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Winter feeding studies on greater horseshoe bats

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Contents

Summary

The objectives of this study were to:

1. relate the extent of winter feeding by greater horseshoe bats of different ages and sexes to climatic data;
2. analyse the winter diet to identify the main insect groups exploited and relate these to foraging habitats;
3. explore regional variation in winter diet, and propose environmental prescriptions for land around key hibernacula.

The quantity of faeces collected from bats of unknown sex and age in each fortnightly period at Woodchester Mansion varied enormously throughout the winter. Many factors probably contributed to this variation, but significant accumulations only occurred during relatively mild weather. The two winters of the study were both very mild, and the impact of severe climate could not be assessed. Only in late December were no significant levels of faeces collected in both winters (less than one gram of dry faeces). This may be a recurring seasonal situation related to a lack of available insect prey, or merely reflect the absence of bats at the Mansion during this period.

The main insect groups eaten by bats at Woodchester, in order through the winter, are: *Aphodius* in early October; *Ophion* in late October; dung flies (*Scatophaga stercoraria*) throughout November and early December; *Ophion* from early January to early March; Moths in early and late March; dung flies & Trichoptera from late March through April; Tipulids in early April. Insects in the winter diet are similar to those found in the summer diet, but secondary prey are dominant. *Geoptupes* beetles occurred at fairly low levels, at times during the winter, especially in early December, in late March and early April.

The sequence of dietary change was similar in both winters, and may be an annual event. It probably reflects the phenology of particular insect prey. In mid winter *Ophion* ichneumonid wasps dominated the diet in both years of the study. The next most abundant prey were dung flies.

Individual bats captured in three other regions, Cheddar, Mells and Winsley, on specific Dates, show that the diet is similar to that at Woodchester at the same time of the winter. However, at two other winter roosts in the Forest of Dean, bats ate significantly more *Geotrupes* beetles than those at Woodchester, and elsewhere. It is argued that these key prey are important in maintaining these populations at a more favourable status than their latitude suggests. The population at Combe Down, Bath, where evidence for winter feeding is sparse, is in decline.

As dietary content in winter is largely comparable with that in summer, essentially the same environmental prescriptions as given by Ransome (1996) are proposed. Bats in winter are likely to forage closer to their roosts than those in summer, so the prescriptions should concentrate in the regions close to hibernacula. However, rather than defining a fixed radius from the entrance, conservation efforts should de directed towards regions that are sheltered from high winds, and on south, or south-west facing slopes.

Introduction

For the purposes of this paper, winter feeding is defined as feeding within the hibernation period. Ransome (1968) first showed that winter feeding by greater horseshoe bats *Rhinolophus ferrumequinum* can occur at times during the hibernation period. As the incidence of mild weather increased, body mass-loss rates decreased, especially in adult males, but also in first-year bats. Rates of mass loss in adult female bats showed no such relationship. From these data it was argued that feeding could potentially have a significant influence on the survival of winter by bats. Ransome (1971) showed that these bats were able to synchronise their arousal timing with dusk on warm days, rather than cold ones. This was achieved by the selection of a site for hibernation whose temperature regime reflected external climatic changes, usually as a result of air-flow through a dynamic hibernaculum. Ransome (1990) presented data on regulated body mass losses by bats in winter, and argued that bats possess a fuel gauge. Bats seem to have a time-compensated energy assessment system which motivates feeding drive throughout the year.

Recent radiotelemetry studies at Cheddar (Park, Jones & Ransome 1999, 2000) showed that most bats tend to synchronise arousals with dusk, and activity remains nocturnal throughout the hibernation period. Although the length of the bat's post-arousal activity was usually significant, it was prolonged by warm weather on the day of arousal. Individual bats with the lowest body reserves synchronised most closely with dusk. As dusk is normally the time when insect availability is greatest on a particular day, at a time when bats are able to forage, these findings support winter feeding.

Overall I suggest the following model of winter energetics for this species:

A bat may store large levels of body reserves in autumn, and use them to sustain itself with little or no winter feeding until April or even May in cold springs. Alternatively it may store insufficient body reserves to survive winter. Such a bat is aware of its deficit, and feeds significantly in winter, motivated by its time-compensated energy assessment system. The former bat is predicted to allow its arousals to free-run; the latter to synchronise strongly with dusk. All bats have prolonged post-arousal activity periods in winter, during which some kind of essential body maintenance is presumed to occur. Successful winter feeding prolongs these periods, and reduces body mass losses to levels which ensure survival until spring.

My unpublished data shows that fat deposition by this species normally occurs rapidly over a ten-day period between late September and mid October, according to age and sex group. Mature females tend to store fat earlier than other groups, and acquire higher reserves. Mature males normally start the winter with the lowest levels, especially if they hold mating territories with a large harem (Ransome 1991). They usually need to feed extensively in winter. First year bats, or young of the year, are the last to leave the breeding roost, especially in years when births are late, possibly because they still have important growth processes to complete. They often leave significant fat deposition until late in October.

If autumn weather is poor, as it was in October 1998, the body reserves of all sex and age groups at the start of hibernation may be insufficient for survival without some winter feeding.

Part 1: Overview of the scientific plan used in the study

Introduction

Collections of faecal pellets, or droppings, provide the most reliable, and least intrusive method of investigating the diets of bats (Whitaker 1988). Droppings can be collected in one of two ways. First they can be collected from beneath clusters of bats which occupy a roost over a specified period of hours, days, weeks etc. Second they can be collected from individual bats placed in clean bags for one or two hours after capture at a roost, or in the field. In both cases the quantity of droppings produced may be estimated by weighing dried pellets, and the diet eaten can be determined by faecal analysis.

Collections of droppings from beneath colonies of bats at regular intervals, if continued long enough, can provide reliable data about the diet of the colony at that location. However such data does not tell us which bats are feeding. In the absence of detailed information about the numbers of bats involved, and the numbers of days when they were present in the roost contributing to the collections, we cannot assess the levels of feeding success.

Greater horseshoe bats feeding on insects in summer may take over 10 hours to process the food they caught at dawn. Dropping production rates are rapid in the first few hours, and taper off gradually until late afternoon (Ransome 1978). If bats become torpid, due to low ambient temperature conditions and/or low food consumption, egestion of the final droppings is delayed and leads to an increase in dropping production rates after arousal. Such bats groom, urinate and defecate just prior to leaving the roost for dusk foraging.

In winter, bats that have fed after arousing from torpidity, frequently enter their next torpor bout with substantial amounts of skeletal remains still retained within the gut. On their next arousal these bats also defecate before leaving to try to forage again. Handling torpid winter bats provokes dropping egestion.

Putting a bat into a clean bag and collecting any dropping produced by it, can tell us which bats have recently fed, and which have not. From the dry mass of droppings produced by a bat, we can roughly judge whether it has recently fed significantly, or only slightly.

Dietary analysis of droppings from bags, allow both the quantity of prey consumed, and the diet to be investigated.

Methods

Site descriptions relevant to dietary studies

Woodchester Mansion This roost is an enormous building with extensive attic and cellar systems. It is fully described by Ransome (1990). The greater horseshoe bat population has been studied over the past 41 years. Recently up to 110 bats have been found in the breeding attic during the peak summer months. However, in winter only from one to eight bats are seen to visit the incubator system provided as a conservation measure, and then often only for a few hours. Continuous time-lapse video recordings were used to confirm that no other species contributed droppings to collections. Occasional captures of bats present show that in October they are young of the year, but later in the winter older bats of both sexes return.

The Mansion is located in a long steep-sided valley with mixed deciduous and coniferous forested edges, some grazed pastures, and a series of lakes. Most of the valley is owned by the National Trust, which is currently implementing forestry and grazing changes which should assist the bat population.

Cheddar This is a complex of caves found within Cheddar Gorge, Somerset, which provide roosts for a large breeding colony in summer, and winter clusters of up to 117 bats in recent winters. Numbers stay relatively stable throughout the winter. Bats born at Brockley (Ransome 2000), and a few from Mells, also hibernate here.
The Gorge has precipitous cliffs with faces sheltered from wind and rain, with scattered trees, often with ivy attached, and patches of grass. The flatter slopes are grazed by increasing numbers of feral sheep. Above the Gorge are mixed woodlands and pastures, leading southwards to the Somerset Levels. Details of the foraging areas are provided by Jones and Billington (2000).

Mells This is a tunnel and cellar system beneath a large old house near the village, which is located south east of Radstock, Somerset. It provides roosts for a very large maternity colony of over 310 bats (Ransome 1998). It is close to a river within a shallow valley, whose sides are wooded. A series of such gently undulating, sheltered riverine valleys exist nearby, alongside and interspersed by fields grazed by cattle, sheep and horses. The flatter land is used for arable crops. A more detailed assessment of the habitat is provided by Ransome (1997a), and Billington (2001) has recently carried out radio-telemetry study of the foraging areas and night-roosts. In early winter torpid clusters of 60 to 80 bats, mostly young of the year, hibernate in the tunnel. In mild winters they remain there.

Winsley This consists of two underground mine/cave systems in Wiltshire which provide an extensive hibernation roost for bats from both the Iford and Mells breeding colonies (Ransome 1998). The number of bats there at any one time of winter shows considerable variation, but numbers can reach 100, with most in a large cluster. The bats are primarily first-years, subadults and mature males.

The systems have entrances located within steep-sided cliffs, within a sheltered deciduous woodland which leads down to a large valley with cattle, sheep and horse grazed pastures traversed by a river and a canal.

Cinderford This is a single large scowle, which is a nearly vertical rift from which iron ore was previously extracted. Partial filling has left a substantial underground system which provides suitable temperature conditions for hibernation throughout the winter. Bats born at the Littledean Hall colony nearby winter here. Clusters containing 60 to 85 bats have been caught recently. They consist of first-year bats and subadults of both sexes, and mature males.

The surrounding habitat consists of a range of forest types, from sparse to heavily-wooded (both deciduous and conifer stands), in steep-sided valleys interspersed with permanent pasture. Grazing is mainly by sheep, but cattle, deer and horses are also frequent. The large numbers of sheep in the forest are permanently grazed among the woods under an ancient common grazing right. It is also adjacent to the urbanised district of Cinderford.

Symonds Yat This consists of a series of disused iron ore mines alongside the River Wye within the extensive mixed deciduous woodland called Lord's Wood. There is good access to sheltered grazed pastures nearby, and sheep also graze within the wood as they do near Cinderford. The numbers of hibernating bats are not high, with usually only from 20 to 30 present over winter. Most are first year bats, older immatures, and adult males. As bats born and ringed as juveniles at Littledean Hall have rarely been recaptured here, it is assumed that the population of greater horseshoe bats which hibernates here originates from the Monmouth colony at Newton Court Stables.

Combe Down Consists of a series of disused limestone mines along the top of a hilly plateau above the city of Bath. It is highly urbanised around the two most important hibernacula, one of which is used as a subterranean summer roost for a small breeding colony. To the south are valleys with steep slopes that are grazed by cattle, sheep and deer. The colony is highly stressed, and has shown significant reductions from 110 to less than 40 in recent years (Ransome 1997c).

