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The management of feeding areas for greater horseshoe bats

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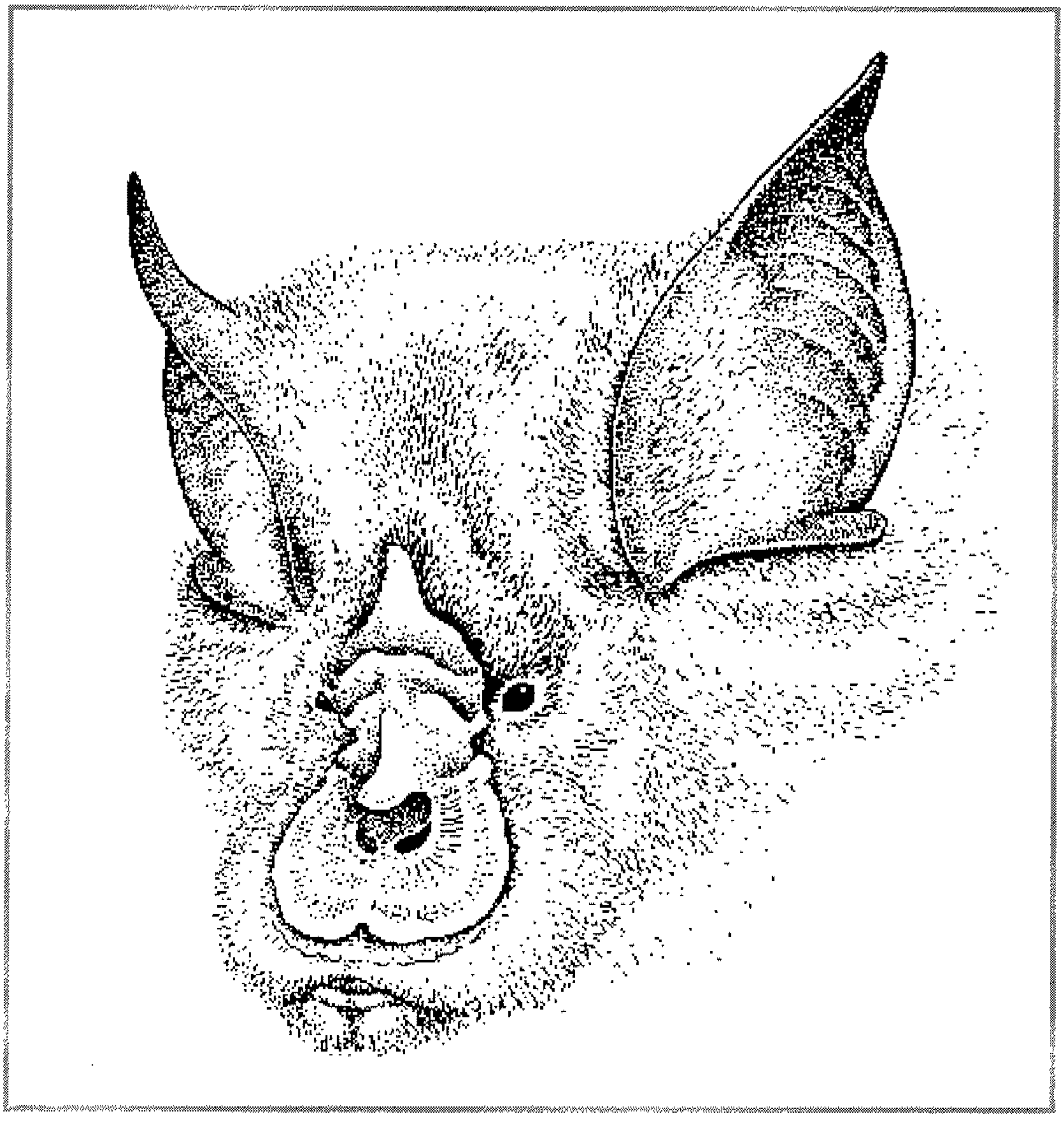

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The management of feeding areas for greater horseshoe bats

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SUMMARY

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

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

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

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

INTRODUCTION

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

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

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

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

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

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

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

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

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

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

PART 1: DIETARY REQUIREMENTS OF THE GREATER HORSESHOE BAT

Introduction

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

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

Methods

Geographical area covered

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

Periods of faeces collection beneath maternity clusters

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

Periods of faeces collected from individual bats

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

Faecal analysis

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

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

Preparation of permanent dry slides

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

The method was as follows:

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

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

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

Results

Dietary content over the geographical area sampled

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

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

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

Diet by month throughout the summer

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

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

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

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

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

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

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

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

Diets of individual mothers and their young on various dates

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

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

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

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

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

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

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

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

Discussion

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

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

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

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

Summary for Part 1

Diet content: geographic and climatic effects

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

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

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

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

Diet content: changes throughout the year

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

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

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

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

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

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

Table 1

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

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

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

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

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

Table 2

Diets of mothers and young in late August after a drought

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

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

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

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

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

Table 3

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

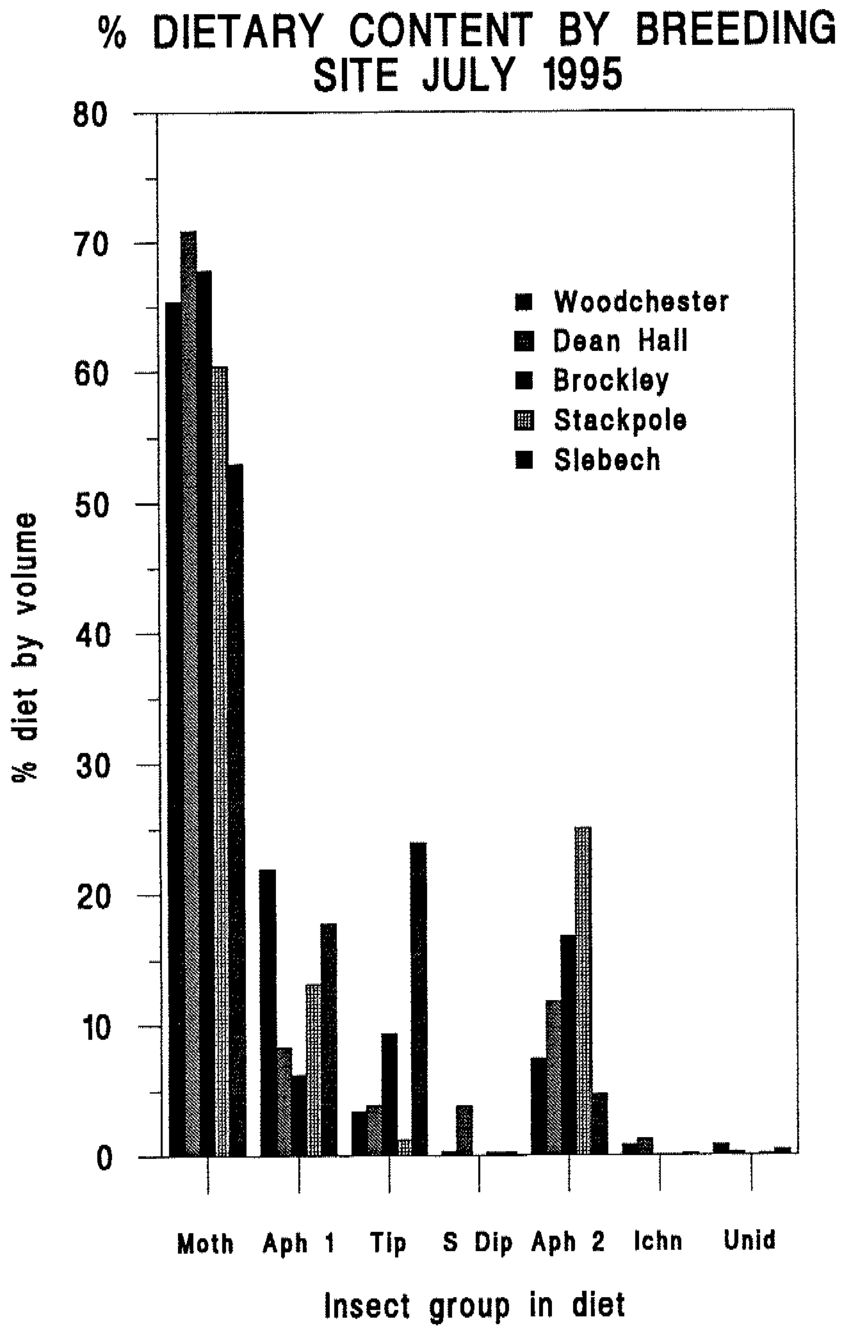
Date	n total (status)	n eating 1 prey item	n eating 2+ prey items	mean n prey items	prey item(s) eaten (n)
WARM DAMP WEATHER:					
12-8-90 (mother)	17	14	3	1.13	moth (14)
1-9-91 (mother)	11	7	4	1.55	Tipl (4) Moth (3)
POOR WEATHER:					
20-8-95 (drought)	24	12	12	1.63	moth (10) Tipl (2)
14-8-94 (v. cold)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

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

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

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

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



% DIETARY CONTENT BY BREEDING SITE JULY 1995

Figure 1

Figure 2(a)

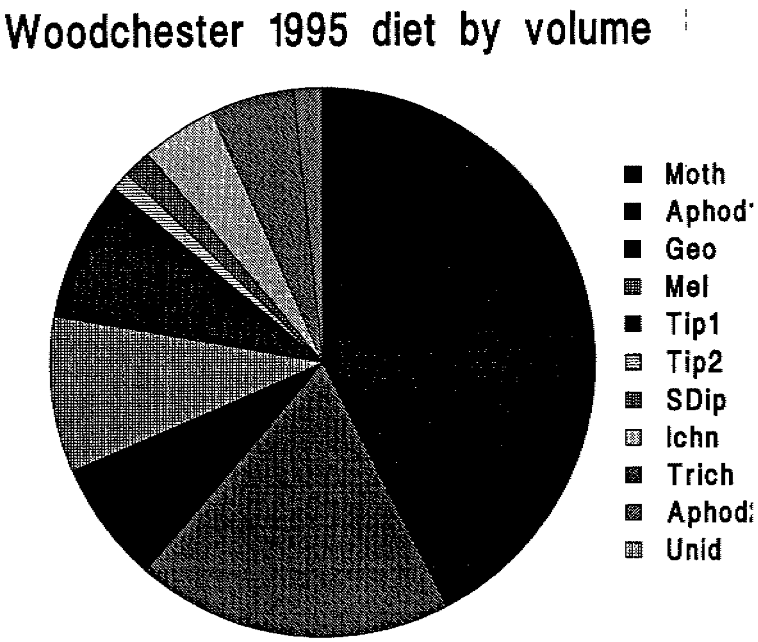


Figure 2(b)

