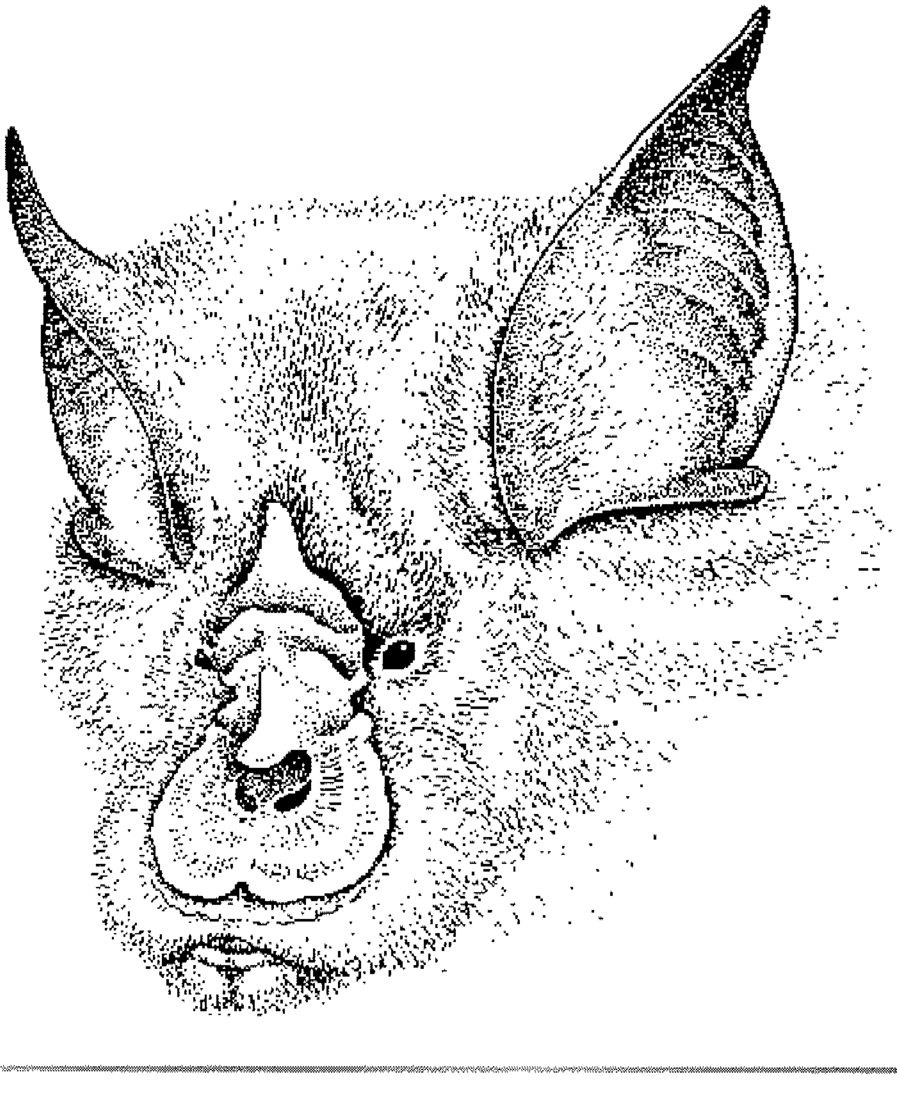
ENGLISH
NATURE

The management of feeding areas for greater horseshoe bats

No. 174 - English Nature Research Reports



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English Nature Research Reports

Number 174

The management of feeding areas for greater horseshoe bats

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ISSN 0967-876X

issue 2

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SUMMARY

The objectives of this study were to: determine the dietary requirements of greater horseshoe bats over a wide geographical range and identify key prey species on a seasonal basis: identify habitat features promoting high densities of key prey species in areas within known foraging range throughout the summer: identify important habitat features influencing movements between roosts and foraging areas: propose land management prescriptions which will integrate with current forestry and farming systems to maintain or enhance foraging areas for greater horseshoe bats.