Climatic data

Temperature data were collected from the garden of my home in Dursley, which is some 9km from Woodchester Mansion. Daily maximum and minimum temperatures were recorded, and wind speed around dusk and dawn estimated on the Beaufort Scale. The degree of rainfall around dusk and dawn were also assessed on a subjective scale.

Collection of dropping samples from Woodchester Mansion

Faecal samples were collected at roughly fortnightly intervals from Woodchester over the winters of 1997/8 and 1998/9, between early October and mid April. A total of 33 samples were collected in total. Droppings fell onto a thick yellow plastic sheet which covered the area beneath the incubator system. This was provided for the bats as a conservation measure to promote population levels (Ransome 1998).

On each occasion the breeding attic was entered, and droppings collected by hand and placed into a polythene bag. Great care was taken not to compress them into a mass, as single pellet analysis was required for this study. Afterwards the yellow sheet was swept clean to ensure that no contamination of the next sample could occur.
The droppings collected were from bats of unknown age and sex.

Collection of dropping samples from winter roosts

Clusters of bats were caught by net and individuals were placed into labelled soft clean holding bags whilst they were being processed as part of a long term ecological and biometric study. They were replaced into the bags afterwards, and all bats released together at the end, about 2 hours later. Consequently all bats in a sample received identical treatment. Bats became active within 40 minutes of capture, and would have egested all of their droppings before release.

Winter surveys to the various sites were mostly carried out annually at a similar time of the winter. The timings varied according to the site concerned, so data was not obtained in a synchronised manner. This restricted the value of the data, and made statistical comparisons among sites inadvisable.

Dietary mass data

Dropping samples from collections or individual bats were removed from the bags, placed on shallow trays and dried to constant mass in an incubator kept at 60 °C. They were then weighed to the nearest gram for large samples (from Woodchester) (>20g); 0.1g for small samples (>1g) and 0.01g for the smallest samples.

Samples collected over variable time periods at Woodchester were adjusted so that the winter was divided up into 13 half-monthly periods. They were early October, late October etc, until early April. The method used was as follows:

Actual data: collection 1 = 4th October to 11th October, dry mass = 53g, n = 7 days
collection 2 = 11th October to 18th October, dry mass = 32g n = 7 days
collection 3 = 18th October to 1st November, dry mass = 8.0g, n = 14 days

Calculations to obtain a total estimate for early October:

A: 53/7 = 7.571g (rate per day, 4-11th October)
B: 7.571*11 = 83.28g estimated for the period from 1st to 11th October;
C: 32/7 = 4.571g (rate per day, 11-18th October)
D: 4.571*4 = 18.28g total estimated for the period 11th October to 15th October
E: 83.28 + 18.28 = 101.6g estimated total early October (1-15)

Calculations to obtain a total estimate for late October:

A: 32/7 = 4.571g (rate per day 11-18th October)
B: 4.571*3 = 13.71g total estimated for period 16th to 18th October
C: 8/14 = 0.571g (rate for period from 18th October to 1st November)
D: 0.571*13 = 7.429g estimate for period from 18th October to 31st October
E: 13.71 + 7.43g = 21.1g estimate for 16th to 31st October

Dietary analyses for insect groups consumed by bats

The methods used in the present study were essentially identical to those used by Ransome (1996, 1997) to produce permanent dry slides suitable for stereo binocular examination and estimation of percentage volume in the diet (Whitaker 1988). Slight adjustments were made to the numbers of faecal pellets analysed. They were reduced from 16 to 12 for collections made at Woodchester, since a re-analysis of the 1996 data showed that this reduction had little impact on the results obtained. Initially four pellets per individual bat were analysed from groups caught in winter hibernacula. As most pellets from the same bat contained the same prey item(s), this was reduced to one pellet per bat. All bats caught had their diets sampled.

Identification to insect orders, families, and in some cases, genera, were carried out as in Ransome (1997a).

As the time periods of collections from Woodchester were not identical from winter to winter, it was not possible to compare data statistically. Neither could data from samples collected from individual bats be statistically compared with the Woodchester samples, as they were collected under an erratic protocol.

Table 1 Mass of dry faecal pellets produced at Woodchester during various periods of winter 1997/8 in relation to climatic temperatures

Winter Period	1997/8 Total dry faecal mass (g)	% days falling below 0 °C	% days falling below 5 °C	% days over 10 °C during period
Early October	64.9	6.7	6.7	100
Late October	22.3	56.3	62.5	81.3
Early November	10.3	6.7	53.3	93.3
Late November	0.4	6.7	26.7	80.0
Early December	0.0	33.3	66.7	40.0
Late December	0.0	12.5	75.0	25.0
Early January	0.4	13.3	60.0	66.7
Late January	0.4	66.7	100	0.0
Early February	30.5	28.6	66.7	60.0
Late February	40.6	7.1	69.2	60.0
Early March	1.2	13.3	60.0	73.3
Late March	14.0	6.3	56.3	100
Early April	23.1	26.7	73.3	66.7

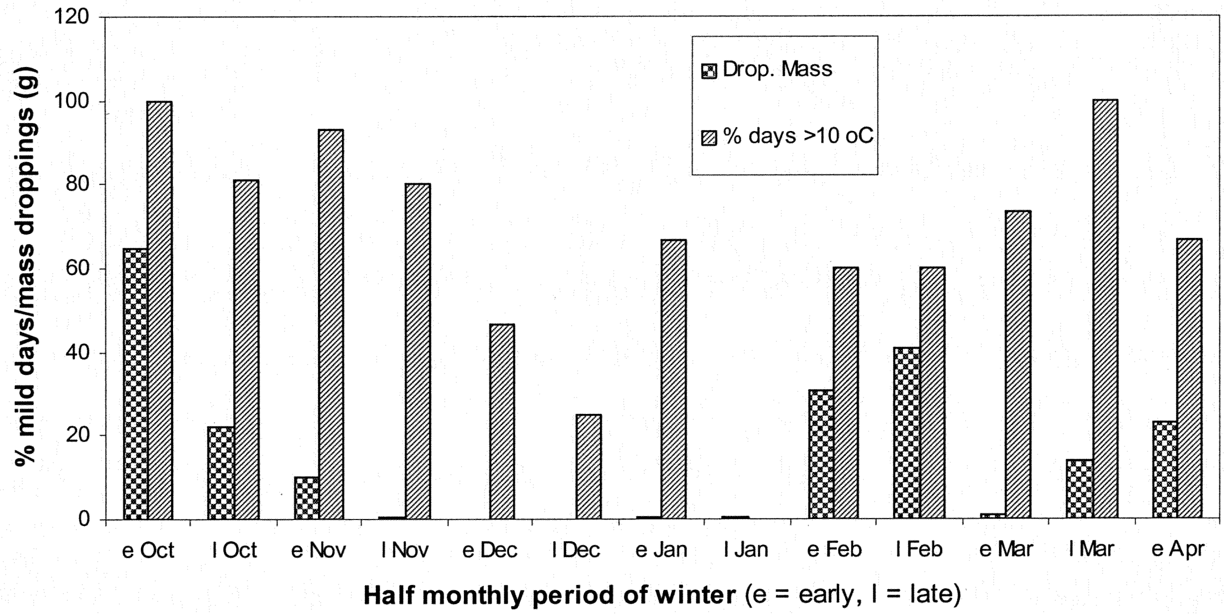

Figure 1 Frequency of mild weather and dropping production at Woodchester in 1997/8

Part 2: Results of winter diet studies at Woodchester Mansion

Introduction

Visits to collect samples at roughly two-week intervals were made as planned. Most visits resulted in the collection of sufficient pellets to allow dietary analysis.

Mass of droppings by winter period and climatic conditions.

Tables 1 and 2 summarise data for the two winters in relation to climatic temperatures.

Figures 1 and 2 show dropping mass production in relation to the frequency of mild days over each time period. A mild day was defined as one on which a temperature of 10 °C was reached. Such conditions were assumed to permit the flight of at least some insect prey, and which was correlated with reduced winter weight loss in certain bats (Ransome 1968). Although high production occurs in mild weather in both Octobers, the association between production levels and mild weather is not strong. Mild weather from late November to early January is not associated with significant production in either winter. The considerable production of droppings in February 1998 occurred under similar conditions to those at many other times of the winter.

Figures 3 and 4 show dropping mass production in relation to the frequency of cold nights. Two levels of coldness are used, below 5 °C and below 0 °C. Both winters were mild, but 1997/8 was slightly colder, with frequent frosts in late October and late January. Otherwise they were similar. Despite this, it was in a mild spell during February 1998, rather than 1999, that production reached its highest winter levels. Overall dropping production for the two winters of 194.5g (1997/8) and 217.6g (1998/9) was very similar. It was the timing of production that differed (figure 5). It may be that the lower levels of prey consumption in October 1997 led to less body reserves in bats at the start of hibernation, and therefore required higher levels of winter foraging to compensate. This is predicted to occur by the energetics model above.

Table 2 Mass of dry faecal pellets produced at Woodchester during various periods of winter 1998/9 in relation to climatic temperatures

Winter Period	1998/9 Total dry faecal mass (g)	% days falling below 0 °C	% days falling below 5 °C	% days over 10 °C during period
Early October	101.6	0	7.7	100
Late October	21.1	7.1	14.3	100
Early November	7.1	6.7	73.3	66.7
Late November	4.6	26.7	80.0	26.7
Early December	1.1	40	53.3	46.7
Late December	0.5	25	68.8	43.8
Early January	2.1	26.7	60.0	33.3
Late January	8.4	12.5	68.8	25.0
Early February	9.3	42.9	64.3	28.6
Late February	2.8	7.1	69.2	42.9
Early March	2.8	13.3	73.3	42.9
Late March	10.5	12.5	56.3	93.8
Early April	71.9	13.3	33.3	86.7