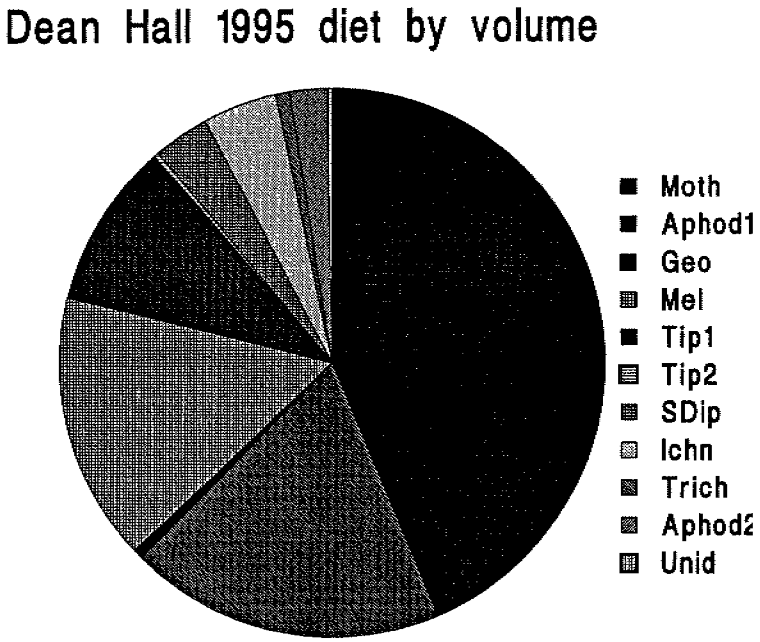
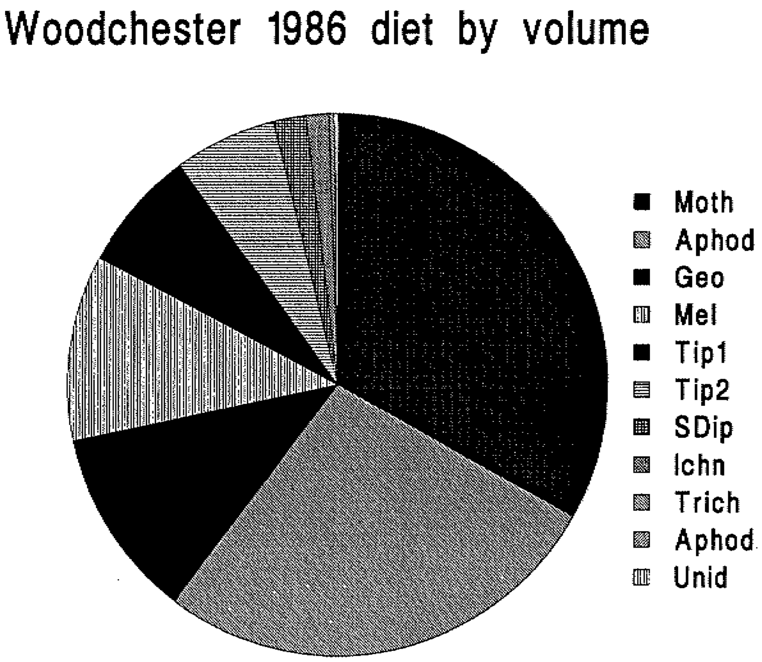
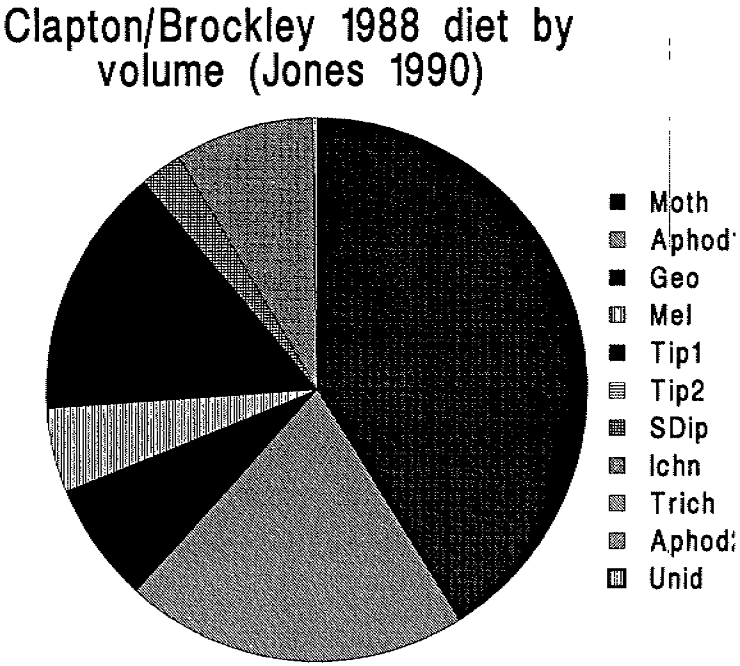


Figure 3(a)



Woodchester 1986 diet by volume

Figure 3(b)



Clapton/Brockley 1988 diet by volume (Jones 1990)

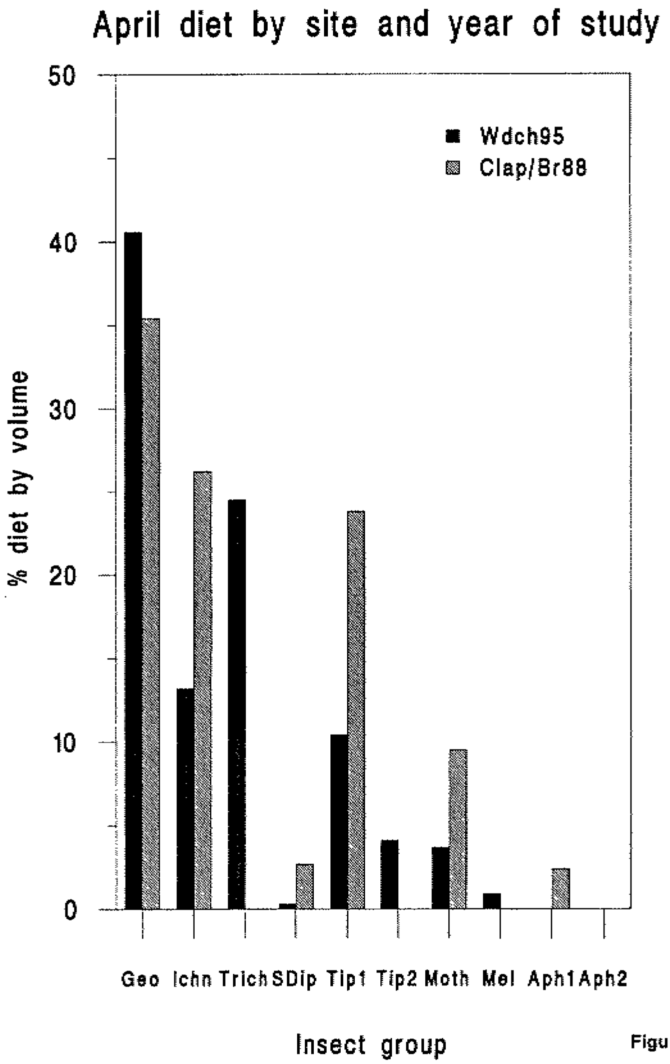


Figure 4

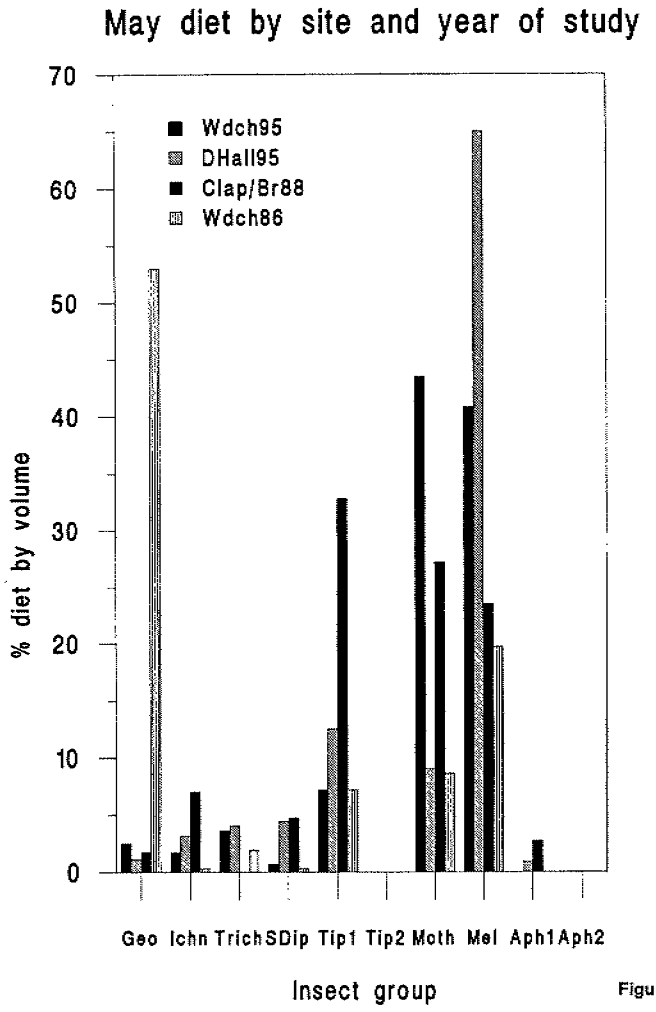
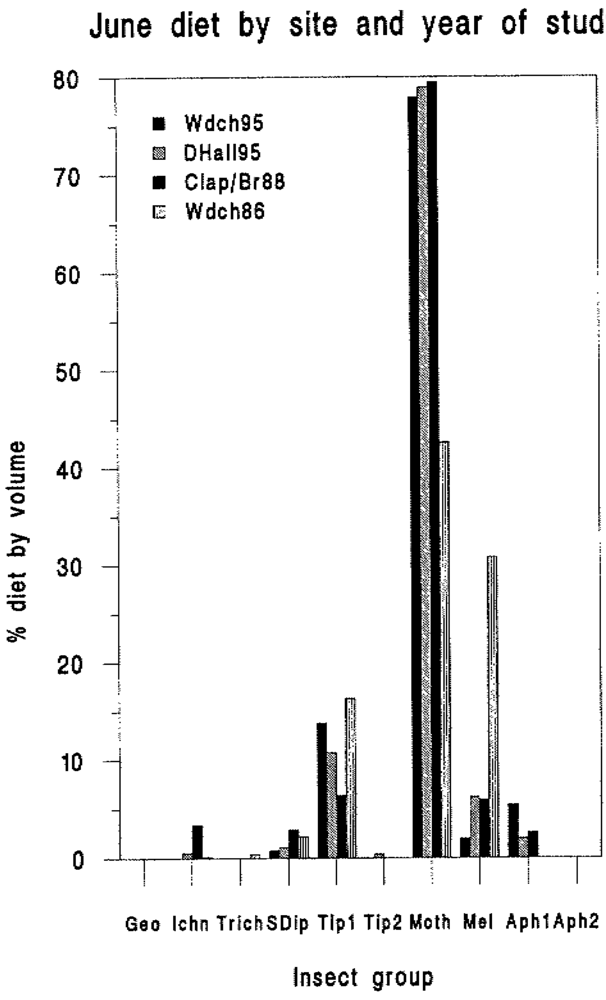


