ENGLISH NATURE

The management of greater horseshoe bat feeding areas to enhance population levels

No. 241 - English Nature Research Reports

CYNGOR CEFN GWLAD CYMRU
COUNTRYSIDE COUNCIL FOR WALES

working today
for nature tomorrow

English Nature Research Reports

Number 241

Species Recovery Programme

The management of greater horseshoe bat feeding areas to enhance population levels

R D Ransome

School of Biological Sciences
University of Bristol
Woodland Road
Bristol
BS8 1UG

A report to English Nature and the Countryside Council for Wales

ISSN 0967-876X

Contents

Summary

The objectives of this study were to:

1. describe the dietary range and population performance parameters of eight widely dispersed greater horseshoe bat populations in the UK;

2. to identify habitat differences between sites and, relate these to dietary differences and measurements of population performance;

3. to make recommendations for improvements to the management of land within the roost sustenance zone of each roost in the light of its dietary state.

The eight sites selected for this study are at the extreme northern edge of distribution for this species. Furthermore, as the year of the study (1996) was climatically severe in spring, it was likely to accentuate dietary and reproductive timing differences among sites. Two sites were in west Wales, and the remaining six were scattered throughout the west country of England. Sites varied in their height above sea level, proximity to the sea, surrounding habitat land-use, habitat topography, roost nature, mean birth timing and population level.

Two main population parameters were assessed by volunteers at each site. They were exit counts of numbers of bats flying out to forage at dusk (NBFD) on seventeen selected dates between April and October, and numbers of young left in the roost after exits by the adults Among sites studied, the number of exiting bats varied from 68 at Woodchester to 199 at Stackpole, and the number of young in the roost varied from 18 at Brixham to 75 at Iford. The number of young in the roost was used to estimate the total young born, and the mean birth date for each site. They varied from 22 at Brixham to 92 at Iford, and 13th July at Woodchester to 31st July at Brixham respectively, among the seven sites where it was possible to obtain reliable data. Two 'plateau' periods of exit count totals were noted, the first in late May and early June, and the second from mid July to mid August, as well as a brief peak in each of these two months. Ratios of NBFD: total young born provided estimates of the numbers of non-breeding bats present in each roost, and allowed the estimation of total colony size in August. These estimates varied from 92 at Brixham to 343 at Iford.

Dietary analysis showed that the same three key prey items, *Melolontha melolontha, Aphodius sp.* (Coleoptera; Scarabaeidae) and moths (Lepidoptera), dominate the diets of bats at all eight sites. Results confirm that this bat is both highly selective and conservative in its diet over a very wide region. The overall importance of these various key prey items, the timing of the appearance of each item, and the levels each reached over the study period varied significantly among sites. This was especially noticeable in spring.

The three secondary prey items consumed, tipulids (Diptera: Tipulidae), caddis flies (Trichoptera), and ichneumonids (Hymenoptera; Ichneumonidae) of the *Ophion luteus* complex, were also eaten at all sites. There were marked differences among sites in the proportions of each secondary prey item consumed, with substantial caddis fly consumption only occurring in either spring or autumn at roosts close to extensive river and lake habitats. Tipulids were eaten in greatest amounts at sites in coastal regions, where milder climates in spring and autumn probably favoured their flight activity. In contrast, ichneumonids were only

consumed in large amounts around inland roosts which were likely to experience frequent cold dawns in spring and autumn due to topographical features near the roost.

The availability of the preferred habitat types, (woodland, with grazed pastures) varied markedly among sites within the 3 km diameter roost sustenance zone suggested by Ransome (1996) following radio tracking study results obtained by Jones and Morton (1992) and Duvergé (in Jones et al 1995). However, stepdown multiple regression analysis of estimated colony size, number of young born and peak exit numbers against approximate % woodland, % pasture (both at 1 km and 3 km radius from the roosts), freshwater and urban rank orders, latitude, and topographical state, failed to detect significant relationships. The most significant combination obtained involved % woodland and % pasture at the 3 km range, together with topography ($p = 0.16$, NS). Larger colonies, with peak exit counts of 100 - 180 adults, and with more than 40 young, currently exist in habitats with a wide range of woodland and permanent pasture levels.

It is argued that these facts are partly explained by variations in the distances commuted by bats to regularly-used foraging areas from specific roosts. Foraging areas are known to be relatively fixed in their structural characteristics from several independent studies both in the UK and other regions of Europe, and are typically along the perimeters of grazed pastures and either woodland or tree-lines, including tall thick hedges. The shape of the RSZ, and therefore the commuting distances involved, may be adjusted in response to the presence of hostile habitats, such as the sea, urban or arable areas, and also in response to the densities of specific insects, especially those of key prey, by foraging bats. They appear to select foraging sites on topographical characteristics, as well as habitat structure, choosing slopes facing south or west.

The topography of the habitat within the RSZ, as well as the latitude of the site concerned, proximity to the sea, and height above sea level all affect micro climatic temperatures near roosts. Topography, however, probably has an important impact upon the timing of the availability of prey items in a local area. If both cold north and warm south-facing slopes occur close together in a region, any prey species with a short emergence period, such as *Melolontha melolontha,* should have its availability period extended in comparison to that of flat regions.

Over 80% of the observed variation in the mean birth timing among sites, in the same summer and therefore under the influence of a broadly similar climate, was explained by the percentage consumption of key prey items, together with percentage woodland at the 3 km range, in multiple regression analyses. More woodland and higher levels of key prey promote earlier births. Topography was also significant in single factor analyses, with steep-sided valleys superior to flat land in promoting earlier births. Key prey consumption, however, was the most important factor.

The percentage key prey items among sites may reflect differences in habitat quality at the foraging grounds. Habitat quality has two aspects, firstly its vegetation and land-management structure, and secondly its temperature micro climate. The latter seems to influence key prey availability in two ways, firstly by altering phenological timing, and secondly via its influence upon flight temperature thresholds. High quality structural habitat within the RSZ, in combination with favourable micro climate and roost conditions, together with short commuting distances to foraging areas, are predicted to promote earlier births and hence more successful survival rates for both the young and their mothers. Over significant periods of

time this should lead to a larger colony size. Conversely, the reverse circumstances are predicted to make a colony vulnerable to a severe population crash, following a single severe spring climate.