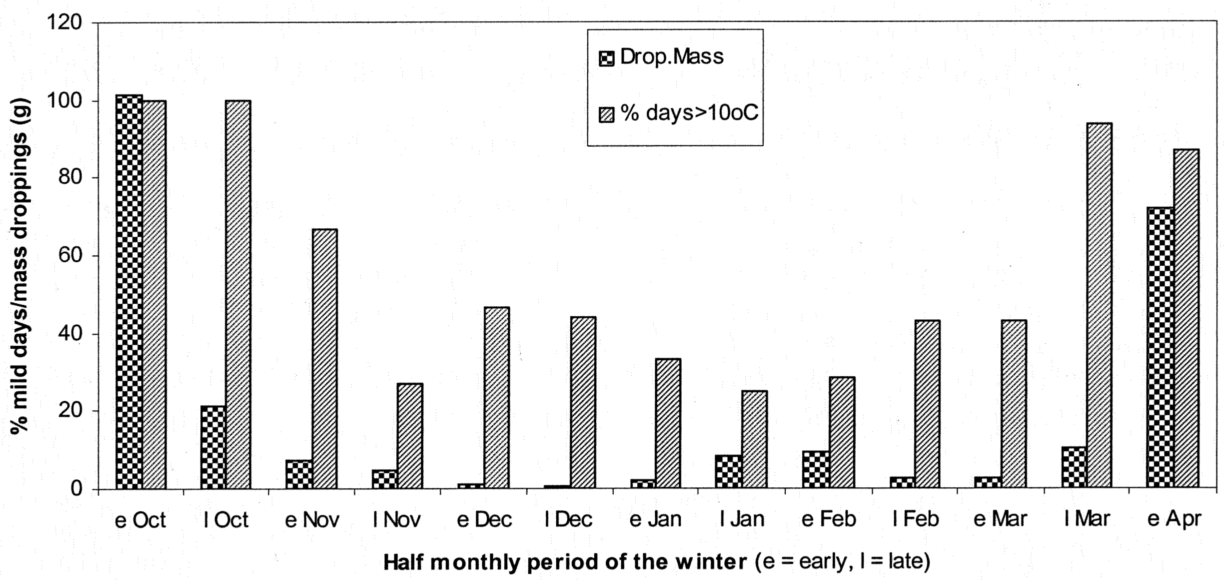

Figure 2 Frequency of mild weather and dropping production at Woodchester in 1998/9

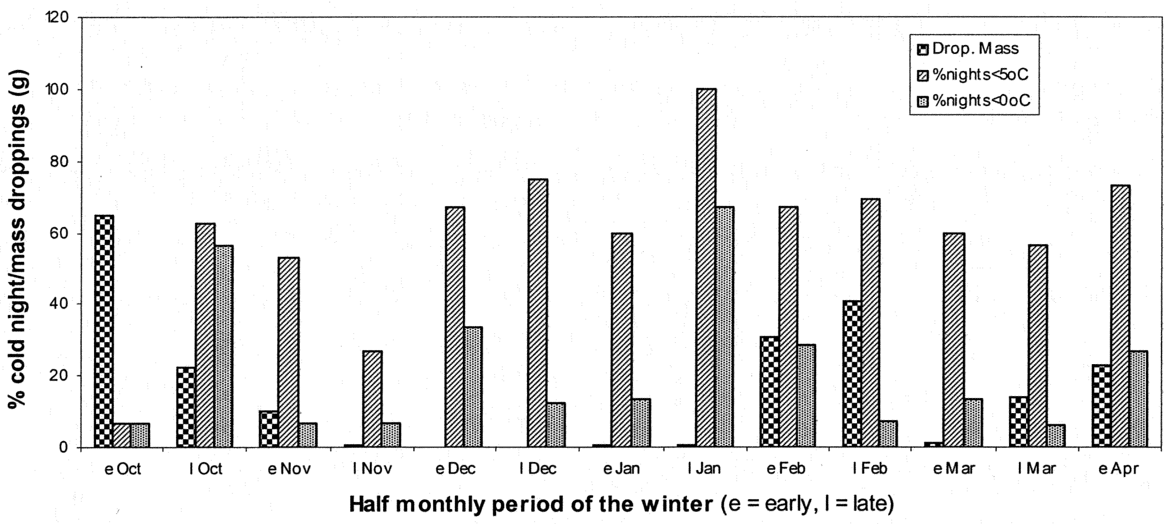

Figure 3 Frequency of cold nights and dropping production at Woodchester in 1997/8

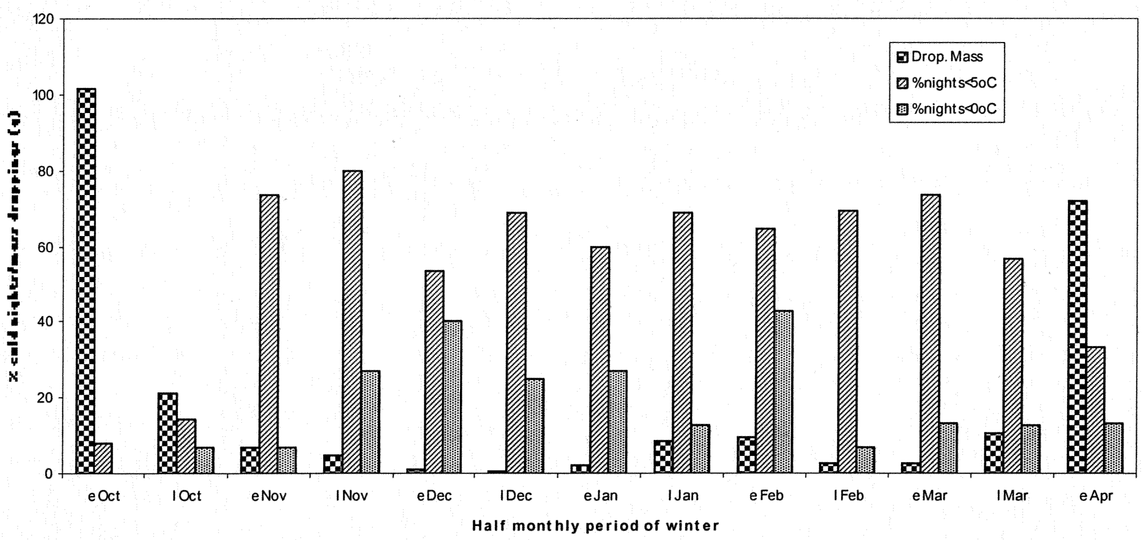

Figure 4 Frequency of cold nights and dropping production at Woodchester in 1998/9

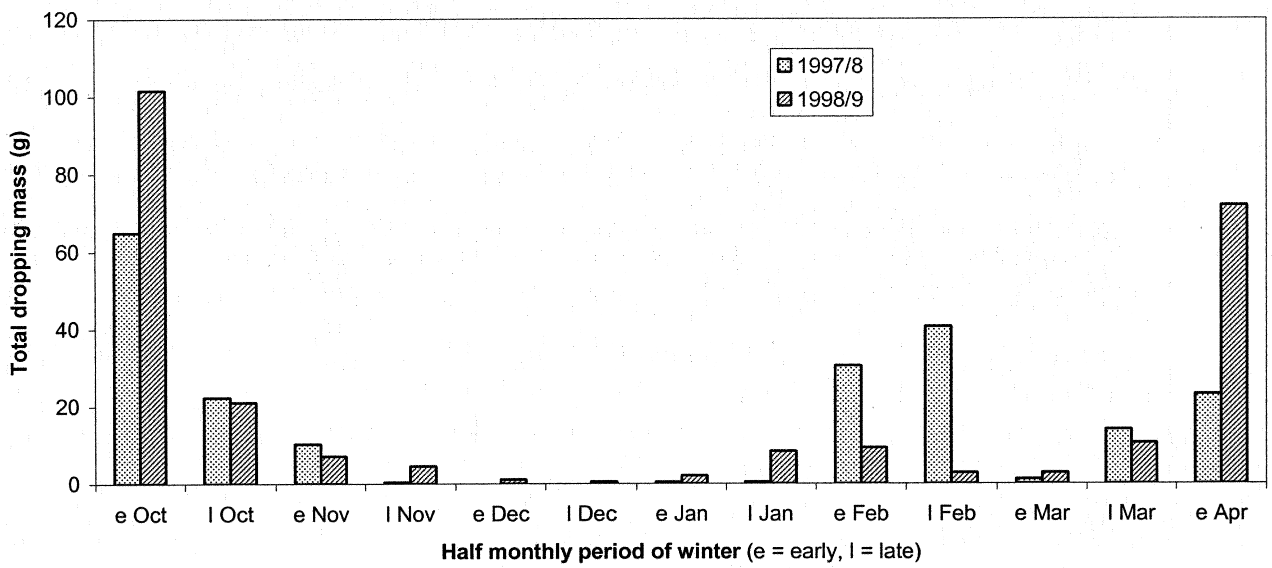

Figure 5 Dropping masses by winter period at Woodchester

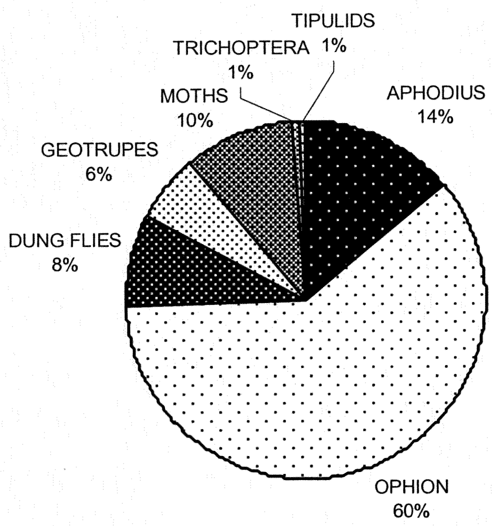

Figure 6 Winter diet at Woodchester 1997/8

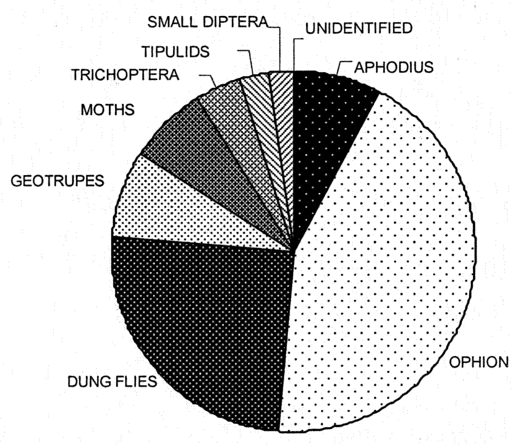

Figure 7 Winter diet at Woodchester 1998/9

Prey consumed by winter period

Total diet for each winter is shown in the pie charts (figures 6 and 7). The prey items, but not their proportions, are the same in both winters, with *Ophion* wasps, *Aphodius* beetles and *Scatophaga stercoraria* dung flies as major prey. In 1997/8 the former two items formed three-quarters of all dropping production, and in 1998/9 they formed a half.

Geotrupes dung beetles and moths were also often eaten. Trichopterans, small Dipterans and Tipulids were also consumed on occasions.