Dietary analysis showed that both mothers and juvenile bats generally fed on a single prey item (species group) at a single foraging bout. Overall, moths and scarabaeid beetles (notably *Aphodius spp.*) dominate the diet, at about 40% each, with tipulids, small dipterans and ichneumonids composing the remainder. The key prey items change through the summer, beginning with *Geotrupes* in April, *Melolontha* in May or June and then moths in June onwards. In August, there is a clear division in diet between mothers and young, with the key prey item for mothers being moths and that for the young being *Aphodius rufipes*. This pattern was consistent across the geographic range of the bats, though periods of inclement weather may force the bats to use less favoured items.

A consideration of the ecology of these key prey species indicated the importance of restricting development or intensive farming close to the maternity roosts, maintaining semi-natural woodland for moths, maintaining grazed permanent pasture for *Aphodius, Melolontha* and *Geotrupes* and limiting the use of avermectins to treat domestic stock. As well as maintaining rich foraging areas for the bats, the maintenance of appropriate habitat features is also critical. Dark areas around roosts, shaded flight paths to feeding areas, large hedgerows with standard trees and woodland features that provide sheltered feeding places with perches for fly-catching all enable the bats to exploit their feeding areas to best advantage.

Management prescriptions are given for two concentric areas around maternity roosts. The area within 1 km of the roost is critical as this is where the juvenile bats learn to forage. Here, particular attention must be given to the maintenance of permanent grazed pasture, with a high density of grazing animals, and hence dung, during July and August when the young bats emerge to feed on *Aphodius* beetles. Outside this area, but within 3 - 4 km of the roost, grazing regimes can be more flexible, provided adequate permanent pasture is available, and longer swards will benefit the larvae of noctuid moths. Overall, efforts should be made to maintain all mature semi-natural woodland, orchards and park lands and, where possible, convert existing coniferous plantations to deciduous woodland with grassy rides and glades. A balance of about 50% woodland and 50% pasture would provide optimum resources for the bats. Pasture should not be ploughed or treated with insecticides and grazing animals should not be treated with avermectins, unless unavoidable. The retention and development of large hedgerows and the creation of smaller fields surrounded by hedgerows or tree lines should be encouraged.

INTRODUCTION

The greater horseshoe bat is one of Britain's largest and rarest bats, with a total population of about 4000 individuals. The species is found only in south-west England and west Wales and only 12 populations are known.

During the summer, female bats form maternity colonies where all the reproductively active female bats from the entire population gather to rear their young. The bats are strongly attached to these traditional maternity sites, which are often located in the roof voids of large abandoned buildings, and will return to the site annually. In winter, the bats hibernate in caves, mines and other cave-like places.

Until now, conservation of this species has focused on the protection of the maternity sites and hibernation sites, but it is recognised that this alone will not ensure the survival of the species. Attention must now turn to ensuring that sufficient food resources are available to maintain the population.

The feeding areas around the maternity roosts must be considered highest priority, as these contain the highest concentration of adult bats with the highest nutritional requirements during pregnancy and lactation. These areas are also vital for juvenile bats when they are learning to hunt. Recent research has shown that most foraging activity by adult females is concentrated within 3 km of the roost and that ancient woodland and permanent pasture with cattle grazing are the most important habitat types. Juvenile bats initially hunt mainly within 1 km of the maternity roost and are highly dependent on cattle-grazed pasture. Habitat features such as hedgerows and tree lines are also important as commuting routes for the bats.

Protection of feeding areas through the SSSI mechanism is not necessarily the best solution in view of the areas involved (3 km radius = 28 km^2) and the mobility of the bats. An incentive scheme to encourage land managers to maintain high quality feeding areas and appropriate habitat features may be preferable. In either case, it is a prerequisite to determine what sort of habitats and habitat features provide optimum feeding conditions for the bats and how these should be managed to provide the right prey items at the right time of year.

The study had four objectives, all of which were addressed. As time was relatively short, but required extensive laboratory analyses of bat faeces as well as reviews of the literature, some of the objectives were only partially realised. The objectives relate directly to the parts of the report. They are given in full below.

Objective 1
Determine the dietary requirements of greater horseshoe bats over a wide geographical range and identify key prey species on a seasonal basis.