Recommendations for improvement to the management of land within the known or assumed RSZ of each site are given in detail in Parts 5 and 6. Overall these recommendations concentrate on the generation of high quality habitat, both structurally and thermally, within the 1 km young sustenance zone wherever feasible, to assist the growth and development of the young, and ensure their long-term survival potential, and that of their mothers. Essentially these recommendations add to those previously made (Ransome 1996), but the level of deciduous woodland is reduced to 40%, as this level permits the development of numerous strips or small blocks of woodland adjacent to cattle-grazed permanent pastures. Such habitats provide very high levels of woodland/pasture edge lines, the preferred foraging areas for this species. The 40% level replaces the previous recommendation for 50% deciduous woodland. Woodland strip development, adjacent to grazed pastures, should be encouraged on the south or west-facing slopes near roosts, if they occur.

Ideally radio-tracking studies should be carried out to determine the specific areas utilised as foraging areas by bats from specific roosts. They should then be safeguarded and improved as recommended. In the absence of such information, areas selected for improvement should concentrate on those with topographically suitable aspects, such as sheltered valleys with south or west-facing slopes as above.

In the absence of natural fresh-water habitats, the creation of wetland areas should be considered, and produced as close to the roost as possible, as an insurance against cold springs, or droughts in summer.

Introduction

Conservation of the remaining populations of the greater horseshoe bat in south-west England and west Wales (distribution shown by Mitchell-Jones 1995) initially concentrated on the protection of summer maternity roosts and winter hibernation sites. More recently attention has been focused upon the food resources around maternity roosts during the summer. The quality and quantity of food resources within favourably constructed foraging areas are believed to be crucial in sustaining large numbers of breeding female bats, especially during lactation. Successful growth and subsequent survival of the young are essential if a viable population is to be maintained at each maternity site.

In a previous study of several maternity roosts, diets were compared over limited periods of the summer, (Ransome 1996). It confirmed previous studies (eg Jones 1990) showing that greater horseshoe bats are highly selective in their diet, and also demonstrated that mothers and young usually eat quite different prey, when the young first start to forage for insects. Mothers normally feed on moths from June to late August, and their young feed upon *Aphodius* dung beetles when they start to forage, and continue to do so normally for several weeks afterwards. Poor weather, particularly low temperatures, can affect this dietary separation however. The young remain close to the roost during early foraging sessions, and so the provision of permanent cattle-grazed pasture adjacent to roosts was an important habitat recommendation.

At other times of the year adult bats feed on a variety of prey, but at any one time there is usually only one or two key prey items. Besides moths, they include the large *Geotrupes* sp. dung beetles in April, and the maybug, *Melolontha melolontha*, in May. If these are unavailable, the bats switch to secondary prey items, or mixtures of prey. Secondary prey include tipulid dipterans, trichopterans and ichneumonids. Other insects are occasionally taken, but are insignificant in the overall diet.

A review of the published life-histories and ecology of these insects by Ransome (1996) led to habitat recommendations likely to promote high concentrations of prey items around the roost within the normal foraging range of the bats. This range was called the roost sustenance zone (RSZ).

The current study develops the investigations carried out in the previous study, partly to complete some of its objectives which could not be fully realised, but also to investigate possible links between diet quality, habitat features and population parameters. The objectives for this study, which relate to sections of the report are as follows:

Objective 1

To describe the dietary range and population performance parameters of a range of greater horseshoe bat populations. (Parts 2 and 3).

Objective 2

To identify habitat differences between sites and relate these to measurements of population performance. (Parts 4 and 5).

Objective 3

To make site-specific recommendations for improvements to the management of land within the roost sustenance zone. (Part 6).

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

Introduction

The study was designed to answer the following questions:

1. Do large successful colonies show the same dietary content as small ones?

2. Do colonies show the same dietary content irrespective of their habitat structure and location, and hence likely insect availability differences?

3. Are mean birth timings the same at each breeding roost, and if not, are differences related to diet/habitat?

4. Do gross numbers of flying bats leaving to foraging at dusk show the same patterns of changes throughout the summer, and if not, are differences diet/habitat related?

5. Which of the population data provides the best overall estimate of population level?

6. Do the data support clear recommendations to enhance habitat around specific roost sites which are likely to promote population levels?

Methods

Originally eleven maternity roosts were selected as possible study sites because of their wide geographical spread, varied surrounding habitats and large population ranges. Two were eliminated as permission to obtain data was refused by the owner, and a third proved impossible to study due to logistical problems connected with the site. Hence eight sites were finally included in the study. Each of these sites was visited by experienced volunteers, with one person acting as co-ordinator at most sites.

List of sites involved in the study

- Slebech Park, south-west Wales
- Stackpole, south-west Wales
- Dean Hall, Gloucestershire, England
- Woodchester Park, Gloucestershire, England
- Brockley Hall, Somerset, England
- Iford, Somerset, England
- Mells, Somerset, England
- Berry Head Quarry, Brixham, Devon, England

Participants did not need to catch or handle bats in any way if they preferred not to do so. What was needed was a commitment to visit their roost and count the numbers of bats flying out on certain dates (all Sunday evenings) from late April to early October. After the adults had left, the roost was briefly entered to count the number of any juveniles born (using a red-light torch to minimise disturbance effects where necessary); and collect dropping samples from beneath the cluster using clean plastic bowls. The faecal samples and population data were then sent to the author for analysis.

Detailed methods and advice for carrying out these activities were provided to co-ordinators on separate sheets in an attempt to ensure uniformity of methodology.

The dates selected were:

a. April 21, April 28, May 5
b. May 26, June 2, June 9
c. June 30, July 7, July 14
d. July 28, August 4, August 11
e. August 25, September 1, September 8
f September 29, October 6

These dates covered:

a. early pregnancy;
b. mid pregnancy;
c. late pregnancy/early lactation;
d. mid lactation/late lactation;
e. late lactation/post lactation;
f. prehibernation.

Juvenile growth occurred between periods c. to e.

Summary: Each site involved a total of 17 visits, which generated 11 dropping samples covering the dietary changes from late April to early October. Ten of the samples were adjacent pairs, each of which allowed any short-term changes in dietary content to be determined. Comparison of the diet of a specific colony with habitat data from its RSZ and young sustenance zone (YSZ) should have allowed determination of the extent to which diet is adjusted to local habitat conditions.