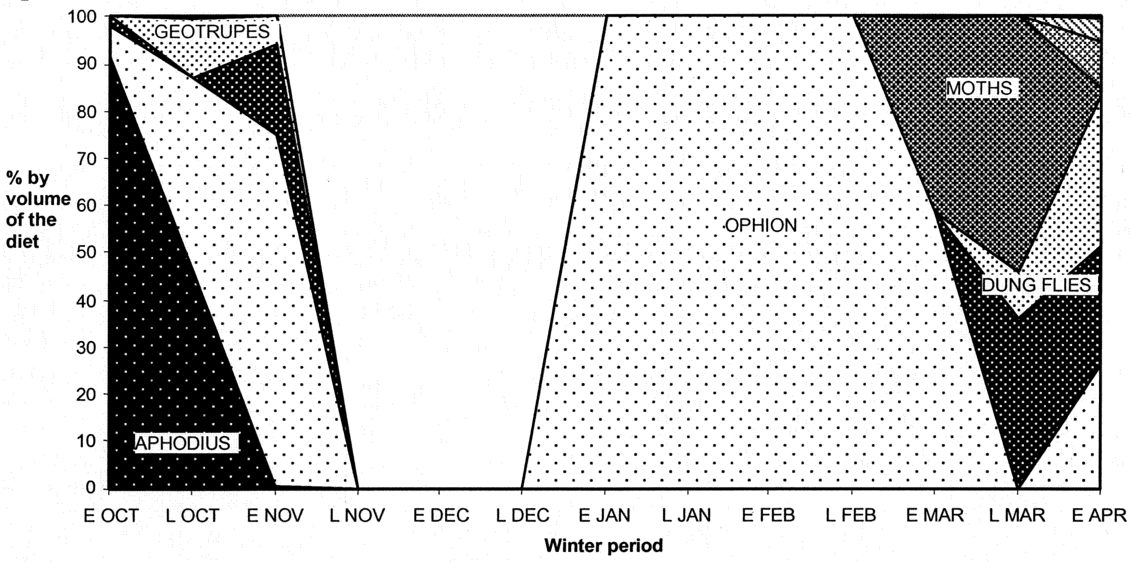

Figure 8 Prey items eaten at Woodchester by winter period in 1997/8

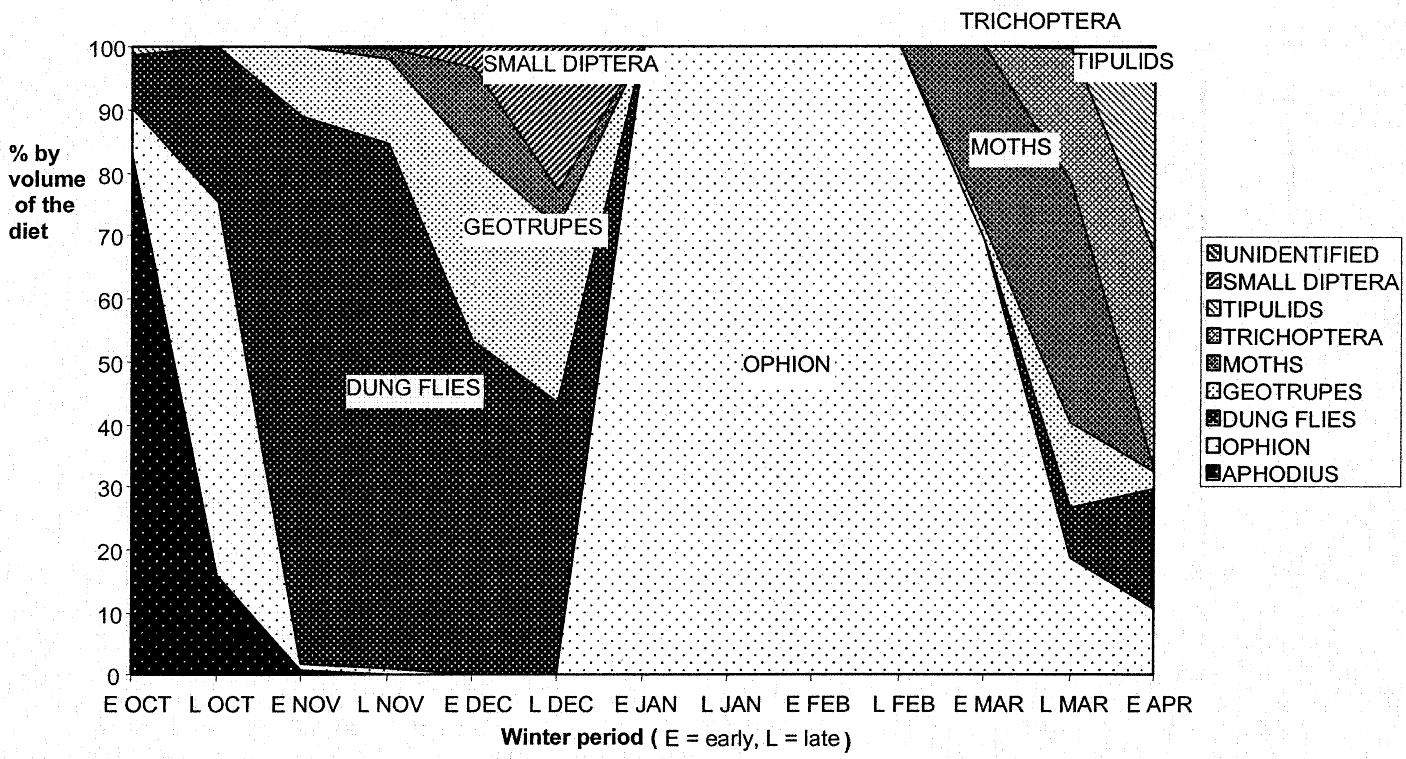

Figure 9 Prey items eaten at Woodchester by winter period in 1998/9

Figures 8 and 9 show how the prey items consumed vary through the two winters. The similarities are very striking, apart from the gap in data in the first winter in December. The number of prey items consumed are greatest at the start and end of hibernation, and some prey occur in both periods (*Geotrupes*, dung flies and moths in the second winter).

Discussion

In both winters December was marked by the lowest levels of dropping production, and bat use of the attic. Possibly there were no prey available in the Woodchester Valley at that time. From late January, through February however, production levels rose at the time that *Ophion* wasps were eaten in significant amounts. In the winter of 1997/8, production in February exceeded that in late October.

As spring approached, and *Ophion* consumption ceased, dropping production fell to low levels again in early March. This happened in both winters, just as the diet broadened. These data suggest that *Ophion* population densities must have been considerable during February 1998.

Dietary prey over the whole winter consisted of eight items, seven of which were also present in the summer diet of bats at Clapton Church and Brockley Stables, south of Bristol (Jones 1990). He considered that these bats were feeding selectively from among other insects flying at the same time. It is possible that some prey items are selected because of their long term availability throughout the year.

Table 3 Diet content and mass of dry faecal pellets produced at Woodchester during various periods of winters 1997/8 and 1998/9.

An * in column 2 indicates the dominant insect type; where 2 * occur, the insects are in more or less equal proportions. From 4th January to 8th March Ophion wasps formed virtually 100% of the diet. Only insects forming more than 20% of the diet at that time are listed.

Winter Period	Major insect group(s) in diet (>20%)	1998/9 Total dry faecal mass (g)	Major insect group(s) in diet (>20% of total)	1998/9 Total dry faecal mass (g)
Early October	Aphodius	64.9	Aphodius*	101.6
Late October	Aphodius* Ophion*	22.3	Ophion* Dung flies	21.1
Early November	Ophion* Dung flies	10.3	Dung flies*	7.1
Late November	Dung flies*	0.4	Dung flies*	4.6
Early December		0.0	Dung flies* Geotrupes	1.1
Late December		0.0	Dung flies* Geotrupes Small Nematocera	0.5
Early January	Ophion*	0.4	Ophion*	2.1
Late January	Ophion*	0.4	Ophion*	8.4
Early February	Ophion*	30.5	Ophion*	9.3
Late February	Ophion*	40.6	Ophion*	2.8
Early March	Moth * Ophion*	1.2	Ophion* Moth	2.8
Late March	Moth* Dung flies*	14.0	Trichoptera* Dung flies Geotrupes	10.5
Early April	Dung flies Geotrupes Ophion	23.1	Trichoptera* Tipulids	71.9

Table 4 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Cheddar 25th October 1997
Dursley the previous day: maximum temperature = 8.2 °C;minimum temperature = - 1 °C;no overnight rain; wind 2 SE

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Third year & older males	Third year & older females
0	16	16	4	2	8	
1-5	2	5	2	1	3	
6-10		1	1	2	0	
11-15		1	1		2	
16-20		1			1	
21-25		1				
26-30						
31-35						
36-40						
40-45						
46-50						
Over 50						

Table 5 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Cheddar 24th October 1998
Dursley the previous day: maximum temperature = 13.2 °C; minimum temperature = 6 °C;slight overnight rain; wind 8 W.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Third year & older males	Third year & older females
0	0	1	5	2	10	0
1-5	2	1	1	3	2	1
6-10	3	2	1	0		0
11-15	1	4	0	2		0
16-20	2	0	1	2		0
21-25	4	2				0
26-30	2	2				1
31-35	2	1				
36-40	1	1				
40-45	0	1				
46-50	1	1				
Over 50						

Part 3: Results of winter diet studies at other roosts

Introduction

As stated above, captures of bats during annual, biannual, or tri-annual monitoring visits to monitor winter roosts, provide opportunities to collect faecal samples from individual bats. These allow the investigation of aspects of feeding, such as which bats feed, and how much do they eat.

Dropping masses and insects consumed at Cheddar

In order to make the data easier to compare, dropping masses were grouped into 5mg classes, by age and sex of the bat. Six age and sex groups were used as follows:

male bats in their first winter; these are incapable of breeding
female bats in their first winter; these are incapable of breeding
male bats in their second winter; these are incapable of breeding
female bats in their second winter; some may have mated
male bats in their third winter, or more; they are capable of breeding
female bats in their third winter, or more; they are usually capable of breeding

All tables are produced to a standard size and pattern to facilitate comparisons.

Tables 4 to 8 present dropping mass data for two October dates, one January date, and two April dates. They show a typical range of results for changes throughout the winter at one site, and are similar during other winters of my study.

Tables 4 and 5 show two extremes for October data. On 25th October 1997 the levels of droppings produced after a cool day and overnight frost (table 4) were much below those of 24th October 1998, after a warm day and night. This was in spite of gale force winds and rain at dawn. The cold weather at dawn in the first winter may explain the much lower dropping production (DP), especially by first year bats. After warm weather they produced the highest levels of the groups represented.

In January 1998 (table 6), there is little evidence of successful foraging for any age or sex group. The droppings produced were all single pellets, and after analysis for dietary content, many showed little or no skeletal remains.

In April (tables 7 and 8), much higher levels of DP are shown, especially after a prolonged period of warm spring weather (1999). However, at this time the greatest production is by mature males, rather than by first year bats of both sexes. Furthermore, the highest levels achieved by mature males do not reach those of first year bats in October under similar warm conditions.

Figure 10 shows a pie chart of the diet on 24th October 1998 from 66 different bats. All seven of the prey items present are also included in the diet for the whole winter at Woodchester (figure 7). Only Trichoptera are missing.

Figure 11 shows a pie chart of the diet in January 1999 and 2000. Few bats produced droppings at this time of winter, and many had no skeletal remains. Of the 27 pellets analysed, 18 had no identifiable contents. The nine bats with skeletal contents had eaten only four prey items, all of which were also eaten in October.