Figure 5



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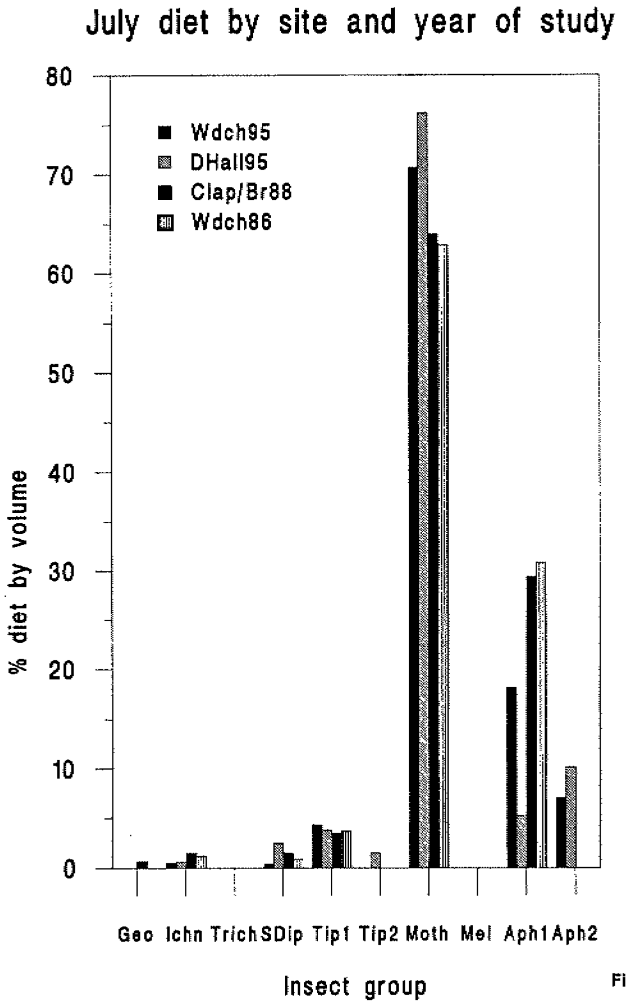

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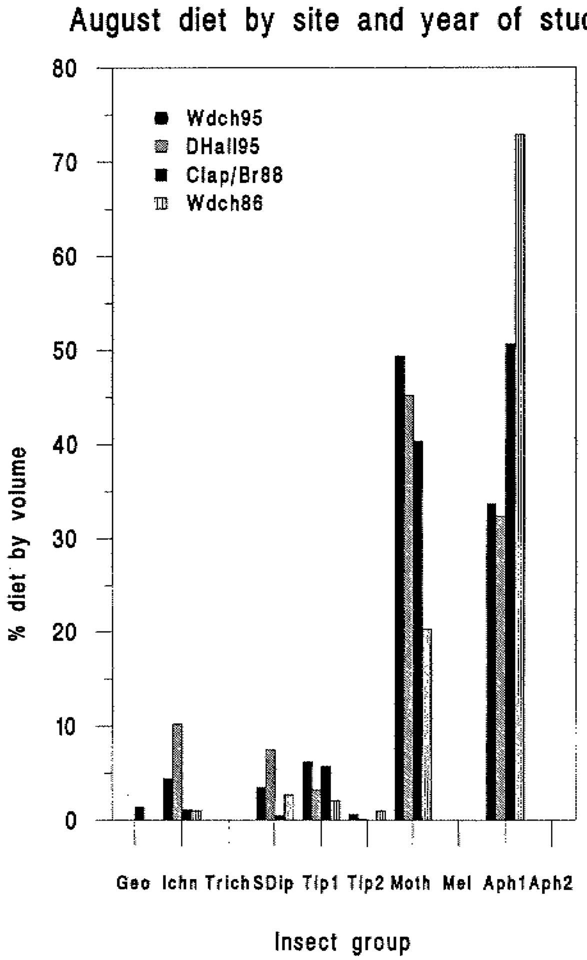