This study was carried out concurrently with the collection of other detailed population parameters and juvenile growth data obtained from a two of the study sites. Together it may be possible to relate any dietary differences to juvenile growth performance and future survival success at these sites.

Part 2: Dietary range of the eight populations studied from April to October

Introduction

The justification for the methodology adopted for investigating dietary content is given in Ransome (1996). The use of faecal pellet analysis to determine the diets of insectivorous bats is a well-established and preferred procedure to other alternatives (Whitaker 1988). Ransome (1978) showed that the bulk of the faeces produced by greater horseshoe bats are voided into the roost, below the cluster, where samples may be collected.

Methods

Volunteers were asked to place clean bowls, lined with clean absorbent paper to remove urine, beneath the cluster on specific dates. The dates were synchronised at all sites. On the next date the faecal pellet samples were collected and air dried if necessary, before being stored in a labelled photographic film canister. After a batch had been collected, it was posted to the author for faecal analysis. If the pellets did not completely fill the canister, it was packed with paper tissues to prevent shaking about during transport. The use of clean bowls and clean absorbent paper eliminated the possibility of contamination of samples by previously produced pellets, and by drying the samples, disintegration or fusing of pellets was avoided.

Period of faeces collection beneath maternity clusters

The dates listed above in Part 1 demarked the weeks of collected samples in 1996. These were numbered from 1 to 11 as follows:

Week 1 was 21 April to 28 April.
Week 2 was 28 April to 5 May.

Week 3 was May 26 to June 2.
Week 4 was June 2 to June 9.

Week 5 was June 30 to July 7
Week 6 was July 7 to July 14

Week 7 was July 28 to August 4.
Week 8 was August 4 to August 11.

Week 9 was August 25 to September 1.
Week 10 was September 1 to September 8.

Week 11 was September 29 to October 6.

The selection of 11 specific weeks, requiring 17 visits for obtaining faecal pellet samples and counts, was to reduce the workload upon volunteers to the minimum thought necessary to obtain worthwhile comparable data on dietary range, and population parameters. It was also to reduce the numbers of pellets analysed to manageable levels. Had all 22 weeks of the

summer from 21st April to 6th October produced samples, some 2816 pellets would have needed analysis.

A significant drawback of using selected weeks from periods during the summer is that diet during the intervening weeks is unknown. Hence total dietary consumption data only refers to the study weeks, not to the entire summer's consumption. This makes comparisons with previously published data (e.g. Jones 1990, Ransome 1996) less valid.

Faecal analysis and slide preparation

Sixteen randomly-selected faecal pellets were analysed per sample, per week of the study. A total of 11 x 8 x 16 = 1408 pellets should have been analysed, had all of the samples been collected. However, the late cold spring in 1996 prevented the first week's sample from being collected at the two Welsh sites, and the last week's samples were also not collected from them. There were considerable difficulties in making collections at Brixham, where the bats used two underground sites erratically, and the cold weather caused them to shift elsewhere. Collections could not be made in weeks 4 and 5, and the sample from week 8 was converted to a mixed sludge by water dripping from the cave roof. The sludge was analysed to produce overall dietary volume estimates, but single-pellet analysis was impossible. These problems reduced the number of samples to 1312, and unfortunately complicated the statistical analyses and comparisons of the data across sites.

The material was treated precisely as in Ransome (1996) to produce permanent dry slides suitable for stereo binocular microscope examination and estimation of percentage volume in the diet (Whitaker 1988). Identification of skeletal remains as far as possible was also carried out as in Ransome (1996), mainly using Chinery (1973) and McAney et al (1991), except that the distinction between the volumes of *Aphodius sp.* 1 (= *A. rufipes*), and *Aphodius sp.* 2 (= *A. rufescens?*) was not feasible due to frequent overlap of the two species in the samples. They were therefore combined as *Aphodius sp.*, however, the bulk of the material belonged to *Aphodius rufipes*. Also no distinction between brown and black tipulid groups was made, as their separation was very onerous, and provided no useful data.

Data were statistically compared, one prey item at a time, among all sites for each week of the study separately. The % volume data for each prey item per sample did not distribute normally, but followed a poisson distribution. Each datum was therefor arcsine transformed to normalise the data (Whitaker 1988), before carrying out a oneway analysis of variance test on the arcsine means for all sites. If the oneway multiple ANOVA test showed significant differences occurred between some of the means, Tukey's pairwise comparisons were carried out at a family error rate of 0.05 probability. Tukey's test is very robust, and copes well with deviations form normality, as long as variance is not too dissimilar (Zar 1984). The chosen family error rate of 0.05, is quite severe, and means that any significant differences shown between sites are very likely to be real. Conversely, Tukey tests at this family error rate level sometimes fail to distinguish significant differences between sites, which are shown by oneway ANOVA to exist. Hence we cannot be confident that, because Tukey tests do not detect significant differences among sites in some weeks, they are necessarily the same.

Results

Figures 1(a) and figures 1(b) to 1(h) show summary pie diagrams for the total diets by volume, for weeks 2 to 10 inclusive, for mean data and for each of the seven sites respectively. Brixham could not be included since data were unavailable for two weeks of this period. Note that the absence of weeks 1 and 11 reduce the levels of both *Geotrupes* and *Aphodius* in the diets presented.

Table 1 shows the major differences between the total diets at each site. The level of each prey item over weeks 2 to 10 of the study period was compared with the mean for all 7 sites, and its standard deviation (s.d.), for each prey item separately. If the total level of a prey item was within 0.5 s.d. of the mean, it was ignored. If it was greater or less then 0.5 s.d. it was included in the table. Although this treatment is not a statistically acceptable procedure, it clearly indicates which prey are important overall at different sites, and helps in making multiple comparisons among the pie diagrams.

Dietary content by site and season

Key prey items

Figures 2(a) to 2(h) show diets for the eight sites by week of the study for each key prey item. These are the preferred prey as defined by Ransome (1996). Figures 3(a) to 3(h) show the same data for secondary prey (Ransome 1996). Note that some weeks are missing from 3 of the sites.