Objective 2
Identify habitat features promoting high densities of key prey species in areas within known foraging range throughout the summer.

Objective 3
Identify important habitat features influencing movements between roosts and foraging areas.

Objective 4
Propose land management prescriptions which will integrate with current forestry and farming systems to maintain or enhance foraging areas for greater horseshoe bats.

PART 1: DIETARY REQUIREMENTS OF THE GREATER HORSESHOE BAT

Introduction

Diets of insectivorous bats are normally determined by faecal analysis, or from culled remains left at feeding posts (Jones 1990), since direct observation of prey capture at night is not feasible, nor is stomach analysis (Whitaker 1988). Faecal pellets contain mostly exoskeletal protein and chitin, both very resistant substances. Skeletal fragments in faeces permit recognition of prey to at least order level, and often to families, species groups and even single species in some cases. Bats eat large amounts of insect food very quickly, digest it rapidly, and egest the bulk of the remains in a few hours. Greater horseshoe bats egest 70% of a full stomach within 8 hours of feeding (Ransome, 1978), most of it within roosts from where samples may be collected. This is particularly true of remains from dawn feeds, since this species is known to night-roost after dusk feeds (Jones *et al.*, 1995).

Collections of faecal pellets from beneath clusters of bats over time poses some inherent problems of interpretation. The individual bats present in the cluster may change, and even if they remain the same, their reproductive state is constantly changing and the level of their contribution to the sample collected alters. Ransome (submitted) has shown that the amounts of food consumed before dawn, as judged by dry mass of droppings produced, varies markedly with reproductive state during the summer. Also, young bats do not feed at first, but show a rapid rise in amounts consumed between 29 and 55 days of age (Jones *et. al.* 1995). Hence samples collected from known individuals at specific times are of great value in interpreting dietary changes. Such samples, however, are bound to be relatively infrequently collected for logistic and conservation reasons, and so cannot replace the colony group collection. A combination of both methods is preferable.

Methods

Geographical area covered

Faecal pellets were collected from five separate maternity sites. Two sites were in south-west Wales and three were in south-west England. The Welsh sites were Stackpole, in a coastal position, and Slebech, located inland in a farming area. The English sites were Dean Hall, in the Forest of Dean, Brockley Court, in rural coastal Avon, and Woodchester Mansion, in a steep-sided wooded valley with lakes.

Periods of faeces collection beneath maternity clusters

Volunteers collected faeces from the different maternity sites using clean polythene sheets in 1995, a year of abundant sunshine, high temperatures and a developing drought during late July and August. The collection frequency varied from daily to weekly, and lacked synchronisation. However, between 4th July and 4th August 1995, complete collections were obtained from all five sites. Collections from Dean Hall and Woodchester Mansion were made from April to October in 1995, mostly at weekly intervals or less. In addition data from Jones (1990) was used for summer 1988, a year of good summer weather without a drought, at a church at Clapton and at Brockley Court. His data was collected weekly from April to October. Also data from Woodchester 1986 was selected for analysis since it was the very cold and wet summer after which the population crashed (Ransome 1989). Populations also crashed in Wales (Ransome and McOwat 1994). Thus the likely extremes of dietary range due to climatic factors influencing insect phenology and availability within the study area should have been covered by the samples used.

Periods of faeces collected from individual bats

The Woodchester Mansion maternity site has been intensively studied for over three decades (Ransome 1971, 1973, 1978, 1989, 1990, 1995). The whole cluster, including mothers with young capable of independent feeding, was caught on one or two occasions in each year since 1990, soon after their dawn feed in August and/or early September. Bats were bagged individually in numbered clean cloth bags immediately after capture, and kept in them until synchronised release about three hours later. Faecal pellets removed from the bags were air-dried and stored separately until analysis.

Faecal analysis

The methods used to analyse faecal pellets from beneath colonies to obtain estimates of percentage volume of each prey in the diet, were essentially those used by Jones (1990). However, 16 pellets per time interval, instead of 20 were randomly selected for analysis. This number exceeds the lower limit of 15 recommended by Whitaker (1988) for collections beneath colonies of bats. This was necessary as Woodchester collection frequencies were very high, averaging every three days in 1995, and so this year alone required the analysis of over 800 pellets. In total some 1600 faecal pellet analyses were carried out.