Table 6 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Cheddar 17th January 1998
All droppings produced were single ones, which contained very little skeletal material; mostly just mucus. Dursley the previous day: maximum temperature = 9.0 °C; minimum temperature = 2.3 °C; no overnight rain; wind 3 NW.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Third year & older males	Third year & older females
0	13	20	10	2	6	2
1-5	9	8	3	3	4	
6-10						
11-15						
16-20						
21-25						
26-30						
31-35						
36-40						
40-45						
46-50						
Over 50						

Table 7 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Cheddar 5th April 1997
Dursley the previous day: maximum temperature = 13.8 °C; minimum temperature = 6.7 °C; slight overnight rain; wind 4 NW. Mild for 10 days.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Third year & older males	Third year & older females
0	10	6	1	4	3	
1-5	2	4	0		0	
6-10	5		0		2	
11-15	2		3		0	
16-20	1		1		1	
21-25					2	
26-30					3	
31-35					1	
36-40					0	
40-45					1	
46-50						
Over 50						

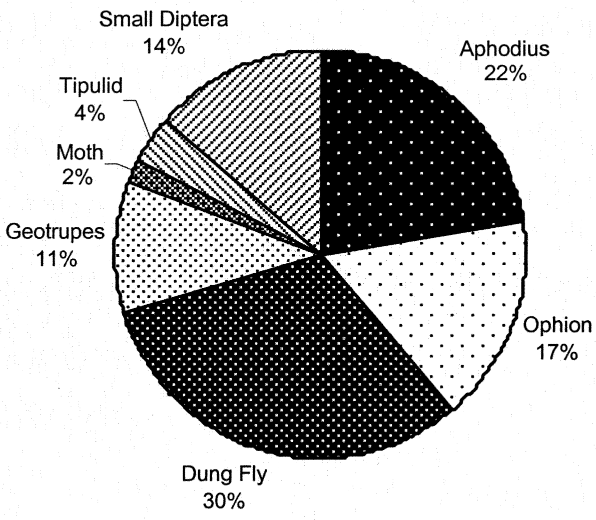

Figure 10 % Prey items eaten by Cheddar bats 24-10-98

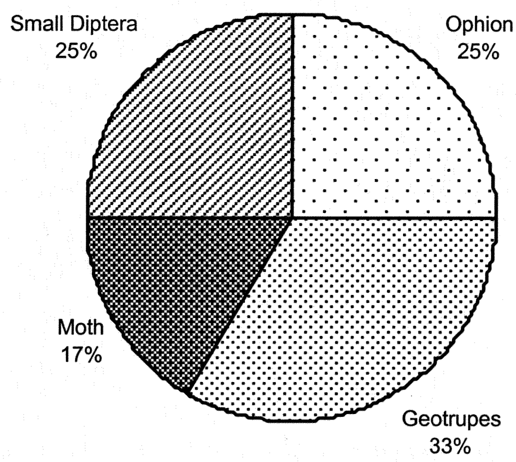

Figure 11 % Prey items eaten by Cheddar bats: January 1999 & 2000

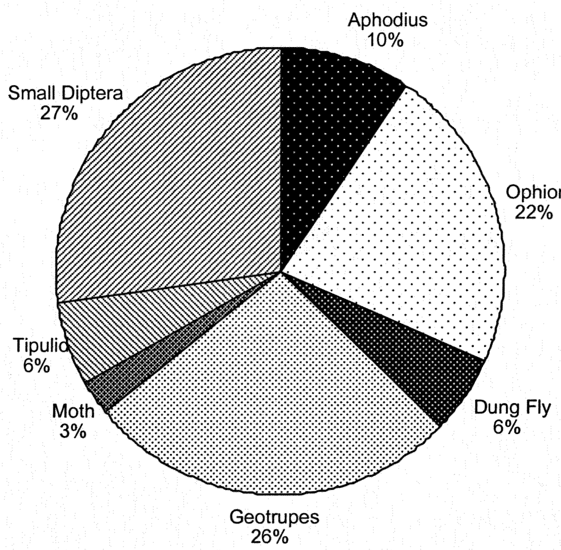

Figure 12 % Prey items eaten by Mells bats 20-10-98

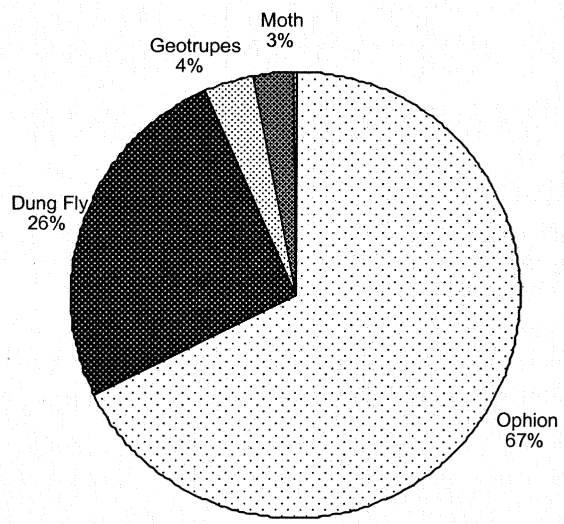

Figure 13 % Prey items eaten by Winsley bats 19-11-97

Table 8 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Cheddar 3rd April 1999
Dursley the previous day: maximum temperature = 16.3 °C; minimum temperature = 4.2 °C; slight overnight rain; wind 2 SE. Very mild for the last 10 days.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Third year & older males	Third year & older females
0	6	5	2	2	1	1
1-5	2	1	1	2	1	
6-10	3	2	3	1	2	
11-15	4	2	2	1	3	
16-20	3	0	4	2	1	
21-25	1	1	0		2	
26-30	2		1		2	
31-35					2	
36-40					1	
40-45						
46-50						
Over 50						

Table 9 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Mells 20th October 1998
Dursley the previous day: maximum temperature = 14.1 °C; minimum temperature = 5.4 °C; no overnight rain; wind 2 NW

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Third year & older males	Third year & older females
0	3	5	5	2		
1-5	2	1	1	4		
6-10	2	3	2	0		
11-15	3	3	2	0		
16-20	3	2	1	2		
21-25	1	1	2	1		
26-30	1	0	2			
31-35	0	0	0			
36-40	4	2	1			
40-45	0	1	2			
46-50	1	0				
Over 50		4 (62mg)				

Dropping masses and insects consumed at Mells

Tables 9 and 10 present data for one October date in 1998 and one November date in 1996. They show typical results for this site. The levels of droppings are very high (both tables), probably helped by the warm weather the day before, and in the previous ten days. Heavy overnight rain did not seem to affect the amounts eaten at this site.

As at Cheddar, first year bats produced very high levels of droppings, but so did certain individuals of the other groups represented.

Figure 12 shows a pie chart of the diet on 20th October 1998 from 57 different bats. Three bats had no skeletal remains. As at Cheddar, the diet shows the same seven prey items. Only the proportions are different.

Dropping masses and insects consumed at Winsley

Table 11 presents data for one November date in 1997. It includes some very high levels of DP, probably again helped by the very warm weather the day before, and in the previous ten days. Heavy overnight rain again did not seem to affect the amounts eaten at this site.

The February data (table 12) show few bats produced high levels of droppings. All were mature males. Most first and second year bats produced no droppings.
The March data (table 13) show low to moderate levels of DP by all age and sex groups, but the sample sizes are small. Levels are much lower than in October and November.

Figure 13 shows a pie chart of the diet on 19th November 1997 from 27 different bats. Four of the seven prey items recorded at Cheddar and Mells in October, are significantly represented in the diet. Two prey items, however, dominate the diet. They are *Ophion* wasps and dung flies.

Figure 14 shows a pie chart of the diet on 16th March 1998 from 11 different bats. One bat had no skeletal remains. The diet shows three of the same four prey items as in November, as dung flies were not present. Once again, *Ophion* wasps dominated the diet here, with some moths and *Geotrupes* beetles.

Table 10 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Mells 4th November 1996
Dursley the previous day: maximum temperature = 14.5 °C; minimum temperature = 9.2 °C; heavy overnight rain; wind 3 SW.Very mild over the last ten days.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Third year & older males	Third year & older females
0	4	3	0	0	1	1
1-5	1	0	1	0	0	
6-10	2	0	0	0	0	
11-15	1	6	0	0	0	
16-20	6	5	1	0	0	
21-25	4	1	0	0	0	
26-30	4	2	2	1	0	
31-35	1	2	0		0	
36-40	0		0		1	
40-45	1		0			
46-50			0			
Over 50			1 (55mg)			

Table 11 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Winsley 19th November 1997
Dursley the previous day: maximum temperature = 14.4 °C; minimum temperature = 10.9 °C; heavy overnight rain; wind 4 W. Mild for the last ten days.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Third year & older males	Third year & older females
0	1	3	2	1	0	0
1-5	1	2	0		0	0
6-10	1	1	1		1	0
11-15	1	1	1		3	0
16-20	3	0	0		0	0
21-25	1	0	1		1	0
26-30	2	0				1
31-35	0	1				
36-40	0					
40-45	1					
46-50						
Over 50						

Table 12 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Winsley 10th February 1997
Dursley the previous day: maximum temperature = 9.7 °C; minimum temperature = 5.5 °C; heavy overnight rain; wind 6 SW. Four days above 10 °C in the last ten days.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Third year & older males	Third year & older females
0	10	12		4	2	0
1-5		1			0	1
6-10					1	
11-15					0	
16-20					1	
21-25					1	
26-30						
31-35						
36-40						
40-45						
46-50						
Over 50						

Table 13 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Winsley 16th March 1998
Dursley the previous day: maximum temperature = 13.3 °C; minimum temperature = 6 °C; no overnight rain; wind 1 SW. Mild with 7 days >10°C in last ten days.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Third year & older males	Third year & older females
0	3	1	2	0	1	0
1-5	0	0	0	0	0	0
6-10	1	0	0	1	0	2
11-15	3	0	0		2	0
16-20		1	0		1	1
21-25			1			
26-30						
31-35						
36-40						
40-45						
46-50						
Over 50						

Table 14 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Cinderford 6th December 1998
Dursley the previous day: maximum temperature = 1.9 °C; minimum temperature = -4.6 °C; no overnight rain; wind 1 NW. Mean maximum temperature 7 °C, with 3 days >10 °C in the last ten days.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Third year & older males	Third year & older females
0	4	10	4	4	9	0
1-5	3	0	2	1	5	2
6-10	1	1	1	0	4	0
11-15	0		1	1	0	1
16-20	0		0	0	1	
21-25	0		0	0	2	
26-30	0		0	1	1	
31-35	0		0		0	
36-40	1		0		1	
40-45	0		0		0	
46-50	1		1		0	
Over 50					1 (51mg)	

Table 15 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Cinderford 12th December 1999
Dursley the previous day: maximum temperature = 10.7 °C; minimum temperature = 3.4 °C; no overnight rain; wind 4 NW. Five days >10 °C in the last ten days.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Third year & older males	Third year & older females
0	5	3	2	1		
1-5	1	3	0			
6-10	0	2	0			
11-15	0	0	0			
16-20	0	0	0			
21-25	0	1	0			
26-30	1	1	0			
31-35	2	0	0			
36-40		0	0			
40-45		2	0			
46-50			0			
Over 50			1 (57mg)			

Dropping masses and insects consumed at Cinderford

Tables 14 and 15 present data for two December dates, one in 1998 and the other in 1999. Although the samples were obtained in mid winter, they include some very high levels of DP by some first year, second year and mature male bats. In 1999 (table 15) foraging was probably helped again by the warm weather the day before, and in the previous ten days. There was no overnight rain before sampling took place. What is surprising is that the sample on 6th December 1998 (table 14) occurred after a very cold day, and a severe overnight frost. However, in the previous ten days, three exceeded 10 °C, and the mean temperature was 7 °C.