Figure 8

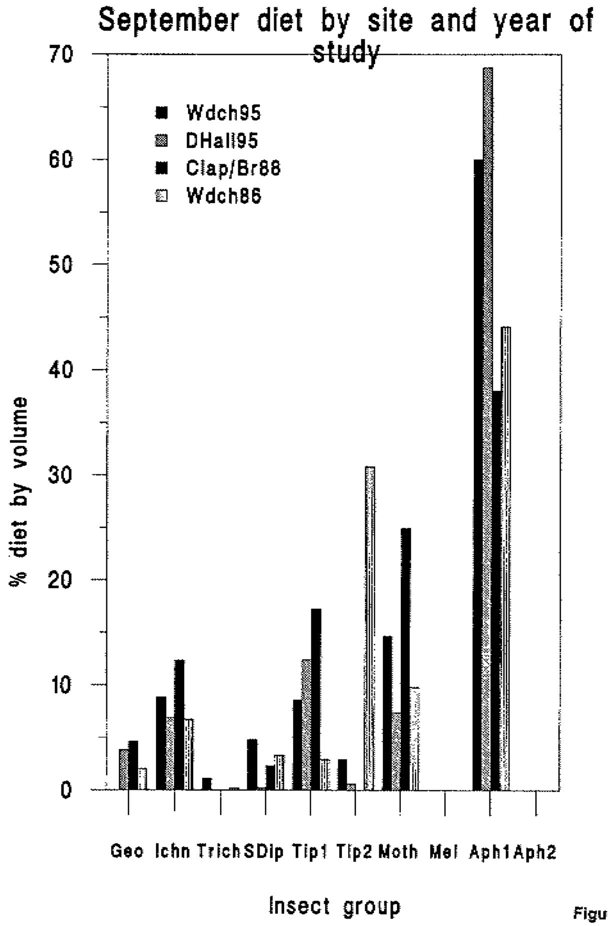

Figure 9

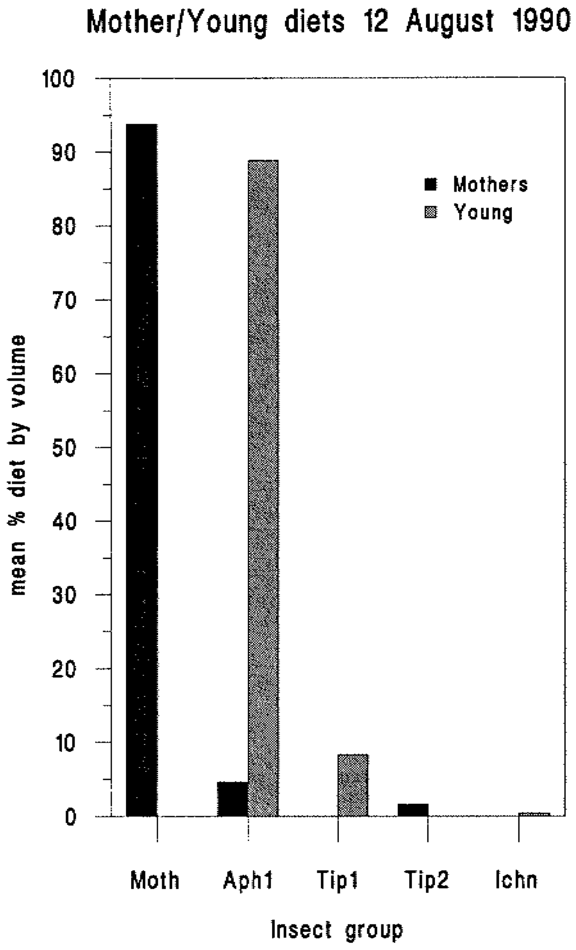

Figure 10

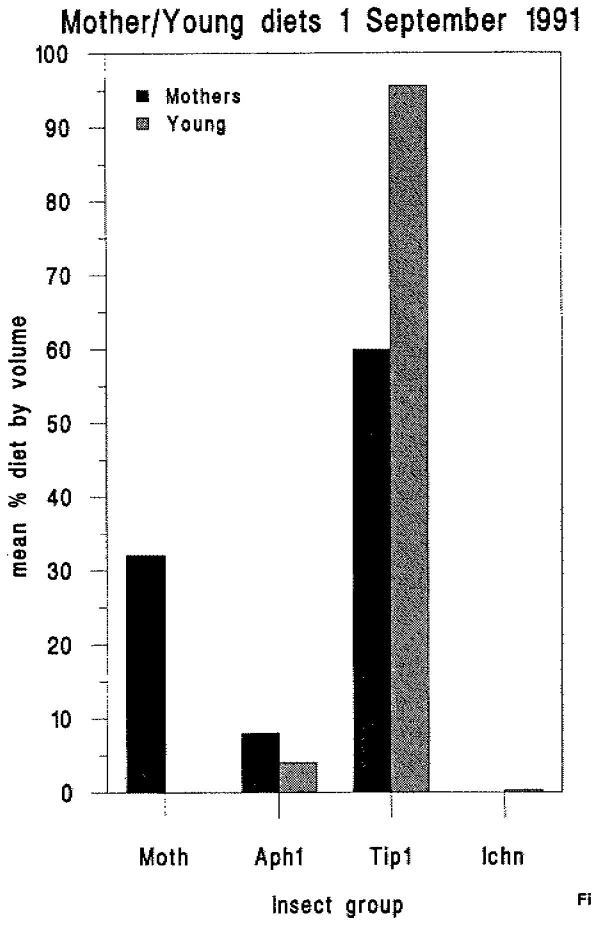

Figure 11

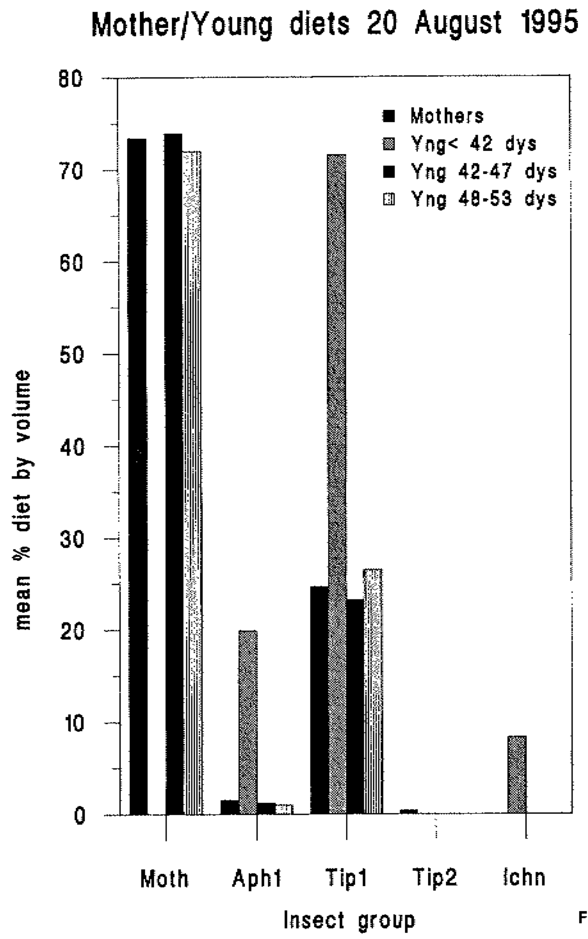

Figure 12

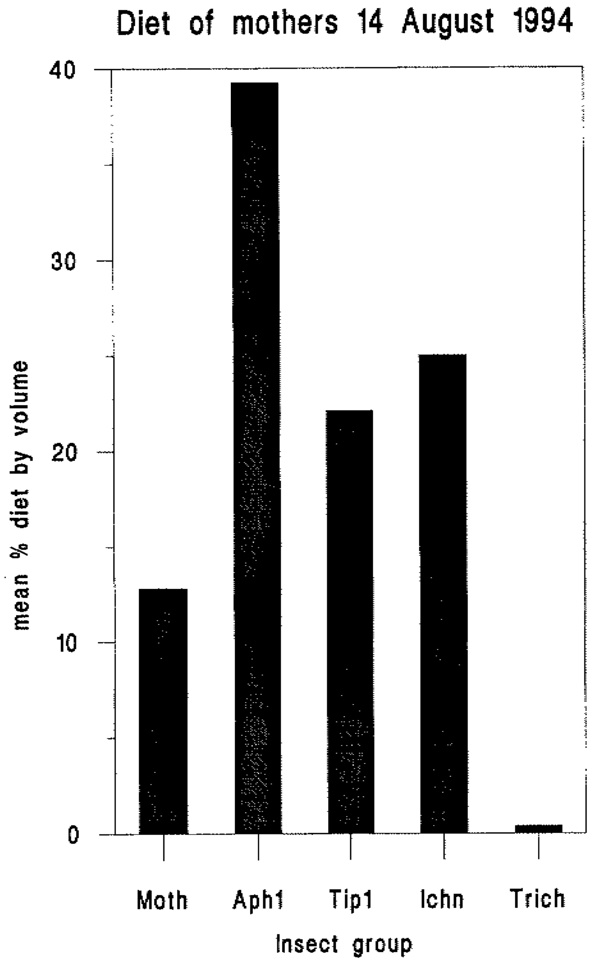

Figure 13

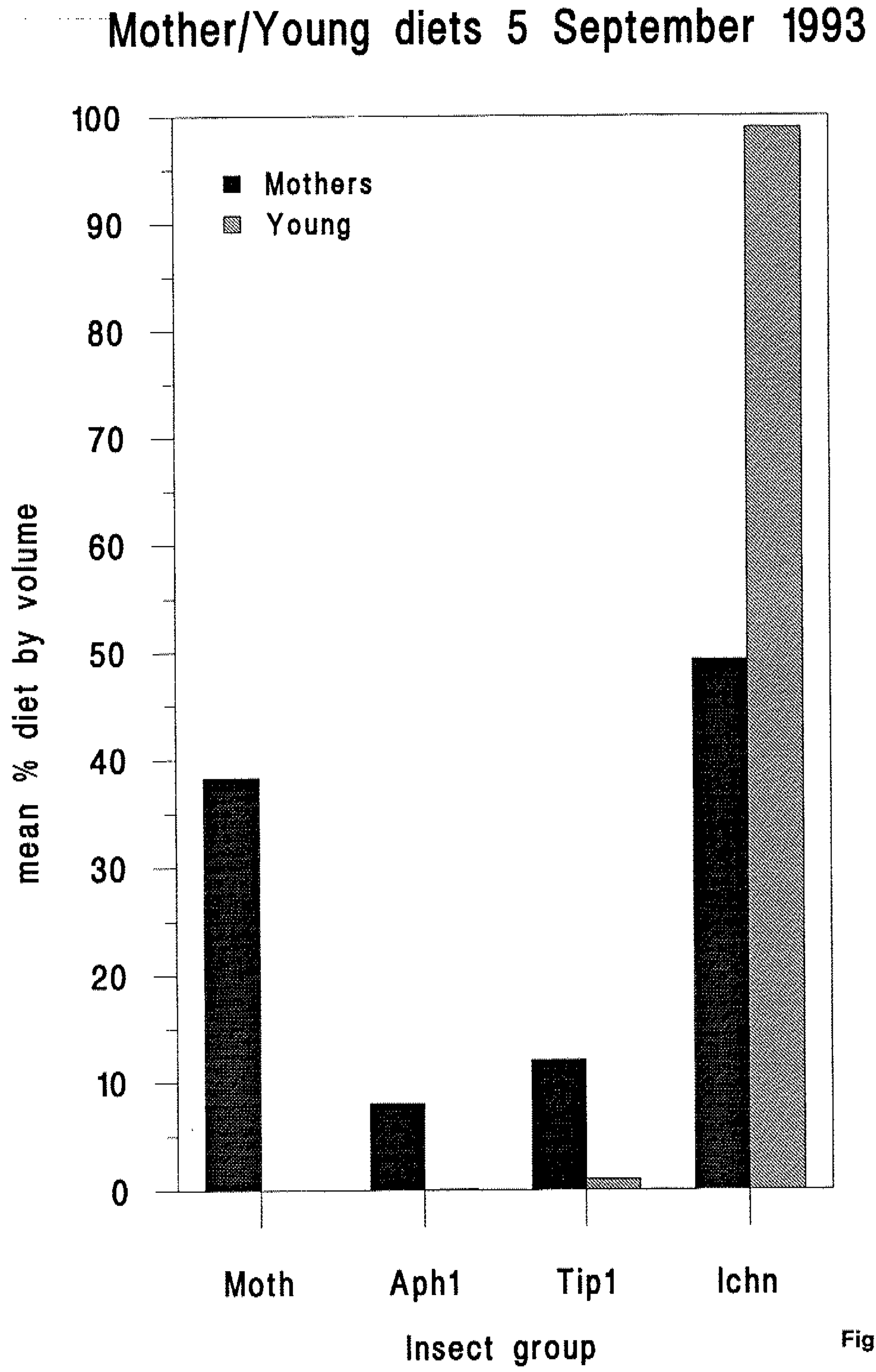
Mother/Young diets 5 September 1993
mean % diet by volume
100
90
80
70
60
50
40
30
20
10
0
■ Mothers
▨ Young
Moth
Aph1
Tip1
Ichn
Insect group

Figure 14

PART 2: HABITAT FEATURES PROMOTING HIGH DENSITIES OF KEY PREY ITEMS WITHIN KNOWN FORAGING RANGE THROUGHOUT THE SUMMER

Foraging Range

Radiotracking studies carried out by Jones and Duvergé (Jones *et. al.*,1995) at three different maternity sites near Bristol have established the typical foraging range of this species. After the first year of life they average between 2 and 3 km distance from the day roost to feeding sites, sometimes exceeding 4 km. Within these ranges the mean total distance travelled by females varies with reproductive state, ranging from about 7.5 km in pregnant females, rising to 12.9 km during lactation, and falling to 8.1 km during post-lactation. They considered that the conservation of foraging areas up to 3-4 km from the maternity roost should be considered crucial for the maintenance of populations of this species.
Young bats, radiotracked simultaneously with their mothers, were shown to feed independently of their mothers. They make exploratory flights at about 24 days of age, and begin to feed soon afterwards, rapidly increasing the amounts captured from 29/30 days up to 55 days. During their early feeding flights (age 30-50 days) they travel increasingly farther, between about 0.3 and 1.5 km, averaging 1 km at age 40 days. At this age growth of forearm length ceases, and soon afterwards the young have fully developed ultrasonic capabilities, permitting them to catch the whole range of their prey items. Between age 50 and 55 days they rapidly increase their range to adult levels (mean 2.8 km).

Foraging Habitat Used

Jones and Morton (1992) in a study of a single maternity site near Bristol established that this species forages mainly in, or at the edges of, ancient woodland during the spring, and over pastures during late summer. Duvergé, in a follow-up study at three maternity sites (Duvergé, unpubl.) supports this finding. Both studies confirmed the suggestions made by Stebbings (1982) after preliminary radiotracking work in Wales. The habitat shift agrees with the major dietary findings of Jones (1990) and the present study. Young greater horseshoe bats are likely to be particularly dependent upon livestock-grazed pastures close to the maternity roost when they first start to forage for insects, since the small dung beetle *Aphodius rufipes* is their key prey item (Part 1).

Key Prey Species and Habitats

Evidence provided in Part 1 showed that various moths, *Aphodius rufipes*, *Geotrupes* spp. *Melolontha melolontha*, brown tipulids and ichneumonids were either key prey species in different months through the summer, or important back-up prey which may become key items in certain years in spring and autumn. The first two key prey items, moths and *Aphodius*, are probably of greatest concern to population levels, since they provide the bulk of the diet during late pregnancy and lactation, both events causing additional stress to female bats. The others are important in early pregnancy during spring, when climatic temperatures affect birth-timing and subsequent survival of the young of the year (Ransome and McOwat, 1994). Brown tipulids and ichneumonids are normally important secondary prey items if densities of key species fall too low for profitable feeding, such as during severe weather, especially when cold or very wet. They are valuable because they fly for extended periods of the year.

It is therefore important that the habitat for 3-4 km radius from a maternity roost should provide substantial areas of high densities of these prey items annually. The preferred habitat for foraging from April to September includes areas of mixed semi-natural deciduous woodland and permanent pasture habitat.

The following review of the literature concerning key insect species attempts to isolate key habitat features promoting high density populations of key and secondary prey species for bats to reliably feed on.

Habitat Features Promoting Key Prey Species

Moths

Although the present study did not identify individual moth species from faecal analysis, evidence from culled remains (Jones, 1990; *pers. obs.*) suggests that various common noctuid species such as the Heart and dart, *Agrostis exclamationis* (L.), Dark arches, *Apamaea* (= *Xylophasia) monoglypha*, Large yellow underwing, *Noctua pronuba* (L.), and Lesser yellow underwing, *Noctua comes* (Hübner), are important. Moth trapping in the summers from 1980 to 1995 in Dursley, Gloucestershire, some 9 km from Woodchester Mansion, showed that these species dominate light-trap catches in every year, with populations of each species peaking in the same order, as in the list above, from late May (Heart and dart) to early September (Lesser yellow underwing). The populations usually show considerable overlap so that two or more common species are available at any one time or (Ransome, unpubl.).

Taylor & Carter (1961) used suction traps to gain an unbiased set of data on various aspects of moth behaviour. Diurnal flight periodicity and height of flight were highly specific with an interaction between them which was associated with the moth's population level. The typical pattern was a peak after dusk followed by a long tail (Mouse, Beaded Chestnut, Large yellow underwing, Garden dart, Setaceous Hebrew character, Knot grass). Only Dark arches (*Apamaea monoglypha*) was bimodal with dusk and dawn peaks, and it flew at the same height each time with a peak of 6 metres. These data suggest that the Dark arches is especially likely to be available as prey for greater horseshoe bats.

Population estimates of moths

Light traps are generally used to sample moth availability and for population estimations, since they capture much larger numbers than suction traps but they are highly selective

(Taylor and Carter, 1961). The interpretation of the number of moths caught in a light-trap catch is contentious since it has a very uncertain relationship to the local moth population available to predatory bats (see Appendix A for a detailed discussion of this point). Certain species are much less attracted to lights than others. At least some populations of some species show little response to the lamps, and this variable response may be partly due to whether they are in a migratory phase (Baker, 1985). There is substantial evidence suggesting that many noctuid moths, including *Noctua pronuba*,, can be highly migratory, travelling huge distances from their larval habitats. It may be these migrations which result in high and erratic catches in traps (as argued by Gregg *et al.*, 1993, 1994), rather than variable illumination conditions.

As migratory species feature strongly in greater horseshoe bat diets, it may be argued that the local environment around a roost is of little importance in conservation measures taken. This seems not to be the case for the following reasons:

(a) migrating moths travel in surges which seem to be erratic and often of brief duration. They come to rest at intervals and seem to be selective in the choice of site, preferring dense woodland, preferably deciduous (Waring, 1989).

(b) migrating moths, which can result in large densities of moths in an area, have been shown to fly at higher levels than these bats normally feed, as shown by Taylor and Carter (1961), and therefore may only be of use to bats feeding at low levels as they land or take off.

(c) resident moths, possibly derived from larvae in the local area, and therefore subject to plant biomass population restrictions, are the ones more likely to be exposed to greater horseshoe bat predation over long periods

These considerations indicate that it would clearly benefit greater horseshoe bat populations to have high-quality moth habitat nearby in considerable abundance. If the resident moth population is the most important, because it is reliable and available for long periods, then the provision of abundant larval food plants, as well as roosting sites, is essential. Migratory swarms of moths may be worth attracting by providing many roosting sites, but their erratic presence may do no more than provide occasional bat feasts.