Initially 16 faecal pellets were analysed per captured bat for individual diet studies, provided that number was exceeded in its collection. However, since the majority of bats fed on single prey items, and when they did so every pellet showed the same content, this was reduced to 10 and finally to 4 to save time and effort. When bats fed on more than one prey item, this number was too low, as the volume ratios of the prey often varied widely among the 4 slides. However, little use has been made of mixed-prey data obtained to date.

Preparation of permanent dry slides

Every faecal pellet analysed was treated by my own method in order to rapidly obtain dry permanent slides for storage and future reference purposes.

The method was as follows:

1) Soak pellets individually for 3 hours in 2% potassium hydroxide (w/v) in numbered depressions (1 cm^3 volume) on spotting tiles. (Removes soft organic wastes, but not the skeletal parts).

2) Remove potassium hydroxide and wash three times in water using fine hypodermic needles and a syringe.
3) Place each pellet on a slide and spread the clean skeletal fragments evenly in a square or rectangular shape to facilitate volume estimation against a grid (Whitaker, 1988). Check under a binocular microscope to ensure all parts are visible.
4) Label and dry slides in an oven at 60 °C for 6 hours minimum.
5) Spray lightly with hair lacquer to ensure adhesion to slide.
6) Store flat in trays so that the surfaces are not touched.

Besides the relative rapidity of this method compared with others recommended (e.g. McAney, *et al.* 1991), it has the advantage of showing up textural differences in sketetal structures. With a reference collection of parts from known insect prey, and faecal pellets collected from captured bats fed single known insect prey (under licence from EN) treated in the same way, identification of prey in collected samples was facilitated. A stage and eyepiece micrometer was used to measure fragments accurately. Using dimensions and specific characteristics (e.g. hairs, punctures, colouration) of certain parts such as tarsi, palps, antennal segments and abdominal segments, it was often possible to identify prey to families, genus, and even to species of beetle with certainty (e.g. *Geotrupes, Aphodius rufipes, Melolontha melolontha*). Large Diptera were all from the Nematoceran family Tipulidae. They were divided into two sub-groups on the basis of body colour. Small Diptera were usually rarely encountered and so were not identified further. All Hymenoptera were recognisable as Ichneumonids from their characteristic antennae, wing venation and leg fragments. In comparison with collected specimens, they proved to belong to the *Ophion luteum* complex of ichneumonids. They readily show up in faeces due to their bright, evenly translucent orange leg and abdominal skeleton fragments.
Moths were not identified beyond order level, as no simple way of segregating families from the limited parts consumed (abdomen, thorax and rarely parts of legs and antennae) has yet been developed. Time did not permit the labour necessary to attempt this. However, all slides have been retained should this be deemed important and feasible. There are distinctive colour and textural differences between moths from different monthly samples which suggest that some progress may be possible in future.

Results

Dietary content over the geographical area sampled

Figure 1 shows the diet by site during July 1995 when lactating females were present at all sites, and only a few young would have started feeding. Most prey were identified, and in all cases moths formed the bulk of the diet at all sites. All site samples also showed *Aphodius rufipes* (Aph1), another *Aphodius* sp possibly *rufescens* (Aph2), and brown tipulids (Tip1). Traces of small dipterans (S Dip) and ichneumonids belonging to the *Ophion luteum* complex (Ichn) were present in some samples. The similarities between the diets are much more striking than the minor differences, which may reflect local habitat differences.

Figure 2 shows the diets for Woodchester (a) and Dean Hall (b) during 1995 between April and September. Unfortunately collections at Dean Hall started in late April, so the *Geotrupes* beetle contribution peak was missed. Otherwise the summary diets for these two adjacent breeding sites are remarkably similar.