Figures 15 and 16 show the diet for both of these dates. Figure 15 was obtained using pellets from 32 different bats, four of which had no skeletal remains. Figure 16 involved 20 different bats, two of which had no skeletal remains. The same four prey items are represented in both dietary analyses. However, the 6th December sample contained a significant *Aphodius* dung beetle component. This was missing from the sample on 12th December. The dominant prey item in both samples is the *Geotrupes* dung beetle. No samples for any of the sites above showed similar levels.

Dropping masses and insects consumed at Symonds Yat

Table 16 presents data for one February date in 1999. This is the only data available for this site, as I do not usually visit it. Although the sample was obtained in late winter, as at Cinderford, it also includes some fairly high levels of DP. However, they are only shown by mature male bats. There was no overnight rain before sampling took place, but it followed a cool day, and a slight overnight frost. However, in the previous ten days, six exceeded 10 °C.

Figure 17 summarises the dietary analyses carried out on 10 pellets from different bats. As at Cinderford in December, the diet was dominated by *Geotrupes* dung beetles. Only two other prey items were represented, *Ophion* wasps and moths.

Table 16 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Symonds Yat 23rd February 1999
Dursley the previous day: maximum temperature = 7.7 °C; minimum temperature = -0.8 °C; no overnight rain; wind 3 NW. Six of the last 10 days >10 °C.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Third year & older males	Third year & older females
0	2	2	4	4	0	
1-5	1		0	1	0	
6-10			1	1	1	
11-15			1		1	
16-20					0	
21-25					2	
26-30					0	
31-35					1	
36-40						
40-45						
46-50						
Over 50						

Dropping masses and insects consumed at Combe Down

Despite annual visits in early January over many recent winters, and the capture of from 20 to 46 bats on each visit, no significant dropping levels have been recorded from the bags used to hold them. Of the few pellets (8) obtained, all contained no skeletal remains.

It is possible that early January is a time of winter when no prey items are available, even under favourable climatic conditions for foraging. Certainly the Woodchester data (figure 5) shows some of the lowest dropping collection levels at that time. However, the data for Cinderford in mid December, when Woodchester data is also very low, suggests that this is unlikely to be true at all sites.

Discussion

Of the six sites studied within a 50km radius of Bristol, only five produced usable data. Three of these sites showed dietary prey items which closely matched those recorded at Woodchester over the entire two winter period. At Cheddar and Mells, seven of the eight Woodchester prey items were recorded on a single date in October. These dropping samples were obtained from large numbers of different bats, some of which generated large amounts of droppings.

At Winsley, there were only four prey items of any significance in a sample taken in late November. Apart from the dominance of *Ophion* wasps in the Winsley sample, the other prey were the same. Another set of samples taken there in March showed only three prey items, but these closely matched the data from Woodchester at that time of year.

The two sites within the Forest of Dean showed diets that were dominated by *Geotrupes* dung beetles (figures 15, 16 & 17). As their samples were taken in December and February, when these beetles either did not feature in the diet at other sites, or were at very low levels, this is a significant finding. Furthermore the dropping levels at Cinderford in December, included some of the highest of this study, only reached at other sites in October (compare tables 5, 9 & 10 with 14 & 15). As this situation was repeated in two separate winters, it is likely to be a consistent feature

Since *Geotrupes* beetles are the only key prey flying in winter (Ransome 1996), we can conclude that foraging conditions for these bats within the Forest of Dean, a cSAC, are superior to those at all other sites studied. Conditions for winter foraging at Combe Down, Bath, seem to be the poorest. If this is true, it may partly account for the poor body condition of bats found there in mid winter, and the dwindling population (Ransome 1997c).

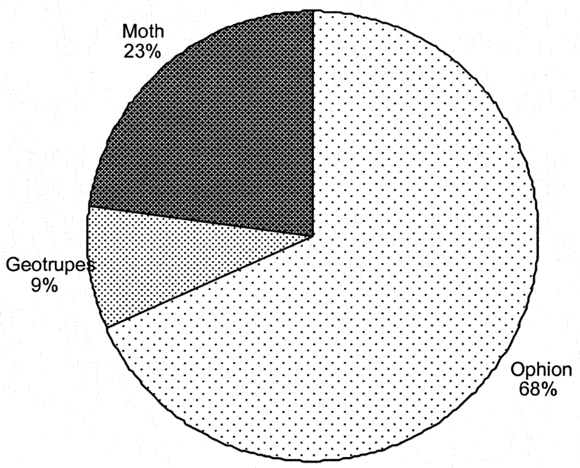

Figure 14 % Prey items eaten by Winsley bats 16-3-98

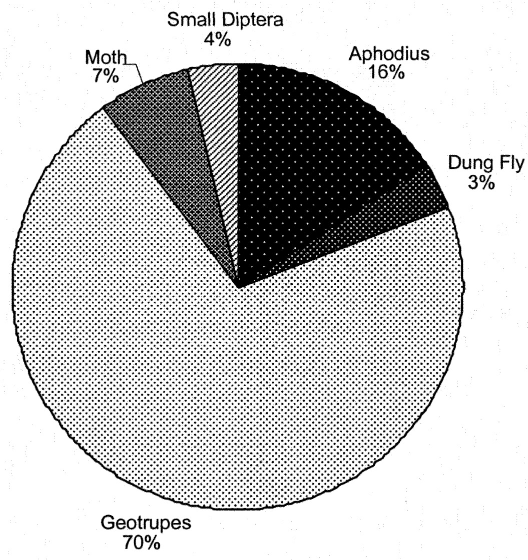

Figure 15 % Prey items eaten by Cinderford bats 6-12-98

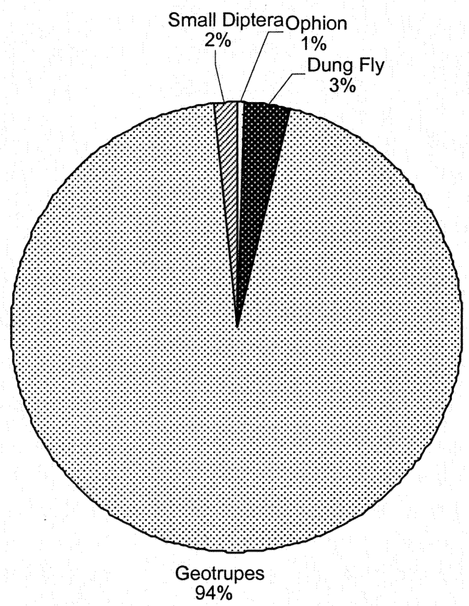

Figure 16 % Prey items eaten by Cinderford bats 12-12-99

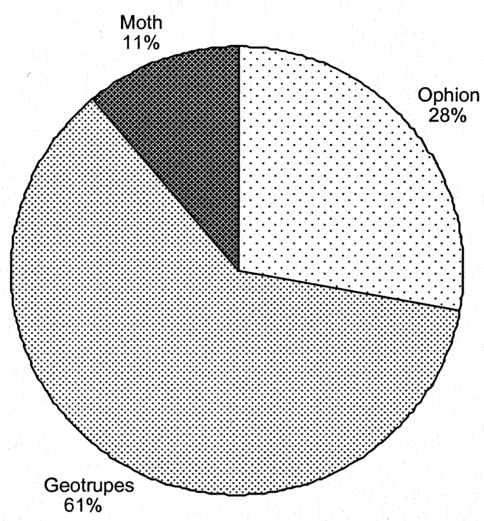

Figure 17 % Prey items eaten by Symonds Yat bats 23-2-99

Table 17 Chi-square tests comparing various age and sex groups dropping production during October and November. Most data are from Cheddar.
P values marked with an * are significant; those with ** are highly significant.

Age and sex groups compared	Degrees of freedom	Chi-square	P value	No. cells with estimates below 5.0	Age /sex with significantly higher levels
First year males & First year females	4	6.469	0.167	0 of 10	N.S.
Second year males & Second year females	4	8.032	0.090	6 of 10	N.S.
First year males & Third year males	3	15.009	0.002**	3 of 8	First year males
First year females & Third year males	3	9.710	0.021*	2 of 8	First year females
First year males & Second year males	5	11.583	0.041*	3 of 12	First year males

Table 18 Chi-square tests comparing various age and sex groups dropping production in October/November with April. Most data are from Cheddar.
P values marked with an * are significant; those with ** are highly significant.

Age and sex group compared	Degrees of freedom	Chi-square	P value	No.cells with estimates below 5.0	Age/ sex with significantly higher levels
First year males	4	34.194	0.000**	3 of 10	October & November data
First year females	4	32.861	0.000**	5 of 10	October & November
Second year males	3	13.030	0.005**	2 of 8	October & November
Third year males	3	9.298	0.026*	4 of 8	April

Table 19 Chi-square tests comparing various age and sex groups dropping production during April. Most data are from Cheddar.
P values marked with an * are significant; those with ** are highly significant.

Age and sex groups compared	Degrees of freedom	Chi-square	P value	No.cells with estimates below 5.0	Age/ sex with significantly higher levels
First year males & First year females	3	3.634	0.162	2 of 6	N.S.
Second year males & Second year females	2	5.148	0.023*	0 of 4	Second year males
First year males & Third year males	3	25.44	0.000**	2 of 6	Third year males
First year females & Third year males	3	27.278	0.000**	2 of 6	Third year males
Second year males & Third year males	3	10.422	0.015*	2 of 6	Third year males

Part 4: Synthesis of winter diet studies

Introduction

Greater horseshoe bats have been shown to be capable of producing similar amounts of winter droppings at the same period of the winter, and consuming a relatively small number of the same prey items, at several sites. This section reviews all of the data obtained, and attempts to integrate the findings of this study into the general ecology of the species, especially aspects relating to population regulation.

Amounts of droppings produced by winter period at Woodchester

Changes in the levels of droppings collected beneath clusters of bats are influenced by both the numbers of bats present, and the feeding success levels those bats have experienced. Neither of these conditions is known using the current methods. However, the data presented in part 2 provide a reliable picture of the prey items in the diet throughout hibernation, under a consistent protocol. The similarities shown in the two winters suggest an annually repeated pattern obtains.

Bats may vacate the Woodchester breeding attic, despite the presence of a warm incubator system, if their other needs are better served by occupying another roost. Two key aspects to be considered are proximity to suitable food supplies, and the availability of suitable conditions for hibernation. Woodchester Mansion is situated 135m above sea level, within a steep-sided valley. It experiences a more severe climate than the south-facing slopes of Minchinhampton Common, nearby, where major hibernacula exist. Many of the Woodchester bats occupy them in mid winter (Ransome 1968). We cannot, therefore, easily interpret the causes of the presence or absence of bats from the maternity roost.