Resident moth levels are likely to fluctuate less than migratory ones, but will be subject to variations caused by the vagaries of climate, diseases and also other predators besides bats, or parasites such as ichneumonid hymenoptera (which have been shown to be important secondary prey items at low climatic temperatures in Part 1).

Factors influencing moth densities

Taylor, French and Woiwod (1978) investigated the effect of various habitats upon the numbers and diversity of moth species over many years, using data collected from light traps from 172 sites around Britain. A series of sites in the north and south of the country were graded from woodland to urban habitats (range: woodland, gardens, arable land, buildings).

They showed that moth numbers declined dramatically from thousands to hundreds across this series. The diversity index used was more stable, but also showed declines, especially in the south. The most obvious feature of their results was the similarity in the abundance of species in all of the woodland sites, and the drop between them and the typical agricultural site. This was often explained as being due to the loss of larval food plants in the case of resident moth species.

Waring (1989) showed that there were lower moth populations in a conifer plantation and a fresh coppice region than in adjacent dense deciduous coppice. The differences may have been greater than he detected, because he used corrections to his data based on Bowden & Morris (1975) who assumed a large zone of attraction operates around light-traps. Waring thought that the availability of suitable roosting sites is a likely explanation for the high numbers of *Noctua pronuba* in the overgrown woodland he showed were present in 1984. Hence it may be the quality of a habitat in attracting migratory moths for temporary resting stops, as well as its capacity to generate its own resident populations, which determine the overall densities of moths available to foraging bats.

Requirements of important prey species of moths

Besides the resting habitats necessary for adult moths, it is important to provide conditions promoting the successful completion of the life-cycle. Details of some of the larval foods, habitats and life-cycles are given in Appendix B, so only a brief summary is given here.

The larvae of *Agrostis exclamationis* and *Apamaea monoglypha* can all tolerate a wide range of open land habitats, including gardens, waste ground, fields and meadows. The first moth can feed successfully on a wide range of low herbaceous plants such as dandelion, chickweed and dock, with various grasses, and the second one feeds entirely on grasses. *Noctua pronuba* and *N. comes* needs similar habitats, but can also occupy mature, open woodland as they feed on primrose and other woodland herbaceous plants as well as dandelion, chickweed, dock and various grasses.

Management objectives to sustain high densities of important moth populations near roosts

1) Restrain creeping urbanisation into the 3-4 km area around breeding sites (the roost sustenance zone) by opposing building developments through planning procedures.

2) Restrain agricultural practices such as intensive arable cultivation within the roost sustenance zone by financial inducements.

3) Encourage the planting of extensive areas of deciduous woodland up to 50% of the area within the roost sustenance zone, if low woodland cover exists. Replace coniferous plantations with deciduous trees gradually over a period of time, avoiding extensive clear-felling. Woodlands should be permeated by grassy rides, and surrounded by regions of permanent pasture, especially close to roosts.

4) Strongly oppose the removal of mature ancient semi-natural deciduous woodland within the roost sustenance zone. Use statutory protection and/or financial inducements.

Aphodius rufipes

This is the major *Aphodius* species utilised by greater horseshoe bats, especially the young (Part 1), despite the fact that 19 species occur in England (Denholm-Young 1978). Many of these other species are very common. This apparent selection appears to be due to a combinations of characters. It is large and therefore a profitable food item (10-13mm length; 93 mg wet mass; 30 mg dry mass), exceeded only by *A. fossor* in dry mass (37 mg dry mass). Most *Aphodius* species in Britain are <8 mm long and <15 mg dry mass. It is one of the few *Aphodius* species which is truly nocturnal (Landin 1961), and will fly throughout the night if ambient temperatures permit flight (>9 °C.). *A. fossor* is diurnal, and although there are other nocturnal species, they are <6 mg dry mass. It is abundant in pastures in late summer, with up to 63 adult individuals per cow pat and an average of about 100 larvae per cow pat (Holter 1975). It is also common in European woodlands (Hanski 1979).

Although it is seasonal, it is long-lived, and is usually readily available to feeding greater horseshoe bats in large numbers from late July until October, usually with a peak in early August, at a time when young bats start to feed, and female bats are in the last third of lactation, and often greatly stressed. Thus it provides a safety net if moths, the preferred dietary item of the mothers, and brown tipulids, are both in short supply. It does well in a cold wet summer as its preferred temperature range is 14 - 17 °C.

Population estimates of Aphodius rufipes

These may be made using two types of method, but only the first avoids the difficult identification of different species of larvae, although there are few large larvae present in cow pats in late August which are not *Aphodius rufipes* as other large species breed earlier in the year.

Baited traps may be excavated in fields containing bowls of fresh dung (about 2 kg) beneath wire mesh grid covers (about 4 mm prevents penetration to the dung) to catch them as they arrive. To sample *Aphodius rufipes* and not other species, traps should be operated at dusk in early August, and observed frequently after dark by torchlight for the arrival of adults over a fixed time period if quantitative comparisons with other sites are needed..

Aged cow pats can be examined for larvae after 21 days to find the levels of populations present in late August, by which time they should be present in large numbers. The dryish pat is lifted whole and sealed in a large plastic bag. In a garden or laboratory it is broken up finely and soaked in a 12 litre bucket fitted with a 5 cm diameter pipe. Running water flowing into the bucket causes effluent to run out through the pipe into two stacking sieves with mesh sizes 2 mm and 1 mm. Larvae can be removed from the finer sieve to a white tray for identification (Strong submitted). At 21 days they should be in their third stage, and be about 15 mm long. This involves a system of pat marking which is not hazardous to grazing animals, and is not easily destroyed, as well as larval identification.

Factors influencing adult <u>Aphodius rufipes</u> densities

Its potential abundance may be due to its capacity to feed on many types of herbivorous dung (in order of preference: cow, horse, sheep (Landin 1961)), and because it will utilise dung in a wide range of habitats, from exposed open fields to dense forests (Landin 1961).

It shows a wide range of habitat utilisation which gives it considerable protection against climatic extremes. In droughts shaded habitats will act as refuges allowing the survival of adults and the successful growth of the larvae. In severe prolonged droughts larvae may be killed within dung in most habitats, and adult survival may involve entering the soil. The adults are not killed, but reproduction is delayed for up to two months as occurred in Sweden in 1959 (Landin 1961). In prolonged heavy rain dung is washed away into the soil killing the larvae in exposed habitats, but dung remains intact in forests (Landin 1961). Hence shaded habitats act as refuges against climatic extremes. In normal climatic conditions exposed cow pats may be the most suitable for successful growth, and horse dung can produce successful development in shaded conditions such as forests, orchards and park lands (Landin 1961).

High densities of *Aphodius rufipes* are promoted by high densities of dung from grazers. As this species can only feed on fresh dung, which it leaves within a day or two, it means that a constant fresh supply from grazing animals, especially cattle, should be kept close to maternity roosts (< 1 km) to benefit the growth of the young by improving their insect capture success rates when they start foraging. Adult beetles find dung by smell, flying into the wind, and Landin argued that they are attracted by wind scent from considerable distances, possibly up to 10 km.

Denholm-Young quotes mean figures from 15 studies as follows. Grazing season = 188 days; average stock level (cattle) = 1.4 per ha; pats/cow/day = 11.9.

This translates into 16.7 pats/ha/day, and a maximum of 1052 adult beetles/ha/day. At 93 mg wet mass/adult this represents about 98 g/ha/day of adult beetles or about 0.1 kg/ha/day. Adult bats eat about 3-4 g of wet mass of insect food/feed, or 6-8 g/bat/day. Juveniles eat from 0 to 3 g/bat/day between 29 and 45 days of age whilst they feed close to the roost at a mean distance of 1 km. This range covers an area of 314 ha. If all the area were grazed pasture 0.1 x 314 = 31.4 kg of adult beetles could arrive at fresh pats per day. 100 pre-weaning young bats eating 3 g/day would consume 0.3 kg adult beetles/day if they ate no other food. This represents about 1% of available beetles if they were at maximum densities in the pats.

In practice stocking levels of 2-3 cows/ha can be maintained from mid July to late August in most years, so only 50% of the close surrounding habitat of a roost is needed to be grazed pasture to keep predation levels at about 2%, and allows for 50% woodland areas to favour moths for the adults to feed on. There are allowances for lower levels than the maximum in the pats, since predation levels can probably reach 5%. Furthermore, since juveniles are normally born over at least a three week period, and since they steadily increase their foraging range after they are 30 days old, several hundred juveniles are likely to be supported by these stocking levels.

If 157 ha of the land around a roost up to a distance of 1 km (50%) is grazed by cattle at up to 3/ha it means that 471 cattle (maximum) should be kept to sustain a bat colony with 100 young. Smaller colonies may require lower stocking levels, but it is probably inadvisable to drop much below 220 cattle within the young sustenance range (1 km). This is because low densities of fresh dung from grazers are much less attractive to colonising dung beetles than high ones, and population levels of adult beetles may fall disproportionately.

Adult greater horseshoe bats travel much further than pre-weaned young - up to 4 km; mean 2.84 ± 0.91 km (Jones *et al.* 1995). At 3 km radius, the minimum range which should be conserved for colony safeguarding, individuals may feed over 2828 ha. This area is the roost sustenance zone. It subsumes the young sustenance zone. 50% of the roost sustenance zone outside the 1 km range as grazed pasture represents 1257 ha of grazed pastures (2828 - 314 = 2514 ha; 2514/2 = 1257 ha). With 1.4 cows/ha and adult beetles = 0.1 kg/ha/day available it represents 126 kg of adult beetles/day. A colony of 700 adults eating 8 g/bat/day within this range would consume 5.6 kg beetles/day if they ate nothing else. This represents about 4.4 % of those in the area. Since fresh dung may attract beetles from a distance of many kilometres (see 8) above in Research Findings) the removal of a part of the local population by bat predation may promote immigration from further afield, if grazers are abundant there. Furthermore, in most years adult bats feed mainly on moths (Part 1) so the densities of cattle could be lower than 1.4 /ha without serious risk of shortages, especially as moths are only likely to be in short supply in cold wet summers. Such weather promotes the levels of *Aphodius rufipes*.

The key requirement to promote populations of greater horseshoe bats may be the presence of abundant grazers, especially cattle and sheep, within the 1 and 3 km radii. The most crucial for juvenile growth and survival, as well as helping reduce commuting distances for lactating females, will be 2-3 cows/ha, or 11-16 sheep/ha, in the 157 ha of grazing pastures which should be available (50% of 314 ha @ 1 km radius from roost). This area can support 314-471 cows for a the period between July and August, in normal summer weather, and up to 220 long-term. Equivalent sheep levels would be from about 1727 to 2512 sheep in July/August, and 1256 long term.

If sheep are used instead of cattle, which is the less preferable option, especially in dry weather because their dung rapidly dries out, they should be kept at levels of at least 11-16 sheep/ha, depending on grass productivity, to generate sufficient beetles. Mixed grazing in rotation with cattle is preferable, as it helps control nematode parasitic infections and reduce the need for drug treatment with anthelmintics (Appendix D).
Horses may also be beneficial in small numbers, especially if grazed in park land, orchards and grassy rides within woodland. Their dung also rapidly dries, and may become useless for breeding beetles, so the shade in these habitats should reduce desiccation rates.