Figure 3 shows the diets for Woodchester (a) in 1986, the cold, wet summer, and Clapton/Brockley in 1988, a warm moist summer. Allowing for the fact that Jones (1990) did not distinguish between brown (Tip1) and black tipulid (Tip2) groups, the similarities are more striking than the differences. When both are compared with Fig. 2(a), it seems that differences between summer climate, rather than site location, has the greater effect. The cold wet summer of 1986 produced lower moth volumes and higher *Aphodius rufipes* volumes than 1988 or 1995. Cockchafer volumes also varied, showing the lowest levels in 1988. This is to be expected in view of the cyclical nature of populations of this species, and may not be a special feature of the diets of bats at the Clapton/Brockley site.

Diet by month throughout the summer

Figures 4 to 9 show the monthly diet summaries from April to September for 3 sites over 3 summers. Woodchester data appears twice, making four samples in all. Unfortunately April data was missing for Woodchester 1986, as the cold spring prevented serious feeding, and bats did not return to the breeding site until May. Dean Hall data was incomplete as previously mentioned.

April diets (Fig. 4) for the two sites show *Geotrupes* is the major prey genus at about 40% by volume, together with significant levels of ichneumonids and tipulids. Woodchester, perhaps because of its proximity to several lakes, showed good levels of caddis flies, which did not feature at Clapton/Brockley in 1988.

May diets (Fig. 5) for three of the four samples show varying levels of cockchafers (*Melolontha*), with from 24-65% by volume. In 1986 *Geotrupes* and cockchafer activity seems to have been delayed, possibly by low temperatures, by about a month. Hence the former was consumed in May, and the latter in June (Fig. 6). Levels of moths and tipulids also vary considerably, possibly due to the same effect, but they can be important prey in some years.

June diets (Fig. 6), apart from 1986 data, show much more consistent dietary similarities as the brief cockchafer period ends. Moths dominate at nearly 80% by volume in the warm summers sampled, with only small amounts of tipulids, *Aphodius rufipes* and ichneumonids.

July diets (Fig. 7) continue to be dominated by moths, but at a slightly lower level (60-70%), even in the cold wet summer of 1986. However, *Aphodius rufipes* volumes start to rise, and in the dry summer of 1995, a second, smaller species was seen for the first time (*A. rufescens*?) as noted in Fig. 1.

August diets (Fig. 8) show that two prey items are important at about 30 to 50% by volume, but only in 1986 did one seriously dominate the other. They are moths and *Aphodius rufipes*.

The proportions of each usually changes as the month progresses, with moths steadily declining and *Aphodius* rising. In 1995 the drought delayed the peak activity of *Aphodius rufipes* until early September, but the wet weather of 1986 probably favoured their populations (see discussion on dung beetles later).

September diets (Fig. 9) show a further decline in the importance of moths and the continued high level (40-70% by volume) of *Aphodius rufipes*, especially in 1995. However other prey types, such as tipulids, ichneumonids and *Geotrupes*, begin to become more important again, as they were in the spring. (In mid October 1995 ichneumonids became the dominant prey consumed - Ransome, unpublished data).

Diets of individual mothers and their young on various dates

Analyses of droppings from individuals were carried out on only five separate dates. These were selected because the mean age of the young needed to be sufficient for substantial independent feeding (about 45 days of age), and before too many of the mothers had left the maternity roost. Mothers usually leave at about 55 days post birth if their young survive, but may leave earlier if their young dies (*pers. obs.*). Hence the date of capture was decided by birth-timing considerations, plus the need to catch the cluster on a Sunday morning, when voluntary helpers were available. Hence the weather preceding a capture was essentially randomly selected.

Three captures were in August and two in early September. The August captures followed a warm moist night (12-8-90); a cold night falling to 5.7 °C (14-8-94) when the young failed to feed at dawn, and a warm dry night after a long drought (20-8-95). The September captures followed a warm moist night (1-1-91) and a cold night falling to 4.5 °C (5-9-94) when very few bats fed successfully, and many left the roost. Hence the sample sizes varied.

Figures 10 and 11 summarise the mother/young diets after favourable weather for both insect flight and bat foraging. On 12 August 1990 86% of the bats (n = 29) showed a single prey item (defined as one occupying at least 95% of the diet volume), and the remainder showed that a single prey item dominated the diet. Hence the mean percentage of the diet volume of a single prey item was 90 for young and 94 for mothers. However, the former ate *Aphodius rufipes* and the latter moths. If this is the normal diet consumption in August, it would explain the pattern shown in Fig. 8. The dietary segregation between mothers and young was almost complete on this occasion.