Which bats feed in winter?

Dropping production by a torpid bat, provoked to arouse, is evidence of successful foraging after the bats previous arousal (see above). In autumn, arousals are very frequent averaging every two to four days (Saint-Girons, Brosset and Saint-Girons 1969). In mid winter the previous arousal may have been up to 12 days before it was caught (Park, Jones and Ransome 2000). In spring, it is again likely to be only a few days earlier (Ransome 1971).

Tables 4 to 16 show that all age groups and both sexes may feed and generate droppings during the winter at one time or another. Data for mature females is quite sparse, as they generally are not found hibernating with other age groups (Ransome 1968). However, Ransome (1995) showed that early breeding females, which gave birth to their first young much later than older breeding females, had lower body condition in the following October than in their previous October. They subsequently suffered higher mortality than non-breeding immature female bats of the same age. They may therefore have a need to feed significantly later in winter as well.

Tables 17 to 19 show the results of chi-square analyses comparing dropping production data for various age and sex groups, other than mature females. In order to carry out these analyses, the bats were grouped into 10mg classes, rather than the 5mg used in tables 4 to 16.

This was necessary to achieve larger numbers in each size class. Chi-square tests become unreliable if a significant proportion of cells contain less than 5.

Table 17 shows that, in autumn, there were no significant differences between production by the sexes in either first or second year bats. However, they did exist between both first year sex groups and mature males, and also between first year males, and second year males. The first year bats produced the highest levels of droppings, and the mature males the least. Second year male bats were intermediate.

Table 18 compares data between autumn and April production by specific age and sex group. In the first year bats of both sexes, and also in second year males, production is highly significantly greater in autumn, than in April. The situation is reversed in the mature males, which produce higher levels in April.

Table 19 compares data from different age and sex groups in April. As in autumn, there are no significant differences between data from first year males and females. However, such differences do occur between second year males and females. The most significant differences occur between the mature males and both first year sexes, with the mature males producing more droppings. They also produce more than the second year males.

First year bats are the last to leave the maternity roosts and enter hibernacula, and they are usually the last to deposit their body fat reserves, apart from the mature males (Ransome 1990), and young females giving birth late in the summer (Ransome 1995). Mature males usually have the lowest body reserves, as they are actively mating at or around that time (Ransome 1990, table 6.9), and may preferentially devote less time to foraging. Later in the winter they have to feed to compensate for their low reserves, and so show some of the highest levels of DP (see tables 7, 8, 11, 12, 13, 14 and 16). These data further confirm the evidence put forward by Ransome (1968), that mature males are the most effective at regulating their body weight (mass) losses during mild winter weather periods. Their effectiveness probably derives more from their increased motivation, rather than from a superior capacity to feed effectively in winter, compared with other age and sex groups.

If prolonged cold spells occur, it is the mature males and young first-time breeding females that are most likely to die from starvation in late winter, rather than older mature females. The numbers of mature males show significant falls in hibernacula after a series of cold winters, which are linked to late birth timing (Ransome 1989). The ratio of the number of bats emerging to forage at dusk in July (=NBFD) to the number of young born at a maternity roost is primarily influenced by the number of mature male bats present (Ransome 1997a). This ratio also falls after severe cold winter weather, and prolonged cold springs. These delay births and also alter the birth sex ratio in favour of males (Ransome and McOwat 1994). Importantly the Littledean Hall colony, whose major type 1 hibernaculum is in a very favourable winter-foraging location, showed the highest ratio of all 8 colonies studied by Ransome (1997a). In contrast, Woodchester's ratio was the lowest (closely followed by Iford), despite the short distance between the two maternity roosts, and therefore similar climates. Population recovery since the last crash after 1986 has been faster at Littledean Hall, than at Woodchester. Superior winter feeding conditions within the Forest of Dean is a likely major contributory factor to these differences.

How much do bats eat in winter?

Captive single bats fed various amounts of mealworms egested most of their faeces derived from the meal before becoming torpid (Ransome 1978). However, on their next arousal they egested further pellets. About 7% of the total faeces egested were retained through the first torpidity period, irrespective of the amounts eaten. The more food that was eaten, the greater the amount of droppings produced. If provided with no further food, the following arousal generated no more pellets.

On the assumption that these circumstances operate with wild animals in the field, we can calculate from the 7% figure, an approximate total estimated dropping production (EDRPS – as in Ransome 1997b). The dry faecal production from a bat handled in the field multiplied by 14.3 (100/7), is the EDRPS.

For a bat producing 5mg of dry droppings EDRPS is 71.5mg; for one producing 20mg it is 286mg; for one producing 30mg it is 429mg, and for one producing 60mg it is 858mg.

In summer EDRPS, obtained as described in Jones, Duvergé and Ransome (1995), is about 250mg dry faeces for bats which are experiencing only maintenance energetic demands, rising to about 460mg in lactating females, and even to 950mg in certain individuals on a specific day (Ransome 1997b). No assessment of the dietary content of these faecal samples has yet been made, although this may be an important factor influencing dry mass. For instance, for every 20g of mealworm larvae eaten, one gram of dry faeces result (pers. obs.), whereas for adult beetles, it is closer to 2g. Possibly adjustments will need to be made between bats eating moths, and those eating dung beetles.

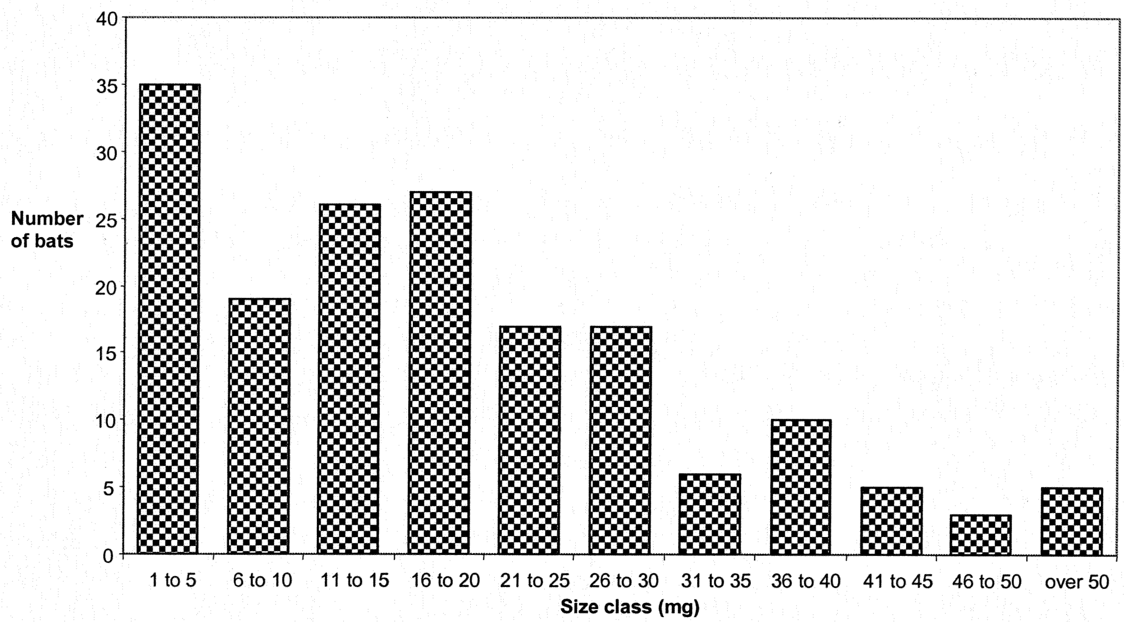

Figure 18 Frequency distribution of dropping production by torpid bats

Tables 4 to 16, and figure 18, show that it is relatively rare for winter bats to produce more than 30mg of dry droppings. The modal class of the frequency distribution for all data combined in the tables (excluding bats that produced no droppings) is 16-20mg, if the 0-5mg class is also omitted. The latter class includes many droppings that have no skeletal remains. Of the 170 samples obtained, 141 (83%) are at or below the 30mg figure. If the calculations are reliable, they suggest that, in winter, most bats eat the amount of insect prey that generates about 250mg of faeces. However, up to about 430 mg is a fairly common level. Exceptionally about 860mg may occur, but only normally in October and November, when fat deposition is occurring (except for the Forest of Dean sites). These estimates show surprising agreement with summer data, and suggest that bats may eat the same quantities of food in winter as they do in summer. It is the frequency of successful feeding, that seems to be the major difference between winter and summer, in this species.

Whatever the accuracy of these estimates in relation to what bats actually consume during a single winter feeding bout, it is clear that these bats are not merely making feeble efforts to eat anything in a desperate effort to avoid starvation. They may consume substantial amounts of prey, which may consist of only one, or a few types, suggesting that prey is strongly selected, as in summer.

Dietary changes by winter period at Woodchester and among sites

Many of the pellets analysed contained only a single prey type. Jones (1990) and Ransome (1997a) found that eight prey items featured in the summer diet of this species (late April to the first week of October). Apart from the cockchafer, *Melolontha melolontha*, the other seven prey items also feature in the winter diet. However, the two dominant prey items in winter are *Ophion* wasps and *Geotrupes* beetles, instead of moths and *Aphodius* dung beetles that are eaten in summer.

Figures 6 and 7 show that seven or eight types of prey were consumed by bats at Woodchester in the two years of continuous winter study. Figures 8 and 9 summarise the changes occurring from October to early April. Early in each winter, about four prey items were eaten, with first *Aphodius* dung beetles and next *Scatophaga* dung flies dominant. *Geotrupes* dung beetles, small Diptera and moths also occurred. In mid winter the diet was almost exclusively *Ophion* wasps. In late winter moths, dung flies and *Geotrupes* beetles reappeared in the diet, with small amounts of Trichoptera and Tipulids.

Habitat types producing high levels of winter prey

The state of the external habitat around a winter roost must be a crucial factor to hibernating bats that are experiencing body reserve shortages. As discussed above, first year bats of both sexes in October and November, and mature males throughout the winter, have the greatest need to feed. Individuals of other age and sex groups may also need to feed.

The habitat determines the types of insects that are potentially available to bats. Two major factors influence their actual availability as prey. Firstly the climatic temperature at the time when both the bats and insects fly (normally dusk). Secondly the population level of the insect. The habitat affects the population levels of insects, and also the potential of bats to utilise them as a food supply. Greater horseshoe bats have been shown to hunt mainly by hawking and perch-feeding (Jones and Rayner 1989). They are highly conservative foragers, which select a habitat structured with key linear features (Jones, Duvergé and Ransome 1995). The phenology of each insect determines the time of year when it becomes available.

Of the eight prey items identified in winter, three are dependent upon the dung of grazing animals, especially cattle. They are the *Geotrupes* beetle, the *Aphodius* beetle and the *Scatophaga stercoraria* dung fly. *Geotrupes* and *Aphodius* beetles were classified as key prey species by Ransome (1996). The latter is only important in October, but seems to contribute crucially to fat deposition at that time. Dung flies become important as *Aphodius* beetle consumption falls, presumably as their populations decline. They may only be eaten in the absence of sufficient *Geotrupes* beetles, as secondary prey.