Avermectin usage and its potential effect on dung insects

Avermectins belong to a family of compounds derived from a naturally-occurring soil actinomycete fungus, *Streptomyces avermitilis*. They were discovered in the mid 1970's. It includes the brand ivermectin marketed by Merck, Sharp and Dohme.

Ivermectin is a broad spectrum antiparasitic drug introduced onto the international animal health market in 1981. In Britain it is approved for use in cattle, sheep, goats, pigs and horses. It is particularly effective against gutworms and lungworms, and also some arthropod ectoparasites. It is absorbed systemically after administration by drench (pour-on), injection or stomach bolus, and is excreted mainly in the faeces. Residues of ivermectin in cow dung have been shown to reduce the number and variety of insects in the dung. This includes certain types of fly larvae, and various dung beetles which are important in promoting the rapid decomposition of dung. Besides delaying dung degradation, leading to pasture fouling, there is concern over the effects that long-term ivermectin usage in any area could have upon populations of these insects. Since they occur in significant numbers in untreated cattle-grazed pastures, the loss of their biomass may have important consequences to bird and mammal predators (McCracken and Bignal JNCC).

Control programmes recommended by Merck, Sharp & Dohme.

This company produced and marketed the first avermectin in 1981. They called it ivermectin. It contains two chemically-modified avermectins (at least 80% 22,23-dihydroavermecinB_{1a} and no more than 20% of the equivalent B_{1b} homologue). The brand names used for sales are Avomec^{R} injection for cattle, and Ivomec^{R} oral dose for sheep.

First season animals:

Strategic: (i) Up to 3 treatments, minimum 5 weeks apart early in grazing/transmission period.
(ii) treatment at the end of period of transmission e.g. housing, entry to feedlot, start of dry season.

Evasive: Treat once in mid season.

Therapeutic: Treat as clinically required.

Second season animals:

Strategic: Treat at a lower frequency than for first year animals.

Adult cattle:

Beef cattle: Treat occasionally strategically. Dairy cows are rarely treated; if so it is at drying off.

Since cattle need to be kept at high densities in the vicinity of greater horseshoe bat breeding sites to boost *Aphodius rufipes* and *Geotrupes* spp. beetle availability at certain critical times of year. High densities of cattle/sheep/horses are likely to lead to increased risk of heavy nematode parasite burdens, especially in young animals. These burdens need reducing by effective measures if a healthy herd is to be maintained. Young animals need more anthelmintic treatments than adult livestock, as they are immunologically naive and highly susceptible to parasitic infections at first. Ewes need treatment at lambing as they show rising levels before birth, as do mares.

Ivermectin is a broad-spectrum anthelmintic which is currently approved for cattle excluding milking herds, as pour-on and injection formulations. Most (98%) of the drug lost from the body does so in the dung. It takes several weeks for all ivermectin to be excreted from a single dose treatment, but peak levels normally occur within 2 days of treatment, followed by a slow decline.

Ivermectin-treated cattle dung has been shown to have ecotoxic effects on dung inhabiting insects, especially cyclorrhaphous dipterans and larval *Aphodius* (Strong 1993). It probably also has similar effects on *Geotrupes*. Further studies by Strong and his collaborators have shown that ivermectin-contaminated cow pats are at least as attractive to adult beetles as control pats, and that they lay eggs in it. The eggs hatch into larvae which are unable to complete development to pupae. Hence the life cycle is terminated by ivermectin, although the adults show low sensitivity to ivermectin poisoning. With drench and injection treatments all dung produced remains toxic to larval development for at least 10 days, and structural defects have been noted in larvae growing in pats 16 days post treatment. Furthermore ivermectin in large cow pats degrades very slowly with no significant losses after 45 days. Possibly in the smaller, thinner pats from young animals degradation is more rapid through the action of sunlight penetrating the surface. Sunlight causes rapid breakdown of ivermectin. In comparison to pats, degradation in soils is more rapid, and it binds strongly to particles, reducing its toxicity. In water it also binds to particles which reduce the likelihood of damage to wildlife generally, though it is highly inadvisable to dispose of empty containers directly into water habitats as fish and water fleas (*Daphnia*) are especially vulnerable.

Clearly cattle fitted with a rumenal bolus designed to release ivermectin slowly over 120 days would produce dung which is unusable for the life-cycle of dung beetles and other insects. If routinely fitted to livestock herds on a widespread basis it would potentially do enormous damage to dung fauna populations in time, and have wide effects on the ecosystem. The use of ivermectin boluses in cattle should not be permitted anywhere, not only on the grounds of damage to wildlife, but also since their use will promote the rapid development of drug-resistant parasites (Herd 1993).

Management objectives to sustain high densities of Aphodius rufipes near roosts

1) Promote the development/retention of permanent grazing pastures within 1 km of maternity roosts (the young sustenance zone) at a 50 % level, which is 157 hectares. Some of these pastures should be as close to the roost as possible, subject to the need for some close woodland cover to comply with flight behaviour needs. Improved or semi-improved pastures of low conservation value should be improved by non-hazardous methods, to provide high levels of grass productivity. This is needed to cope with high densities of livestock in August.

2) Stock the young sustenance zone pastures with cattle, sheep and possibly a few horses at up to 1.4 cattle/ha, or 8 sheep/ha early in the season as weather permits and rotate between cattle and sheep in specific fields (March -May). This represents up to 220 cattle or 1256 sheep, but mixtures of both are preferred. They should be enough to keep the grass sward short, without serious pasture damage in wet or cold conditions. Rest fields in June for grass growth recovery, and do not permit silage or hay cutting. Graze at 2-3 cattle/ha or cattle mixed with at least 11-16 sheep/ha (level depending on quality/quantity of grass), from the first of July until late August at least. Continue at lower levels if necessary into October as the grass state permits. In July and August these figures mean 314-471 cattle or 1727-2512 sheep (or pro rata mixtures of the two). If weather permits, continue grazing at lower levels to suit grass growth into early October.

   NB stocking levels will always have to be adjusted in the light of climatic conditions influencing the growth of grass. Numbers of livestock assume 157 hectares of pasture are available within the young sustenance zone. These figures are estimated to be required to sustain a colony with 100 young (see Part 1).

3) Ensure that cattle used from July onwards are primarily mature animals, as small ones produce small pats which dry rapidly and cannot sustain *Aphodius* larval development to viable pupae.

4) Promote the grazing of cattle at further distances up to roost sustenance zone limits (up to 3-4 km, but especially 3 km) to generate high productivity of surrounding beetle populations. At 3 km range, and about 50% grazing levels this means about 1760 cattle or about 10,000 sheep should ideally be present in the roughly 2,500 hectares of land beyond the young sustenance zone. Stocking levels and patterns will have to be more flexible enough to allow the logistics of 2) above. Livestock will need to be moved between the outer roost sustenance zone and the young sustenance zone.

5) Prohibit the use of avermectins as anthelmintics to treat livestock kept within the young sustenance zone. Recommend alternative drugs such as the milbemycin **moxidectin** (sold as Cydectin^R, Cyanamid), the benzimidazoles **fenbendazole** (sold as Panacur^R, Hoechst) or **oxibendazole** as alternatives, together with rotation of cattle with sheep, as part of a coherent programme to control parasites, without

generating drug resistance. Moxidectin and fenbendazole have been shown by Strong, Wall and colleagues to permit successful completion of the life-histories of both *Aphodius* and cyclorhaphous flies.

6) Prohibit the use of bolus, slow-release, avermectins on livestock in the wider roost sustenance zone beyond (and elsewhere), and recommend the alternatives above in 5). Allow injections, pour-on and drench formulations of avermectins if strongly recommended by vets as part of a mixed programme to control parasites and avoid resistance to these drugs developing. If used at all, avermectin treatments near bat roosts should be carried out only in the spring at recommended frequencies.

Other key prey species

At certain times of the year some *Geotrupes* species, Cockchafers (*Melolontha melolontha*), tipulid and ichneumonids become important prey items. They may be significant for relatively short periods between April and September, but their densities could have important implications for the survival of bats in the spring or autumn and pregnancy in adult females. Tipulids and ichneumons may enhance the growth of the young if *Aphodius rufipes* populations are reduced by drought or cold weather.

Since the recommendations for moths and *Aphodius rufipes* populations largely determine the overall nature of roost sustenance areas, there is a danger that specific additional recommendations for alternative prey items will overcomplicate advice to landowners. However, a mixed woodland/permanent heavily grazed ecosystem is likely to promote the populations of all of the other key prey species.

The following accounts of each key prey item are brief summaries of their ecology, inasmuch as the information may be useful as background for advisory bodies.

Geotrupes

1) *Geotrupes* is a tunnelling genus of dung beetle digging 30 cm below the soil surface to bury dung. The genus is seasonal, appearing in spring and autumn, and is relatively scarce compared with *Aphodius*, with only 1-2 individuals per cow pat. Very large adult insects (13-25 mm length) with strong spiky legs. It is important in the diet of greater horseshoe bats in spring, but not so much in the autumn, when other prey, such as *Aphodius*, are available. It may be more important in winter when other prey do not fly, in which case cattle grazed pastures near hibernacula may be important for winter feeding (Ransome, 1968, 1971).

Three common species, others rarer. All are nocturnal.:

(a) *G. stercorarius* (L) (16-23 mm; up to 1 g wet mass); common and widespread. Some authors say it prefer horse dung but others say cow dung. It breeds in spring, during April and May, flying from February until May. Two adults per pat maximum.

(b) *G. stercorosus* (=*G. sylvaticus* of Fowler; = *Anoplotrupes stercorosus* Scriba); (13-17mm). Uses cow, human, horse and sheep dung. Spring to summer breeder. Common and widespread, and is said to be forest loving.

(c) *G. spiniger* (Marsh) (16-25 mm; up to 1g wet mass) Common; autumn breeder, flying from late August until late December, but does not breed for 2 months. Its flight period suggests it could be important to feeding during hibernation. It prefers cow dung in semi-shaded sites towards field edges or in sparse woodland. One adult per pat maximum. It has been shown to colonise up to 44.4% of pats in the breeding season. It overwinters as larvae, pupae or as adults.

Life history of Geotrupes

On emergence adult beetles are very frail and light, and must feed for several weeks or months. This period has been called the 'maturation feeding period' (Halffter & Matthews 1966). This may be due to the fact that the protected nest contains only a limited amount of food, enough for larval and pupal development, but not enough for egg maturation. *Aphodius* sp. show the same delay.

Dung is found by olfaction, by flying for unknown distances. During maturation feeding, high nitrogen content of dung may be more important than carbohydrate, and explains the habit of visiting omnivore dung at this time in some species, whereas breeding takes place using herbivore dung. Protein is needed to build up muscles in both sexes, and eggs in females. At the end of the maturation feeding period the body mass has increased substantially, and females would be especially nutritious. Possibly greater horseshoe bats wait until then before feeding on Geotrupes - would be in late October or April according to species.

Cockchafer: *Melolontha melolontha*

Adults are very large beetles (20-25 mm long); males: mean mass = 872 mg wet mass; range 695-1055 mg (n = 11); females even larger). Its large size and thin chitinous skeleton makes this a highly profitable prey species as it is also highly nutritious (Hoese and Schneider, 1988). Greater horseshoe bats seem to prefer this species to *Geotrupes* or moths when numbers are high.