The total of key prey consumed at each site rises from low levels in weeks 1/2 to high levels by week 5, and involves the same prey items in sequence. However, the levels reached, and the timing of the occurrence of specific key prey items is very variable. The extremes are shown by Slebech (fig. 2(a)) and Iford (fig. 2(f)). Key prey form over 50% of the diet by week 2 at Iford, compared with 8% at Slebech. Also *Melolontha* consumption spanned weeks 1 to 4 (total span at least 7 weeks including the 3 weeks between samples) at Iford compared with weeks 3 to 5 (total span at least 6 weeks) at Slebech. Both the timing and levels of contribution of specific key prey items to diets at specific sites clearly vary among sites, even though the same items are consumed.

Consideration of figures 2(a) to 2(h) and tables 1 and 2 show that the same four key prey items occurred at seven of the sites, and only *Geotrupes* was missing from Brixham samples. *Geotrupes'* importance was probably underestimated as the various species fly mainly in late winter/spring, or in autumn/winter. However, the total amounts of the various key prey, their relative proportions, and the timing of their appearance and disappearance, was highly variable among sites. There are many factors which could influence the significant differences between the consumption levels of specific key prey shown by Tukey tests among sites during different weeks. Hence the details will be discussed in Part 5.

Table 1. Total prey dietary content differences from mean levels of total diet in 1996 by site. (Data from weeks 2 to 10 of the study only.)

Site	Prey mean +0.5 SD	Prey mean -0.5 SD
Dean Hall	(Geo.) Moth	Aphod. Trich.
Slebech	(Tip. Trich.)	(Moth Ichn.)
Woodchester	(Aphod. Ichn.) Moth	(Mel. Tip.)
Stackpole	(Tip.) Trich.	(Ichn.) Moth Aphod.
Brockley	(Aphod.) Mel. Ichn.	(Trich.)
Iford	(Moth) Ichn. Mel.	(Trich. Aphod.)
Mells	(Mel. Aphod. Ichn.)	(Tip.)

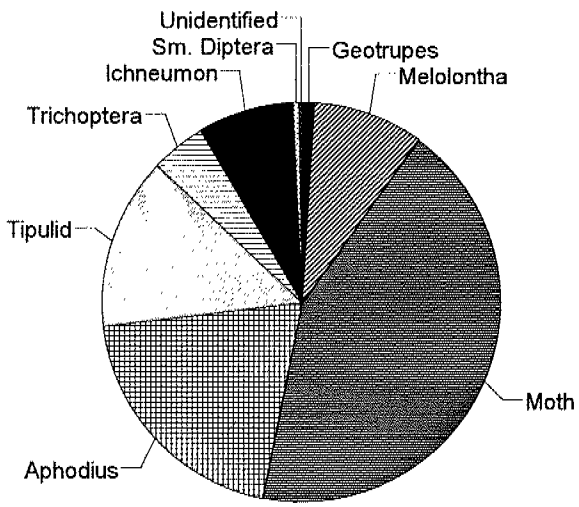
Key: Geo. = *Geotrupes* sp; Aphod. = *Aphodius* sp; Mel. = *Melolontha melolontha*; Trich. = Trichopterans; Tip. = Tipulids; Ichn. = ichneumonids. Prey in parentheses were recorded at levels of 1 standard deviation or greater from the mean for all 7 sites. Underlined prey items are key prey. No data presented from Brixham for reasons explained in the text.

Table 2. Tukey test results for dietary differences between sites for key prey items by week of the study

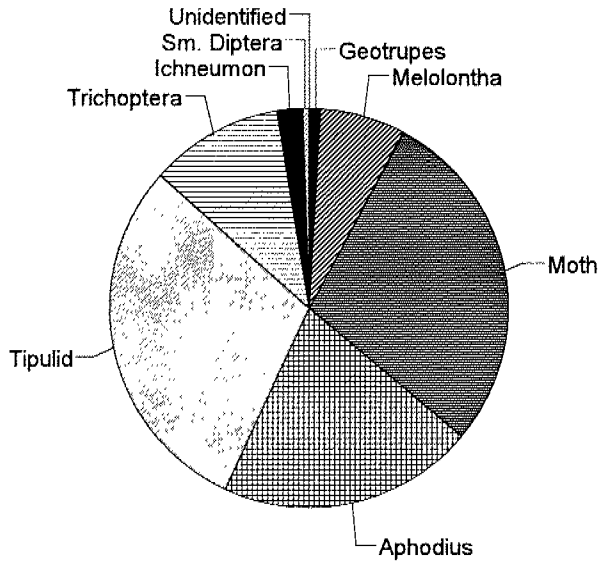
Week of key prey item study		Sites showing significant differences
1	*Geotrupes*	Wdch. > Mells & Brixh.
3	*Melolontha*	Mells > Wdch.
4	*Melolontha*	Mells > Wdch. DHall Iford & Slebech Stackpole > Wdch. & DHall
3	Moths	Wdch. > DHall Brock. Iford. Mells Stack. & Sleb. Brock. > DHall Stack. & Sleb.
4	Moths	Wdch. DHall & Iford > Mells Stack. & Sleb.
5	Moths	DHall Iford & Mells > Sleb.
6	Moths	no sign. diffs. detected (8 sites)
7	Moths	DHall > Brock. & Sleb. Iford Mells Brixh. & Stack. > Sleb.
8	Moths	no sign. diffs. detected (7 sites)
9	Moths	no sign. diffs. detected (8 sites)
7	*Aphodius*	no sign. diffs. detected (8 sites)
8	*Aphodius*	Wdch. Mells & Sleb.> Stack.
9	*Aphodius*	Mells & Stack. > Iford
10	*Aphodius*	no sig. diffs. detected (7 sites)
11	*Aphodius*	DHall & Mells > Wdch & Brixh.

KEY: Brock. = Brockley, Brixh. = Brixham, DHall = . Dean Hall, Sleb. = Slebech, Stack. = Stackpole, Wdch. = Woodchester.
NB Brixham data were absent from weeks 3 4 5 & 8. Stackpole and Slebech data were absent from week 11.