On 1 September 1991 the young again fed primarily on a single identical prey item, but it was brown tipulids, not *Aphodius rufipes*. The adults were less restricted to a single prey item, and those that were, split between moths and brown tipulids. The dietary segregation was much reduced, and was restricted to the absence of moths in the diet of the young.

Table 1 summarises data for these two dates. Although mothers tended to feed on more prey items (up to 4 per faecal sample) the differences were not significant (chisquare = 2.508; d.f.= 1; n = 52; $p<0.25$ NS). Differences between the single-item diets of all mothers and all young after good weather was highly significant (chisquare = 30.994; d.f.= 2; n = 43; $p<0.001$).

Figure 12 summarises the mother/young diets on 20-8-95 after a long hot dry summer which apparently delayed the activity of adult *Aphodius rufipes* in a manner recorded by Landin (1961) in Sweden during 1959. The maternity colony was showing signs of food-supply stress before this capture, with small total dropping collections, loss of young born early in the season, and very early emergence times (Ransome unpublished data). Hence this data represents an abnormal sample. I have divided up the young into three age classes since there was a clear segregation of the diet between bats younger than 42 days, which did not feed on moths and those older that did. I further divided the older juveniles into two equal-sized groups to see if increased age continued to result in dietary changes. Fig. 12 shows they did not, so data in Table 2, which summarises aspects of the data, just contains two juvenile groups. Clearly young older than 42 days are capable of catching moths, since they were the exclusive diet of all those that ate single prey items. As on 12-8-90, most mothers fed on moths, but two ate exclusively brown tipulids.
The percentage of individuals feeding on single prey was less than after good weather conditions at 56.8% of the total sample (n = 44), but chisquare tests showed the differences were only just significant for the young (chisquare = 4.768; d.f.=1; n = 44; $p<0.05$; but 2 cells showed expected frequencies of 4.9 and 4.1, which are below the accepted limit of 5). Hence more data is needed to determine whether the number of prey items increases as drought stress rises.

Figure 13 shows only the diet of 11 lactating mothers which fed on 14 August 1994 after a cold dawn, which prevented successful feeding by all young and many mothers. The mean age of the young was 33.3 days (n = 24; range 22 - 45 days) so many would normally have been expected to feed (Jones *et. al.*, 1995). The mothers showed a low tendency to feed on single prey items (36.4%; n=11), and those that did ate ichneumonids (2), brown tipulids (1) and *Aphodius rufipes*(1), at a time when primarily moths would be expected. Five mothers ate two prey items, one three and one four, which was the most seen in the present study.
Figure 14 shows mother/young diets on 5 September after a very cold dawn prevented all but seven bats from feeding (4 young; 3 mothers). Five of them, including all young, ate single prey items (71% single prey). All young fed almost exclusively on ichneumonids, whereas one mother fed entirely on moths, and two others on 71-76% ichneumonids plus some brown tipulids, *Aphodius* and moths.

Figures 13 and 14, together with Table 3, help to show some aspects of weather effects on the diets of mothers. By combining samples as after good or poor weather, significant chisquare tests could be successfully carried out to detect the effects of poor weather at similar times of the year. Poor weather, especially if cold, significantly increases the number of prey items captured by mothers (chisquare= 5.504; 1 d.f.; n = 63; $p<0.025$). Although ichneumonids were only found in the diet after cold dawns, the differences between the single prey item diets after good and poor weather were not significant. This may have been due to small sample size which results from the fact that many bats abandon feeding during cold dawns.

Discussion

Taking all data from the monthly summaries from the colonies, with Figures 10-14 and Tables 1-3, the following working hypothesis seems to explain dietary changes:

(a) Mothers normally feed on moths, their key prey, throughout August, and avoid *Aphodius rufipes* even when they are abundant as long as moths are in good supply. Moth supplies may fall steadily due to phenological population declines, or rapidly at a particular dawn or dusk due to temporary low temperatures. If either happens they switch to alternative, or secondary, single prey items, or combine moths with them. Brown tipulids are often the first alternative, but *Aphodius rufipes* is also taken. In very cold spells ichneumonids, which are dominant prey in October, and seem to be able to fly at low ambient temperatures, are used as a last resort.