Life history of cockchafers

Adults fly from May to June normally, but only for a brief period of a few weeks. Exceptionally fly in mid April. In some years they may swarm. Adults feed on deciduous tree leaves, cutting large holes in the margins, and females fly to pastures with short grass to oviposit and return to woodland to feed again. Bats catch them in transit, swarming near trees or close to the ground when ovipositing. A clumsy flier which is probably easy to catch by bats. Eggs take 5-6 weeks to hatch, and larvae feed on roots of grass, herbs, shrubs and trees, taking four years to develop (Linssen 1959).

Tipulids

In order of frequency in a continuous study over four years by Robertson (1939), who incorporated data previously collected by R.D. Pinchin and J. Anderson, the species over grassland are:

Tipula paludosa (57.4%); *T. obsoleta* (14.4%); *Pales maculata* (7.6%); *P. flavescens* (6.7); *T. pagana* (5.7%); *T. marmorata* (3.7%); *T. oleracea* (3.3%); rest (10 other species.) <1%. each and never more than 2.6% of totals captured.

Life history of tipulids

All species winter as larvae underground. No adults were caught between mid November (16th) and early May. Earliest dates were: 6, 20, 5 and 22 May in sequence of 4 years. Coulson (1962) found that 90% of female *T. paludosa* oviposited within 18 hours of emergence, and daily mortality was high at 29-71% for males; 55-88% for females, so both are very short lived. Barnes (1937) found that *T. paludosa* males lived for 7 days and females 4-5 days, and that about 75% of females mated and oviposited within 24 hours of emergence. All species need short grass for oviposition. Egg hatching and larval success rates benefit from damp conditions, and some species have aquatic larvae.

Robertson (1939) showed a minor maximum peak of populations occurs in May, and a major peak in September. The May peak was due to *P. maculata*, and the September peak to *T. paludosa*. The two extra years converted the May peak to June, but they had no effect on the September peak. The change was due to the reduction in catches of the May-flying *P. maculata*, and the much greater abundance of *P. flavescens*. This seems to be the normal pattern, as only in 1933 was there a May peak. October was the only month in which females predominate over males. This was due to the fact that *T. marmorata* and *T. obsoleta* fly then, and both show a preponderance of females attracted to light traps.

Phenology

Tipula oleracea - flies from early May/early June to end September, or late October. Evidence of 2 broods/year in either May/June or August/September each lasting about 6 weeks.
Pales maculata - first species to fly each year - from early May to end of June mostly.
P. flavescens - flies from early June to late July/early August.
T. paludosa - a few in late June to the end of July, then an increase throughout August and a peak through September (max.- 14th) and a rapid fall in October with a few specimens up to early November. Of 1949 caught only 101 were outside the

August/September period. Possibly two-brooded, but no evidence for a break in adult numbers.

T. marmorata - few from mid September increasing in late September and lasting until late October (32 days activity); single brooded.

T. obsoleta - starts in v. late September and peaks throughout October, suddenly ceasing in early November (30 days activity).

T. pagana - builds up in early October to a short peak in mid-late October and tails off in early November (26 days activity).

Data on the effect of temperature on flight activity is poor, but few seem to fly below 10 °C. All tipulids fly low over the ground, and are clumsy fliers, so are likely to be easily caught by hunting greater horseshoe bats.

Ichneumonids

Only one type of ichneumon was identified in faecal samples, the Yellow Ophion, *Ophion luteus*. It may not be a single species, but a parasitic complex. It is a large ichneumonid (15-20 mm long) which is thought to parasitise noctuid moth larvae. These larvae are subterranean and nocturnal, feeding at ground level from mid summer until late December, before diapausing overwinter. They continue development in the following spring. Hence the parasites are especially active in late autumn, early winter, and in spring. They appear to be able to fly at very low climatic temperatures (Part 1). In order to parasitise their prey females must hunt them at ground level. This may make them vulnerable to greater horseshoe bat predation in a similar manner to tipulids.

Management objectives to promote these key prey species

The management objectives already proposed to sustain high densities of moths and *Aphodius rufipes* provide good conditions for high densities of *Geotrupes*, Cockchafers, and tipulids by either providing dung or tree-leaf food supplies, or short grass on permanent pastures which aid oviposition. High noctuid moth densities will promote the levels of the Yellow Ophion. There are therefore few additional objectives to propose.

They are as follows.

1) Encourage the retention of permanent pastures in order to permit the long life-cycle of the cockchafer to be completed, as well as those of tipulids and *Aphodius rufipes*. Pasture ploughing should be strongly discouraged, at least within the young sustenance zone. In the wider roost sustenance zone permanent pastures should be encouraged as much as possible. Furthermore, no insecticide treatments should be permitted to control cockchafer larvae, leatherjackets (tipulid larvae) or wireworms (larval click-beetles) in pastures. These would seriously affect important prey items for greater horseshoe bats.

2) As tipulid larval development is favoured by damp conditions, any aquatic environments and/or marshes should be retained, or their development encouraged. This would be particularly advantageous fairly close to the roost. Aquatic environments will also favour the production of adult caddis flies (Trichoptera) in certain months, particularly May and late August/September, when other food supplies may be erratic.

PART 3: IMPORTANT FEATURES INFLUENCING BAT MOVEMENTS BETWEEN ROOSTS AND FORAGING AREAS

Introduction

The provision of rich foraging areas within the roost sustenance zone will be of little use if the behaviour of the bats does not permit access to them. Observations of greater horseshoe bats leaving to forage from maternity roosts show that this species strongly adheres to regular flight paths which may extend for considerable distances. Flights are close to the ground and mostly beneath vegetational cover. Paths may be changed during a summer season, such as when the bats switch from woodland to pasture feeding, but recur annually with a similar pattern unless vegetational features change substantially.

Roost exit flight paths are never directly out into open areas unless bats have no alternative routes. This behaviour is in contrast to exit flights of many vespertilionid bats which emerge out directly into open areas at high levels, and disperse rapidly in many directions. The flight behaviour of greater horseshoe bats may result from predation pressure (Speakman, 1990, 1991), and would account for the tendency for this species to emerge later than pipistrelles. Pregnant greater horseshoe bats, which progressively lose agility as pregnancy progresses, emerge when it is almost completely dark just before giving birth. In contrast, early in the spring and when in mid to late lactation, they often emerge in much lighter conditions (*pers. obs.*). These periods are both times of nutritional stress, and indicates that these bats are constantly having to choose between the risks of predation and those of starvation. Certainly, exits from roost buildings always shows frequent circling behaviour by the first individuals which leave, suggesting that light-sampling behaviour is taking place. When in the field they fly fast across open well-lit spaces and head for cover.

Habitats around roosts should therefore reflect these behavioural restraints, which may restrict or prevent access to favourable foraging sites. Since in my experience practical problems vary with roost distance, I will consider habitat features in two sections; those close to the roost, and those away from it.

Important habitat features close to roosts

Jones *et. al.*(1995) found that emergence times of bats from two maternity roosts separated by about 2 km varied by from 5 to 37 minutes in the summer. The earlier emergence occurred at the site within woodland, which was much darker than the one located in the roof of a house. If this also affected returns at dawn, it would mean that bats may lose up to an hour's foraging a night as a result of high natural light levels at roost exits. Since darkness only lasts about 5 to 6 hours in late June, this may have serious consequences by delaying births of pregnant bats. Birth-timing has been shown to be crucial to the long-term survival of cohorts of greater horseshoe bats, and bat populations

(Ransome, 1989, 1995). Clearly no artificial lighting should be present around roost exits since they would make emergences even later.

Outside the roost exit, suitable cover should be present to provide darkened flight paths to assist safe departure into the wider habitat. Problems are most likely to arise at roosts located in occupied buildings, especially if extensive open lawns surround them. Lines of trees, tall shrubs or fences and buildings may all be suitable for cover.

Important habitat features away from roosts

Jones and Morton (England), Duvergé (England), Bontadina (Switzerland) and Pir (Luxemburg) have all carried out serious and extensive radio-tracking studies of greater horseshoe bats. The behavioural features of travelling and hunting bats they describe, both published and by personal communication, are remarkably consistent. They are briefly summarised in the following account.

Greater horseshoe bats travelling away from the roost towards foraging grounds (commuting) at distances of up to 4 km radius from the roost, do so along distinct flight paths. Up to three main flight paths radiating in different directions can be used by a single colony, with varying proportions of the colony using different ones through a single summer, possibly as different foraging areas became profitable. The majority (about 70%) of flight paths run along the edges of woods, woodland rides or tall hedges, only rarely crossing open fields. When they do cross open fields, it is normally well after dusk, and rarely on clear moonlit nights. In all cases commuting bats keep close to vegetation or buildings, some of which are used as night roosts, or resting perches for culling insects. They travel at about 1 metre height above the ground or away from vegetation edges.

Hence contiguous lines of vegetation of sufficient height and thickness to provide darkness in the early part of the night, and before dawn, when light levels are still relatively high are highly desirable for commuting bats. These lines should link up important foraging areas to ensure bat accessibility to them. As bats may travel up to 4 km radius from the roost, and woodland blocks are relatively small in many parts of this country, the most effective method of linking such blocks is by tall hedgerows or tree lines.

Features promoting successful foraging by bats

Greater horseshoe bats capture prey by two main methods; continuous hunting on the wing (hawking), and by flycatching from a perch (Jones and Rayner, 1989). Hawking over pasture occurs at low levels, usually between 0.6 and 1.5 m and close to woodland edges or hedgerows. About 95% of all hawking occurs within about 10 metres of hedgerows or woodland edge (L. Duvergé, *pers. comm.*). Perch feeding involves hanging from a suitable projection, such as the end of a bare branch. This is usually at about 1.5-2 metres from the ground, and sheltered by an overhead screen, such as the leaf canopy above it. This behaviour seems to confirm the predator avoidance behaviour seen at roost exits. The bat scans the area in front of it with long constant-frequency ultrasonic pulses, whilst rotating its body axis through 360 °. The short distance from the ground of feeding perches may be set by the minimum detection distances of a range of prey size (Walters *et. al.*, 1995), and also the higher concentrations of many of its prey species close to ground level (referred to in Part 2). The bat intercepts detected prey as it flies past, returning to its perch, where it may cull captures of large prey with inedible or less edible parts.

All radiotracking studies confirm the extensive use made of woodland edges. Duvergé notes, in addition, the use of hedgerows as perching sites, in which case they almost always use the leeward side. Hedgerows are also features along which bats hunt on the wing. It is well known from the work by Lewis (1969a, 1969b, 1970) that hedgerows have important effects upon the distribution of aerial insects. These effects include reduction of windspeed, concentration of insects from adjacent habitats into regions of drag, particularly on the leeward side, during winds, and the generation of substantial numbers of insects from hedgerow plant biomass. These benefits require the hedgerow to be sufficiently broad and thick. The advantages increase with taller and thicker hedges.

Livestock make good use of the shelter provided by hedgerows, woodland edges and specimen trees in park land. They tend to rest near or below such features, and their dung concentrates at these places. This behaviour means that concentrations of dung beetles are likely to form near sites favoured by hunting or perching bats.

The edge effect, which results in high concentrations of fauna at the junction of any two different habitats, is well known. A tall thick hedge is a very efficient method of generating a maximum level of insect prey items using a minimum area of land. Besides promoting access to major foraging areas for commuting bats, hedgerows can be important creators of the physical conditions that enhance insect concentrations and reduce windspeeds for economical hunting flight.