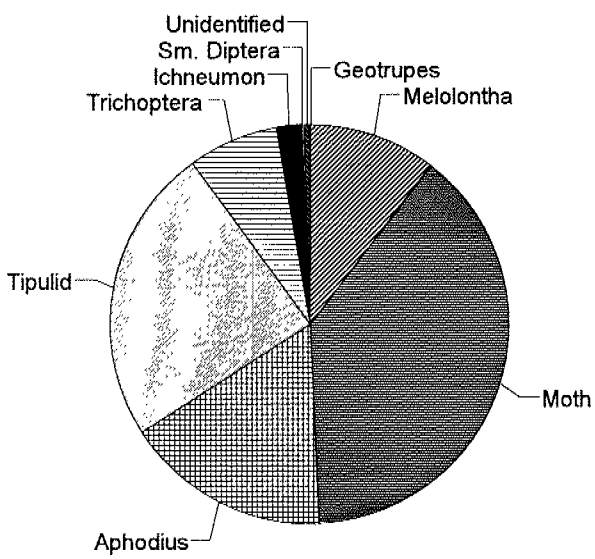
Fig 1 Total diet by volume



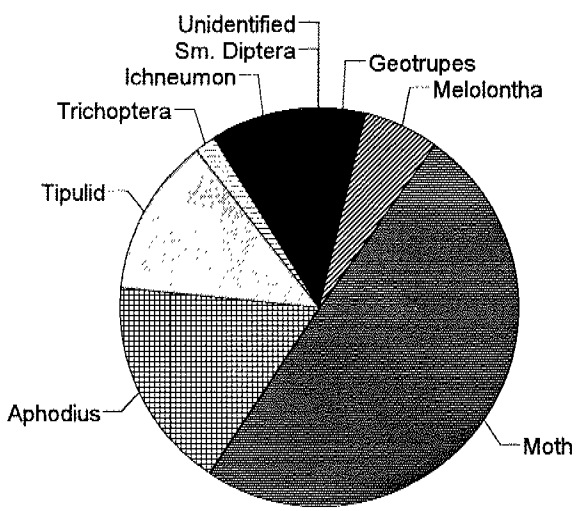
a) Mean total (7 sites)



b) Slebech

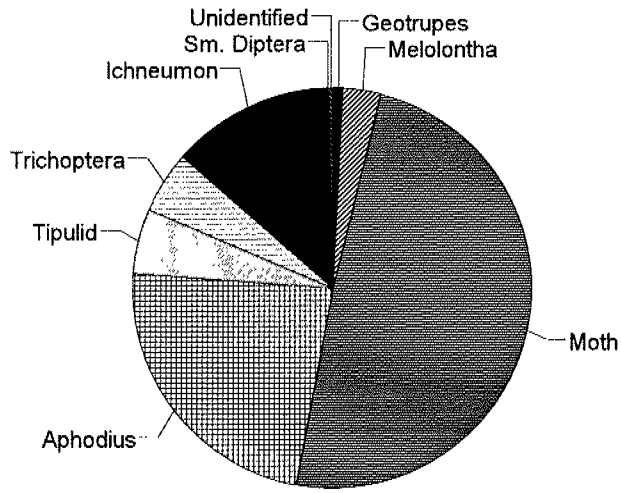


c) Stackpole

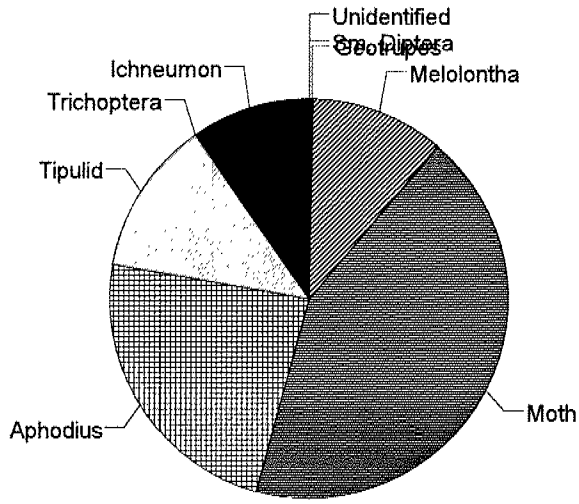


d) Dean Hall

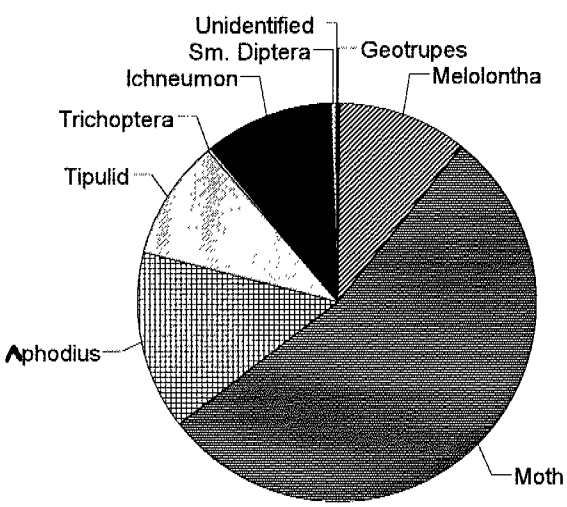
Fig 1 (continued)