(b) Young do not feed at all until they are about 29 days old, when they normally feed on *Aphodius rufipes*, which is therefore a key prey species. This is usually a reliable species of small, easily-caught prey, which reaches peak numbers at the time that these young normally start to feed. However, if drought delays its flight activity, or low temperatures prevent flight at a particular feed, they either switch to other secondary prey, or abandon feeding, rather than combine more than two prey types at a single feed. Alternative (secondary) prey is usually brown tipulids, small diptera or ichneumonids until the age of 42 days. After this age moths may also be caught probably because the young can Doppler-shift compensate at about this time (Konstantinov 1989).

This hypothesis (that selective single prey item feeding by both mothers and young on their respective key species is normal if prey is abundant; and that lower levels result in a forced increase in the prey range eaten, and/or prey switches to secondary prey species) agrees with data shown for April and May (Figs. 4 and 5) and September (Fig. 9) summary diets. These months are all ones which display erratic climatic temperatures, and they are therefore predicted to increase the numbers of secondary prey species. Jones (1990) has already shown that the prey diversity of the Clapton/Brockley colony was greatest in spring and autumn, with a minimum in June during late pregnancy.

Summary for Part 1

Diet content: geographic and climatic effects

One major finding of this study is that both mothers and young normally feed on single prey items at a single foraging bout. It therefore adds to the findings of Jones (1990) who identified and quantified the main prey items over a single summer season. They are Moths (Lepidoptera) and scarabaeid beetles (Coleoptera: Scarabaeidae) which dominate the diet at about 40% each, with tipulids and small dipterans (Diptera), plus ichneumonids (Hymenoptera: Ichneumonidae) composing the remaining 20%.

Other insect orders such as lacewings (Neuroptera) and caddis flies (Trichoptera) are occasionally eaten, but form insignificant proportions of the overall diet in most of the sites studied. However, in Switzerland and Luxemburg, studies by Bontadina and Pir (*pers. comm.*) respectively, show that whilst many of the other prey items are eaten, and in similar amounts, Trichoptera can be very important at certain times of the year. This is only possible where access to substantial bodies of water lies within the roost foraging range. In England many of the maternity roosts lie close to rivers or lakes, so Trichoptera may play a more important role in the diets of such bat colonies. Furthermore, the detailed dietary study by Bontadina in Switzerland, showed that moths are even more dominant in the diet than in England. This seems to be due to the practice of moving cattle high into the mountains in summer, and using the grass for hay to ensure winter feed supplies. Consequently *Aphodius rufipes* beetles are not available, and another abundant scarabaeid beetle, *Amphimallon solstitialis* (L.), the summer chafer is eaten instead. This chafer is only locally distributed in Britain, and was not found in my analyses.

This study shows that the dietary content of greater horseshoe bats is remarkably consistent over a wide geographical range of England and Wales, and is similar to continental colonies. It remains stable despite considerable variations in climatic conditions in different years. Extreme climate, particularly low temperatures if prolonged, affect the timing of the emergence of adult insect populations, and probably the their densities. Short term low temperatures, which often occur in spring, and may even occur in summer before dawn selectively removes species as available food supplies (Taylor, 1963), (see part 2). Bats in the wild are therefore frequently and erratically forced, to abandon feeding on their preferred prey items, and to switch to less preferred and profitable prey items, or stop feeding altogether.

Jones (1990) also concluded that this species is a selective feeder, rejecting smaller unprofitable prey (Diptera and ichneumonids) when larger prey (moths and beetles) were abundant. This study confirms his view, and also shows that mothers and their young select different prey items at a time when both items are abundant.

Diet content: changes throughout the year

1) The key prey item in August for mothers is moths, and for young it is *Aphodius rufipes*.

2) The key prey item seems normally to be *Geotrupes* in April; *Melolontha melolontha* in at least a part of May or June, before moths replace them in June.

3) Secondary prey items include brown tipulids throughout the summer, and they usually replace *Aphodius rufipes* during September.