There are three widespread and common species of *Geotrupes* beetles. The only autumn flying species is *G. spiniger*, a 16 to 25mm beetle which can weigh up to 1g wet mass. It flies from August to late December, preferring the dung of cattle in semi-shaded areas, such as sparse woodland, or field edges near substantial hedgerows. Up to 44% of cow pats may be invaded by a maximum of 2 adults, which lay from 4 to 6 eggs in brood chambers some 30cm below the soil surface.

There are two widespread and common spring flying species of *Geotrupes* beetles, *G. stercorosus* and *G. stercorarius*. The former will utilise a wide range of dung, including cow, horse, sheep, deer and even human. It prefers forested habitats. It is slightly smaller than the other two species, but is still a large beetle (13 to 17mm long). *G. stercorarius* prefers the dung of horse and cattle. Both fly from February to May.

Since bats in the two Forest of Dean sites ate very high proportions of *Geotrupes* beetles in both December and February, populations of the genus must have been substantial at those times. Published literature suggests that their populations should have been in steep decline in December, and only just emerging in February. This suggests that conditions for these beetles are excellent, if not optimal for their life cycles. At other sites, dietary samples were obtained in October, November and April. All of these months are well within the anticipated peak periods for the autumn and spring populations. Despite this, *Geotrupes* levels were either low, or absent from the samples. This suggests that it is the management and/or density of the grazers, not only their presence or absence, which is important.

The major difference between the habitats around the two Forest of Dean roosts, and the others, seems to be the existence of large numbers of free-range sheep throughout the year. At other sites grazers, which are kept in open fields in summer, are often removed in winter. They may be kept within buildings where they are fed indoors, rather than out in woodland. Since they are kept on deep litter systems, this practice is predicted to seriously reduce the populations of these beetles, by starving them of access to fresh cow pats on pastures.

The most important other prey item in winter is the parasitic *Ophion* wasp. *Ophion* wasps form a complex of some 17 species. Some occur in almost all months throughout the year, with the exception of late December and early January. Though small (about 35mg wet mass), they occur in dense swarms that hang close above the ground, especially within deciduous woodland, at night. Winter species seem to have a particularly low temperature threshold for flight, and so they remain active, and available to bats, under conditions few other insects can tolerate. Females search out the larvae of caterpillars, thought to be mainly of noctuid moths, in which to lay their eggs.

The only way of stimulating the populations of these wasps is by encouraging the moths whose caterpillars they parasitise. They include those of common noctuid moths, such as the yellow underwing, *Noctua pronuba*. Its caterpillars are subterranean, and emerge from the soil to feed on low plants at dusk. They carry on feeding until mid winter, before diapausing for until spring (March), when they continue feeding. They pupate in May in underground cocoons.

Whichever insect prey are being preyed upon, it is important for bats to be able to emerge to feed at dusk as soon as it is dark enough. Insect densities usually peak at, or just before dusk, and as temperatures fall rapidly afterwards, the earlier bats are able to forage the better their chances of success. These bats are predator sensitive (Jones and Rydell 1994), and their emergence behaviour involves balancing the risks of predation against those of starvation (Duvergé,*et al* 1999). Cover provided at the entrance to winter roosts, either by overhanging cliffs, or trees, especially those with evergreen vegetation, may be an important habitat consideration. In addition, such sheltered cover may enable winter foraging to be successful in mild winter spells, when windy and wet conditions often occur. Ransome (1997b) showed that such conditions in summer, often significantly reduce food consumption.

Discussion

The evidence presented shows that bats at all of the sites produce quite similar levels of dropping production for the same age and sex groups, at the same time of year, with the possible, exception of Combe Down. Apart from this site, most others show a similar range of prey items to those recorded at Woodchester Mansion over the whole of two winters. This suggests that even single-date samples in late October or early November can be of value in determining the diet of these bats, especially if a large sample of bats can be caught. Only the late December to late January period may be unprofitable for this.

The two sites within the Forest of Dean, at Cinderford and Symonds Yat, are exceptional in the very high levels of the large *Geotrupes* beetles consumed, as well as the high levels of dropping production in months previously regarded as unlikely to be profitable for feeding. At other sites *Geotrupes* consumption was either low, or very low, even at more favourable times of the winter with regard to the beetle's phenology.

Changes in agricultural grazing regimes over the past 30 to 40 years must have adversely affected the populations of *Geotrupes* beetles over a wide area, especially around roosts affected by urbanisation. Minchinhampton Common was permanently grazed by many free-ranging cattle in the late 1950s and early 1960s, as was Woodchester Park. *Geotrupes* beetle remains were commonly found at feeding perches near the entrances to the disused mines at Minchinhampton in October, and the tunnels at Woodchester. The mines beneath Minchinhampton were occupied by a population of over 100 greater horseshoe bats at that time (Ransome 1968). Over the past 20 years, not a single beetle fragment has been found beneath the same perches, and the numbers of bats using these mines has fallen to between 20 and 30. In contrast, the numbers of bats occupying the Cinderford scowle has recently reached 85. Each winter, several bats born at Woodchester the previous summer, have travelled to Cinderford to hibernate. In contrast, no Littledean Hall-born bat has crossed the river Severn to hibernate in any of the Minchinhampton mines over a four-year period.

It appears that, in the absence of sufficient levels of *Geotrupes,* the only key prey available during winter, bats at Woodchester and Minchinhampton have been forced to feed on various secondary prey. The major common winter insect group consists of wasps of the genus *Ophion*. They are much smaller insects, that are common in woodland, especially deciduous ones, which support the noctuid moth caterpillars that these wasps parasitise.

Two periods have been identified as important feeding times. For first year bats it is the October/November period when they move into key, type 1 hibernacula (Ransome 1991), for the winter. A rich food supply, with abundant *Geotrupes* beetles in the immediate foraging area, may be a crucial factor in the selection of a specific site at that time. Later in the winter, adult male bats need to have access to good foraging areas, in order to compensate for low reserves in October and November, when mating activities are expensive. They move into type 1, or type 2 hibernacula, leading to the formation of large clusters.

There was no prolonged period of sub-zero temperatures in either of the two winters of the present study, which might have produced a clear correlation with dropping production. In the winter of 1962/3, however, deep snow covered lowland southern England from late December until mid February. It prevented all winter feeding at that time, and produced smooth, steep rates of weight loss in all sex and age groups of bats (Ransome 1968). The following three winters also had prolonged spells of cold weather. Birth-timing in the summers was delayed, and the bat populations fell dramatically over a wide region (Ransome and McOwat 1994). During these population crashes, adult males are particularly severely affected, for reasons that have only become clear through the present study. They show greater declines than the females (Ransome 1989).

In contrast, during the mild spell in February 1998, when substantial accumulations of droppings from *Ophion* consumption occurred, some mature female bats ejected their vaginal plugs onto the plastic sheeting with the droppings. Plug ejection normally occurs at, or after the time of conception (Matthews 1937). Other females delayed plug ejection until early April, a more normal time of year. That summer, births were very early, and as expected (Ransome 1989), the survival of young from that cohort has been very high so far. This suggests that the weather in February may be a crucial factor influencing bat populations, via foraging success at that time. McOwat and Andrews (1994) related birth-timing to February climate, and nearly obtained a significant relationship.

The opportunity of successful foraging during February has two main advantages. Firstly it allows mature males, which may be close to starvation if severe weather occurs in late autumn and mid-winter, to replenish their body reserves. Secondly, it may allow mature females to initiate pregnancy, and give birth earlier in the summer. If these deductions are correct, it is especially important to ensure that these bats have close access to high levels of both *Geotrupes* and *Ophion* populations around key hibernacula, during this month.

Part 5: Environmental prescriptions for land around key hibernacula

Introduction

This study has identified two periods when the availability of insect prey is a likely crucial factor influencing bat population levels and distribution. Firstly from September to November, when bats move into their hibernation sites, and most age and sex groups deposit their body reserves. Secondly from February to April/May, when bats with low body reserves, especially mature males, often need to feed to avoid starvation.

As the grazed permanent pasture/woodland ecosystem generates large populations of suitable prey items in both summer and winter, essentially the prescriptions for habitats around hibernacula are the same as for those around maternity roosts. It is particularly important that whatever land management changes are implemented, they include the structural features proposed by Ransome (1996).

Prescriptions around major winter roosts

1) The immediate area outside winter roost entrances should be sheltered by cliffs, with overhanging vegetation, or be within fairly dense woodland. Some evergreen trees nearby may be an advantage for shelter from predators and rainfall.

2) The habitat close to all type 1 hibernacula should have permanently grazed pastures within parkland, orchards or sparsely-wooded cover. Occasional evergreen, or ivy-covered trees may be an advantage for perching under cover from predatory birds, and heavy rainfall.

3) Grazing regimes should be established in early September, at a time of year when bats search for hibernation quarters, and continue for as long as possible. Ideally it should last until mid December. Cattle are preferred at this time.

4) In early February, grazing regimes should be continued with either cattle and/or sheep, until May. The choice should be made on the grounds of practicality, in relation to problems such as poaching damage, or potential worrying by dogs.

5) The chosen grazers should be kept at the maximum sustainable level determined by the available area of land. Supplementary feeding will almost certainly be required, but the chosen grazers must deposit their dung out in the pastures.

6) Grazers should be provided with shelter against severe weather conditions within open sheds which are adjacent to woodland edge, or tall hedges. If substantial, they will potentially provide night roosts for bats.

7) These measures should concentrate in the habitats immediately around hibernacula entrances, but be implemented at distances of up to 6 kilometres from the entrance of major hibernacula (Jones & Billington 2000), along south, or south-west facing slopes. However, if the only suitable topography is long and thin, these distances may need to

be increased. Slopes with sheltered situations, such as cliffs, quarries or steep-sided valleys should be included.

Prescriptions around male territorial roosts

Recent genetic studies have indicated the importance of genetic variability and breeding behaviour upon the survival of these bats (Rossiter *et al* 2000a, 2000b, 2001). Male territorial roosts, (= type 3 hibernacula of Ransome 1991), are key sites in these considerations. Hence the same prescriptions are recommended for male territorial roosts, which are also frequently occupied by groups of up to eight mature females. These females include many of the oldest ones from a colony. Hence although the numbers of bats using a given territory may be low, those present possess the genes of successful long-term survivors. Furthermore, there is accumulating evidence that the success of a matriline in a colony depends upon the survival of its oldest member.

The prescriptions for grazing regimes should be implemented at least from September to November, and again from February until May. However, the distance from the roost entrance for prescriptions can be significantly reduced. Only a radius of about one kilometre should be needed, if all parts are suitable for foraging, or two kilometres if significant areas are not. Duvergé (1996) found that territorial males travelled the shortest distance from their roost for foraging of any age and sex group.

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