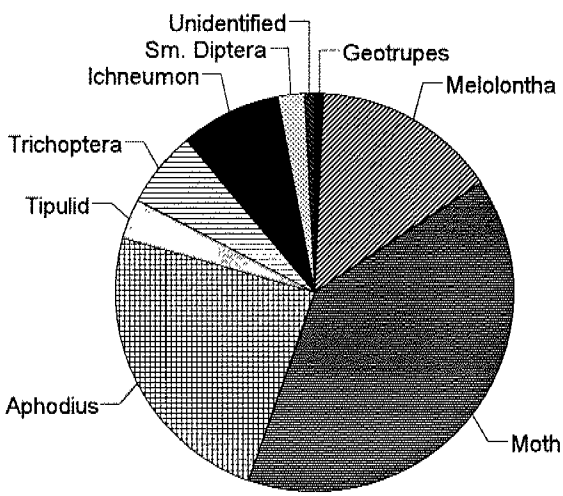
e) Woodchester



f) Brockley



g) Iford



h) Mells

Fig 2 Key prey species 1996

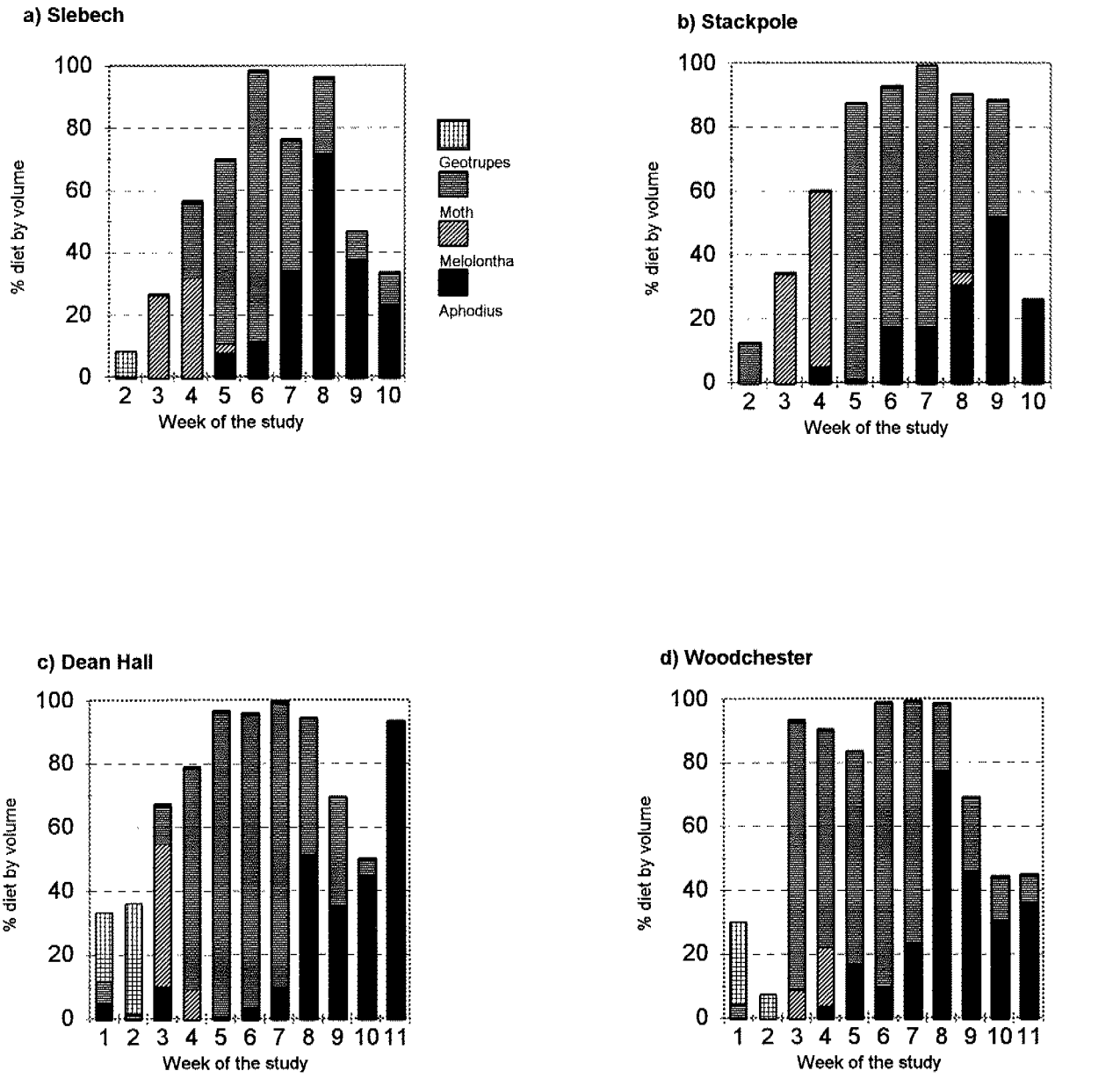
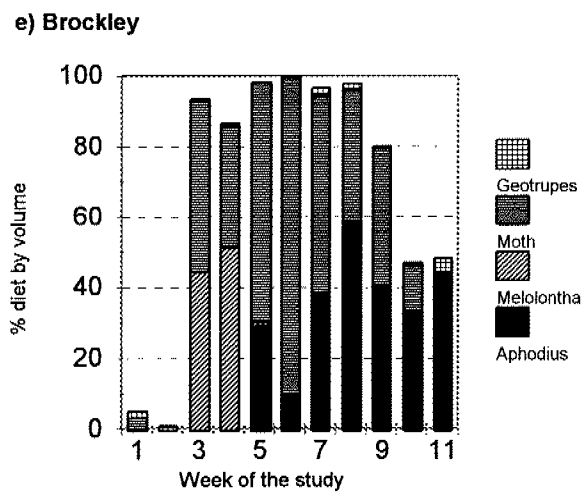
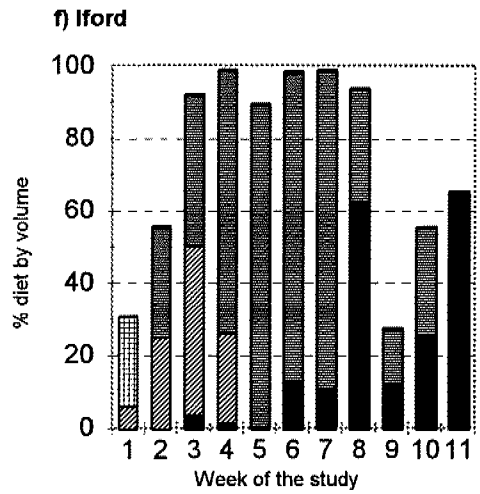
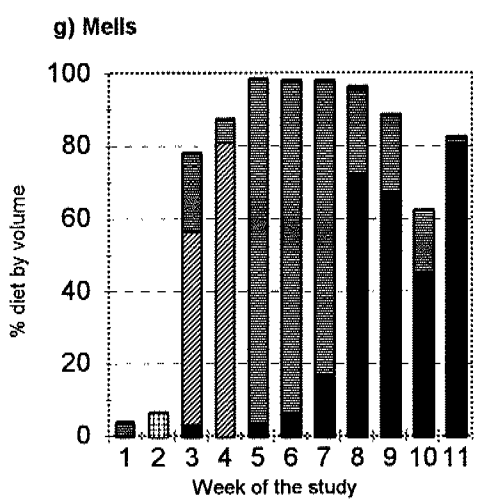


Fig 2 (continued)







