and Ross (1967) showed that little brown bats *M. lucifugus* have fragments of several different insects in their mouths at one time, even though insects are captured singly (Griffin, Webster & Michael 1960). If handling and searching are compatible, and more than one prey item can be handled at a time, then handling time can be considered as zero, in which case unselective feeding is the optimal feeding strategy.

It is difficult to exclude the possibility that either the insect trapping, or the faecal analysis (or both), has been a source of bias in our results. However, Kunz & Whitaker (1983) have established that faecal analysis is a reliable technique for examining the diet

of small insectivorous bats. If the techniques are biased, the fast-flying hard-bodied insects (such as Coleoptera), which may escape the suction trap but whose exoskeleton would survive passage through the bats' alimentary canal, would be over-represented in the faeces and under-represented in the trap samples (Rabinowitz & Tuttle 1982). Yet Coleoptera were commoner in the trap samples than in the faeces. Similarly, weak-flying, soft-bodied Neuroptera and Ephemeroptera would be relatively under-represented in the faeces, yet the opposite was the case. There is no indication, therefore, of obvious systematic bias in our techniques.

Previous studies of insectivorous bats suggest that large species (*Eptesicus fuscus*, *Clootis percivali*, *Lasiurus cinereus*, Black 1972, 1979) feed selectively, whereas smaller species such *Myotis lucifugus* (Anthony & Kunz 1977) are unselective. This difference is probably adaptive in that larger species generally fly faster (Hayward & Davis, 1964; Patterson & Hardin 1969) and therefore have higher encounter rates with all prey items and would therefore be expected to feed selectively (Charnov 1976; Pulliam 1974).

ACKNOWLEDGMENTS

This study was supported by a NERC grant to P. A. Racey. M. I. Avery was supported by a NERC research studentship. We thank J. R. Krebs for useful discussions about handling times.

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(Received 20 February 1984)