4) Other secondary prey items include ichneumonids of the *Ophion luteum* complex which are especially used in cold weather.

5) Changes in dietary prey items with time primarily reflect the phenology of key prey items, most of which are available as flying adults for limited periods of the summer.

6) Lower population densities, even during peak emergence periods of adult prey items, may result from low temperatures or extended dry weather, and complicate dietary patterns.

Table 1

Diets of mothers and young in mid-August and early September during good weather

Date	n total (status)	n eating 1 prey items	n eating 2+ prey items	mean n prey items	prey item(s) eaten (n)
12-8-90 (mother)	17	14	3	1.13	moth (14)
12-8-90 (young)	12	11	1	1.08	Aph1 (10) Tip1 (1)
1-9-91 (mother)	11	7	4	1.55	Tip1 (4) Moth (3)
1-1-91 (young)	12	11	1	1.08	Tip1 (11)
TOTALS:					
mothers	28	21	7	1.25	moth (17) Tip1 (4)
young	24	22	2	1.08	Aph1 (10) Tip1(12)

NB prey item(s) eaten refer only to individuals eating single prey items. They formed 82.7 % of the total sample (n = 52).

χ^2 test between numbers of prey items in the diet of total mothers and total young: $\chi^2 = 2.508$, p = 0.25-0.1 NS.

χ^2 test between the single item diets of total mothers and total young in good weather: $\chi^2 = 30.994$; d.f. = 2; 1 cell with expected frequency <1. $p<0.001$. Highly significant.

Table 2

Diets of mothers and young in late August after a drought

Date	n total (status)	n eating 1 prey item	n eating 2+ prey items	mean n prey items	prey item(s) eaten (n)
20-8-95 (mother)	24	12	12	1.63	moth (10) Tip1 (2)
20-8-95 (all young)	20	13	7	1.35	moth (9) Tip1 (3) Aph1 (1)
20-8-95 (yng<42 dys)	6	4	2	1.35	Tip1 (3) Aph1 (1)
20-8-95 (yng >42 dys)	14	9	5	1.36	Moth (9)

NB As for Table 1. Individuals eating single prey items formed 56.8% of the total sample (n = 44).

χ^2 test between numbers of prey items in the diet of mothers and all young after the drought: $\chi^2 = 1.00$; p = 0.5 - 0.25, NS. Numbers of prey items are therefore similar in both groups after the drought.

χ^2 test between numbers of prey items eaten by young in good weather (Table 2) and after a drought: $\chi^2 = 4.768$; d.f. = 1; 2 cells with expected frequencies < 5 (4.9 & 4.1); $p<0.05$; probably just significantly different (more prey items in poorer weather).

Same test for mothers gave $\chi^2 = 3.483$; d.f. = 1; no cells <5; $p<0.1$; just NS. (Combined mother/young data also gives NS result - see Table 2)

Table 3

Diets of mothers foraging at dawn in August and early September in good and poor weather

Date	n total (status)	n eating 1 prey item	n eating 2+ prey items	mean n prey items	prey item(s) eaten (n)
WARM DAMP WEATHER:					
12-8-90 (mother)	17	14	3	1.13	moth (14)
1-9-91 (mother)	11	7	4	1.55	Tipl (4) Moth (3)
POOR WEATHER:					
20-8-95 (drought)	24	12	12	1.63	moth (10) Tipl (2)
14-8-94 (v. cold)	11	4	7	1.91	Ichn (2) Tipl (1) Aphl (1)

NB As for Table 1. Individuals eating single prey items formed 58.7 % of the total sample (n = 63).

No young fed at dawn on 14-8-94 after a minimum night temperature of 5.7 °C.

χ^2 test between numbers of prey items in the diet of mothers (total) in good and poor weather (combined) = 5.504; 1 d.f.; p 0.025-0.01. No cells <5.0 expected count. Difference significant. Poor weather increases the number of prey items.

χ^2 test between dietary content (single prey items) of mothers between good and poor weather (combined) = 4.0; 3 d.f.; p 0.5-0.25 but 3 cells <1 therefore value very suspect. NS.