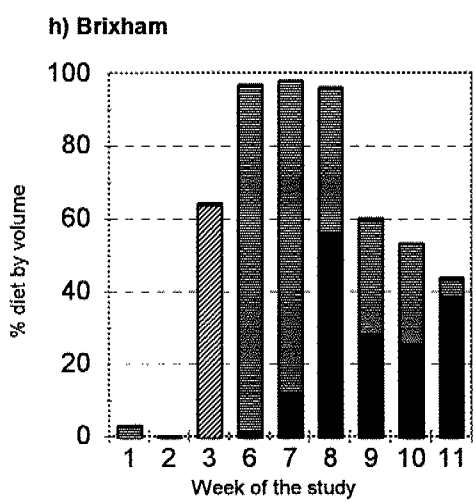


Fig 3 Secondary prey 1996

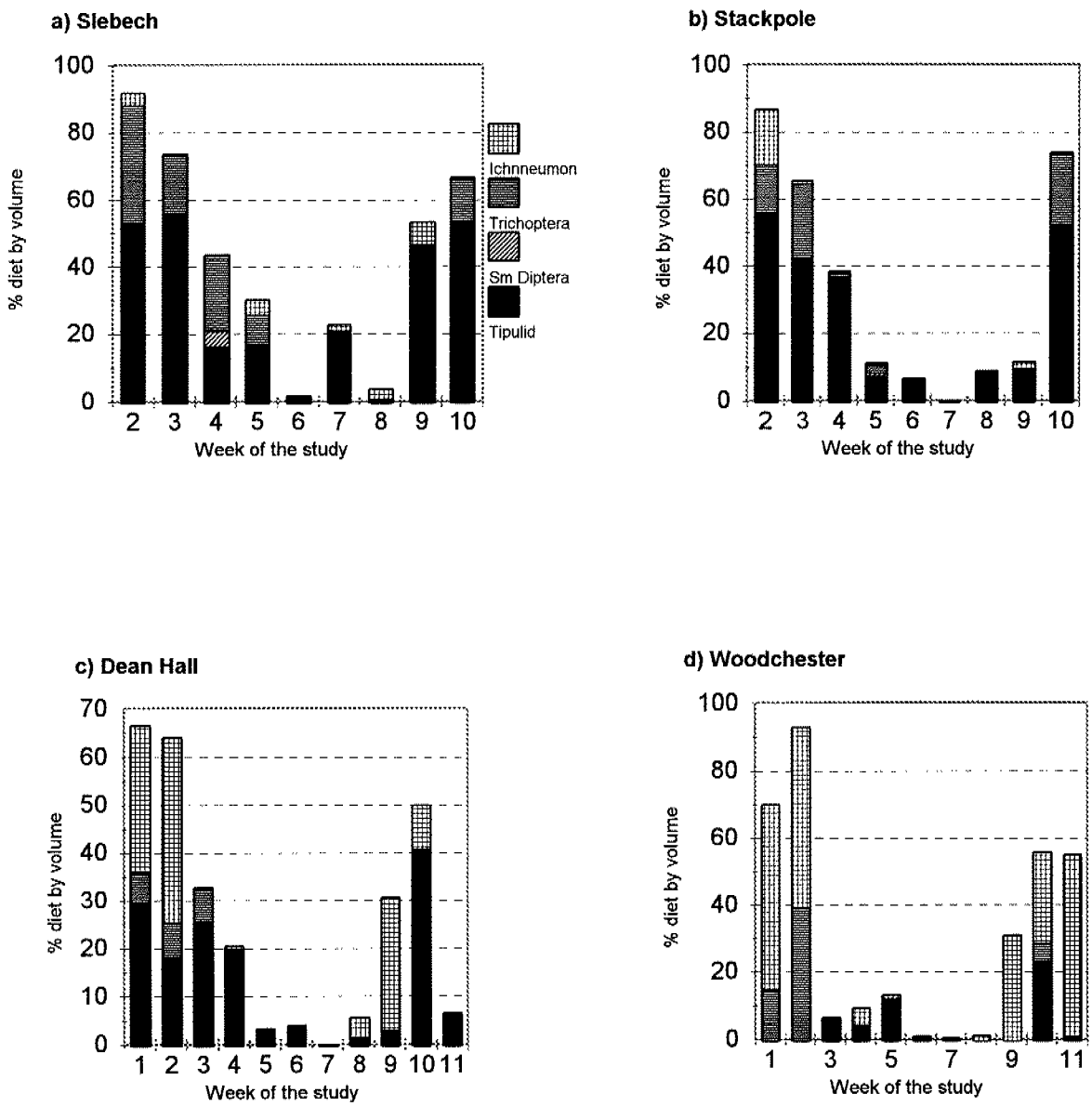
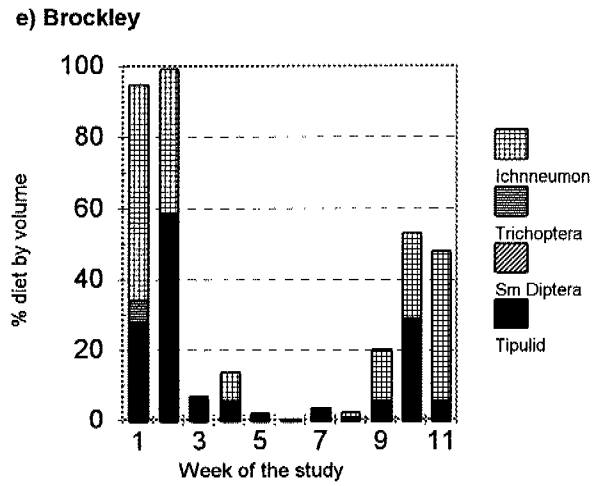
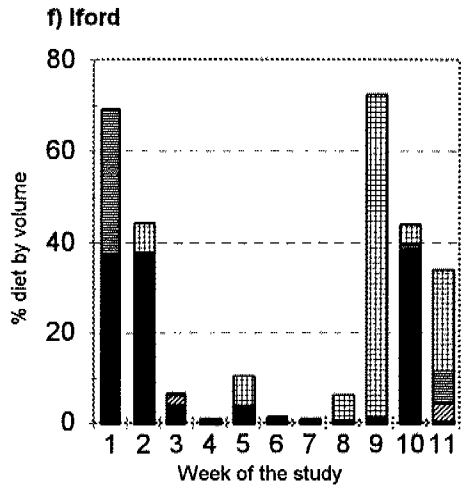
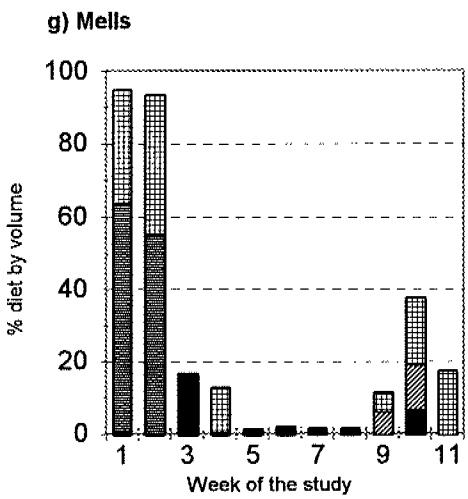
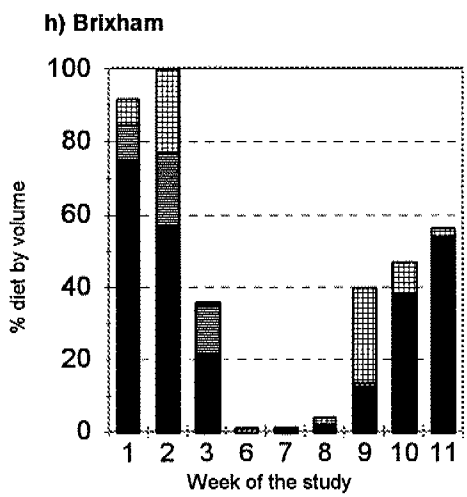


Fig 3 (continued)









Key prey level overall was highest at Iford, and Mells, and appeared earliest at Iford, Brockley and Woodchester, reaching 90% or above by week 3. It took until week 6 for the same level to be reached at Stackpole and Slebech. Slebech had the lowest total key prey levels at 56% of the total diet between weeks 2 and 10 inclusive. Iford and Mells had the highest levels at 79% each, closely followed by Brockley (78%), Dean Hall (77%) and Woodchester (76%). Stackpole showed an intermediate level at 66%. All figures are for the same period. Brixham could not be assessed due to missing data.

The importance of specific key prey varied markedly among sites. *Melolontha*, the largest scarabaeid beetle in Britain, was significantly higher in the diet at Mells (weeks 3 & 4) and Stackpole (week 4) than at Woodchester (weeks 3 & 4) and Dean Hall, Iford and Slebech (all week 4). Although *Melolontha* was not present at very high levels in the diet at Iford, it appeared very early (week 1) and continued in reasonable numbers over a long period (until week 4). This was a much longer period than at any other site. Overall Woodchester was lowest in dietary *Melolontha* levels.

In contrast, moths appeared at very high levels at both Woodchester and Brockley by week 3. The former site showed significantly higher moth levels than all other sites at that time, and Brockley was significantly higher than Dean Hall, Stackpole and Slebech. As time progressed, Dean Hall, Iford, and lastly Mells, showed significantly higher levels than Slebech until by week 6 all sites showed over 75% dietary levels of moths, and no significant differences among sites were detected by Tukey tests. Moth levels fell sharply at all sites between weeks 7 and 8, except for Slebech, where the decline occurred between weeks 6 and 7.

Aphodius levels increased by week 7, and reached high levels by week 8 at most sites, as juveniles started to seriously forage. However, levels were significantly higher at Slebech, Mells and Woodchester, compared with Stackpole (week 8). Mells and Stackpole levels were significantly higher than Iford in week 9. In weeks 7 and 10 no significant differences were shown among sites, but in week 11 Dean Hall and Mells showed greater levels than Woodchester and Brixham.

Secondary prey items

As with key prey, the same secondary prey items, except for small dipterans, occurred in the diets at all 8 sites. Small dipterans were absent from Woodchester and Brockley, and only present at very low levels at other sites. The two major secondary key prey were tipulids and ichneumonids, with trichopterans occasionally important at some sites.

Unlike the key prey, the two major secondary prey, tipulids and ichneumonids, are available from spring to autumn. However, they only featured extensively in the diets in spring and autumn, since bats fed almost exclusively on key prey from weeks 5 - 8, when temperature conditions favoured moth and *Aphodius* flight activity. Trichopterans fly only in the spring or autumn, and so are only periodically available.

The total levels of secondary prey at each site from weeks 2 to 10 is 100% minus the level of key prey (see above). Slebech therefore showed the highest level of secondary prey, and Mells and Iford the lowest. The proportions of specific secondary prey in the diet among sites varied considerably (see figure 1 and table 3).

Tipulids dominated the secondary diets at Slebech, Stackpole and Brixham, and were very common at Dean Hall, Brockley and Iford. Both Woodchester and Mells showed only low levels of tipulids in the diet in any one week, and were frequently absent.

Ichneumonids, though present at all sites, form highly variable levels erratically throughout the study period. Sites with high levels overall include Woodchester, Dean Hall, Brockley, Iford and Mells. The lowest levels were at Slebech, Stackpole and Brixham.

Trichopterans are seasonal fliers, emerging from fresh-water habitats. They were found in the diet at all sites during at least one week of the study, but were most important at Mells and Woodchester in spring (weeks 1/2). At Slebech and Stackpole they appeared in the diet at low levels from weeks 2 to 5 and again in week 10.

Table 3. Tukey test results for dietary differences between sites for secondary prey items by week of the study.

Week of study	Secondary prey item	Sites showing significant differences
2	Ichneumonids	Wdch. > Iford & Sleb.
9	Ichneumonids	Iford > all other sites Brixh. > Sleb
10	Ichneumonids	no sign. diffs. between sites (8 sites)
11	Ichneumonids	Wdch. > DHall Mells & Brixh. Brock. > DHall & Brixh.
1	Trichoptera	Mells > Wdch. DHall Brock. Iford
2	Trichoptera	Wdch. & Mells > DHall Brock. Iford & Stack.
2	Tipulids	Brock. Brixh. Stack. & Sleb. > Wdch. & Mells
3	Tipulids	Stack. & Sleb. > Wdch. Brock. Iford
4	Tipulids	Stack. > Wdch. Brock. Iford & Mells
9	Tipulids	Sleb.> all other sites (8 sites)
10	Tipulids	Sleb. > Mells
11	Tipulids	Brixh. > all other sites (6 total - no welsh ones)

KEY: Brock. = Brockley, Brixh. = Brixham, DHall = , Dean Hall, Sleb. = Slebech, Stack. = Stackpole, Wdch. = Woodchester.
NB Brixham data were absent from weeks 3 4 5 & 8. Stackpole and Slebech data were absent from week 11.