Management objectives to promote early emergence from roosts, safe access to foraging areas, and successful foraging

1) Promote the development of dark regions around the immediate roost exit by restricting the use of artificial lights, and encouraging the development of light screens. These may usefully include evergreen trees and shrubs.

2) Promote the development of shaded flight pathways leading to the nearest wooded areas. These may also be achieved by the use of tree and/or tall shrub lines. They should include species of trees which produce overhanging branches low down in an umbrella-like cover, such as beech, apple or plum trees, not trees like poplar, with vertical branches, which can be spaced out so that their canopy just overlaps. Many small ornamental species would be suitable if the variety has the right shape, and houseowners insist on attractive trees in their gardens.

3) Promote the planting of hedgerows and tree lines across large tracts of fields and pastures to create smaller fields so that hawking bats can utilise a larger proportion of the field area. Convert existing highly trimmed, square-shaped hedgerows into a more bat-friendly state. Hedgerows should be broad (3-6 m across), and at least 3 metres mean height, and include specimen trees at intervals which also grow in an umbrella-like fashion in open conditions. This structure will allow safe perch-hunting over adjacent pastures, and a safe refuge for those that hawk when moonlight levels are high.

4) Promote the replacement of wire fences with hedgerows as in 3).

5) Promote the development of park land, by planting large specimen trees, and groups of smaller ones, on the grazed permanent pastures. If orchards occur with a grazed understorey, they should be retained, with suitable advice on restrictions in pesticide use to prevent insect removal or possible bat poisoning via the food chain. This habitat will also permit sheltered perch-feeding and hunting on the wing.

6) Promote the development of grazed meandering grassy woodland rides with occasional wider glades leading towards other foraging areas, such as pastures. Also create some scalloped indentations into long straight woodland edges. These changes will greatly add to available wind-sheltered edge zone between woodland and pasture, which is highly favoured by foraging bats.

PART 4: LAND MANAGEMENT PRESCRIPTIONS INTEGRATING WITH CURRENT FORESTRY AND FARMING SYSTEMS TO MAINTAIN OR ENHANCE FORAGING AREAS

These prescriptions are divided into three sections. The first section covers prescriptions common to the whole roost sustenance area (up to 3 km around the roost). Sections two and three cover the young sustenance zone (up to 1 km around the roost) and the wider roost sustenance zones separately, since the nature of the desirable livestock management regime of the desirable habitat varies between them.

Prescriptions within the whole of the roost sustenance zone

1) Support the retention of all mature ancient semi-natural deciduous woodland, old orchards and park lands.

2) Support the development of further extensive blocks of deciduous woodland up to about 50% of the total area.

3) Support the replacement of coniferous plantations with deciduous trees gradually over a period of time, avoiding extensive clear-felling.

   NB All woodlands should be permeated by grassy rides, contain grassy glades and be surrounded by regions of permanent pasture, especially close to roosts. They should be managed without insecticide treatments. Glades probably need to be 10 - 15 metres across before they will be used by the bats for feeding.

4) Support the retention of existing hedgerows and tree lines linking areas of woodland. Encourage hedgerow improvement to become 3-6 m wide, mean 3 m high, with frequent standard emergent trees.

5) Support the development of new hedgerows or tree lines, as in 4) above, to divide up large grazed pasture areas to create many smaller fields and link up with blocks of woodland.

6) Support the retention of all grazed permanent pasture, subject to the need to create sufficient woodland and hedgerows.

7) Support the development of further grazed permanent pasture up to 50% of the total area. These pastures should ideally be developed as mixed park lands and small fields separated by substantial hedgerows.

   NB. All grazed pasture should be permanent, and managed without any insecticide use at all. Both are crucial to avoid disrupting supplies of cockchafers and tipulids.

8) Support the retention or creation of marshy or aquatic habitats if feasible.

Prescriptions for grazing regimes within the young sustenance zone

1) If permanent grazing pasture is present at a 50 % level, 157 hectares should be available within 1 km of the roost. Substantial areas of grazed pastures, as park land or small fields with hedgerows, should be as close to the roost as possible. Where there is no other conservation interest, they should be managed to be improved by non-hazardous methods, to provide high levels of grass productivity. This is needed to cope with high densities of livestock between July and September. Unimproved pasture or semi-improve pasture with a high conservation interest should not be improved by the addition of fertiliser.

2) Support the stocking of these pastures with cattle, sheep and possibly a few horses at 1.4 cattle/ha, 8 sheep/ha early in the season as weather permits and rotate between cattle and sheep in specific fields (March -May) to keep a short, but not seriously damaged, sward. This represents 220 cattle or 1256 sheep, which should keep the grass sward short, without serious soil disturbance in wet conditions. Mixed grazing at say 110 cattle and 628 sheep, rotated to reduce parasite problems, is an advantage long term.

   Rest fields in June to allow grass growth recovery which is likely to be necessary, and do not permit silage cutting.

   Graze at 2-3 cattle/ha or cattle mixed with 11-16 plus sheep/ha (maximum level depending on quality/quantity of grass), from the first of July until mid September at least. This represents 314-471 cattle or 1727-2512 sheep if 157 hectares of improved pasture is available. Mixed grazing with sheep, with cattle dominant, is also desirable. If weather permits, continue grazing at lower levels into early October.

4) Support grazing from July onwards using primarily mature cattle; either beef or milking herds.

   NB stocking levels may need to be adjusted in the light of climatic conditions influencing the growth of grass in a particular summer. Numbers of livestock assume 157 hectares of pasture are available within the young sustenance zone. These figures are required to sustain a colony with 100 young (see Part 1).

Prescription for grazing regimes outside the young sustenance zone in the wider roost sustenance zone

1) The roost sustenance zone limits may be up to 3-4 km, but especially 3 km. At 3 km range, and about 50% grazing area levels this means about 1414 hectares of grazed land, of which 1257 ha are outside the young sustenance zone. 1257 cattle, at 1/ha,

or about 6285 sheep at 5/ha, should ideally be present. Mixed grazing of cattle and sheep with rotation among pastures should aid parasite control. At these lower grazing levels longer swards should be freely available to the larvae of noctuid moth species. Stocking levels and patterns of grazing will have to be more flexible than in the young sustenance zone to allow the logistics of the regime specified for that zone.

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APPENDIX A: MOTH POPULATION ESTIMATIONS

There is no method currently available which accurately measures population levels of moths in an area. The problem is exacerbated by two major factors as follows.

1) The moths present in an area consists of resident individuals which have developed locally, and varying proportions of immigrants which may soon move on. The proportions vary with the moth sp. eg Scarlet Tiger moth (*Callimorpha = Panaxia dominula* (L)). lives in discrete residential colonies, the Silver-Y moth (*Plusia gamma*) is largely migratory, moving NNW in spring & summer, and S in autumn (Williams 1958, Baker 1978). The main difference between species is the length of time each spends in its particular habitat before once more leaving to travel across country (Baker 1969). A result of this is that the mosaic dispersion of a species over large geographical regions through time is forever changing (Taylor & Taylor 1977). Despite this mobility, within-habitat stability of numbers of 263 sp. caught at 53 sites was shown over six years (Taylor and Woiwod 1980). Baker 1984 suggested this happens because mobile individuals each make the best decision when to leave an area.

   A consequence of long-distance migration is the smoothing of regional differences in morph frequency of polymorphic species. Large Yellow Underwings (*Noctua pronuba*) has a more or less constant morph frequency throughout Britain (Cook & Sarsam 1981); are long-lived in laboratories (55 days males; 75 females; Singh & Kevan 1965); and probably travel at least 100km (Baker 1985). Baker made this claim partly from the very low recapture rates of moths at Woodchester Park.

2) Traps have different efficiencies in capturing moths, and the relationship between catch numbers and population levels is usually unclear.

   There is a debate about the effective range of light traps. Baker & Sardovy 1978 argue from mark-recapture experiments that the range of attraction is just 3 m to a trap 0.6 m above ground level, and that the angle of elevation is more important than brightness. Other workers argue that the attraction range near the ground is from 100-500m, and that brightness and contrast with background illumination are the critical factors (Hartstack *et al.* 1968; Bowden and Morris 1975). Gregg *et al.* (1994) report personal communication with V.A.Drake and R.A.Farrow who observed radar views around ground-level light traps which showed plumes of insects extending up to 200m from the traps. However, Muirhead-Thomson (1991), after crosswind trapping experiments argues that, although light traps are perceived and influence flight behaviour at much greater distances, they are not effective at catching moths over more than 10-25m. This distance is similar to the findings of Sotthibandhu (1978), who tethered moths and exposed them to a 125 W mercury-vapour lamp raised 9m above ground level. They responded between 10 and 17m.

   Baker (1985) argues that light traps are highly selective to moths, even when they have the right spectral composition (Mikkola 1972), and intensity (Bowden &

Morris 1975). In addition, for a moth to make a mistake and enter the trap its lamp must satisfy critical elevation and vertical dimension criteria. These must mimic the moon's size and position in the sky, so that it affects the dorsal ommatidia of the eyes. Even these factors were not sufficient, as he argued the moth must also be in a physiological state to make use of moon orientation (i.e. in a migratory phase). Supporting evidence for his views included: there appears to be a better correlation between light-trap catch and volume of migration as shown by radar (Schaefer 1976) than between light and suction-trap catches (Taylor & Carter 1961); light-traps are ignored by adjacent nectar-feeding moths (Baker unpubl. data); males, which are probably more migratory than females (Baker 1978) predominate in light catches. Exceptions to the latter include *Noctua pronuba*, in which females have a long pre-ovulatory period (Singh & Kevan 1965) and are probably more migratory.

Most moth migration occurs at heights of tens or hundreds of metres above ground level (Schaefer 1976; Riley *et al.* 1983). If it is the migrant population that is being caught it is likely to be during the low-flying phase at the start or end of migration (Baker & Sadovy 1978). This would be consistent with the findings of Taylor & Carter (1961) that moths fly lower at low densities, and higher at higher densities, if high densities reflect additional concentrated migrating individuals.

I offer the following hypothesis in an attempt to explain these conflicting views. Some species of moths are affected by similar circumstances to locusts when in the larval phase. They remain solitary and resident in an area normally, but become migratory if overcrowded as larvae, possibly in response to low food supplies dwindling in certain 'outbreak areas'. Migratory moths, since they are physiologically programmed to orientate by a distant light source, normally the moon or stars, are most vulnerable to capture in light traps.

Trap capture likelihood, and distance of effective attraction, even in migratory individuals, is also influenced by at least the following factors.
(a) The lamp intensity and vertical size; (b) prevailing contrasting illumination intensities; (c) its elevation from the moth's flight path; (d) competing point sources of light which may distract; (e) screening by obstacles especially nearby, which allow escape; (f) levels of cross-wind. The flight power of the moth species is also likely to be a factor in its capture rate.

Clearly some moth species are always resident (eg Wood Tiger), and others highly migratory (eg Large Yellow Underwing and other noctuids), but not completely so. If the migratory urge is variable as suggested, and related to population densities in outbreak areas, probably to the south of Britain, in continental Europe, the great variation in migration levels observed may be explained.

APPENDIX B: FACTORS INFLUENCING POPULATIONS OF SOME IMPORTANT MOTH SPECIES

(Data mainly from Carter & Hargreaves, 1986 and South, 1961)

1) ***Noctua pronuba* (L.) (Large yellow underwing)**
Habitat: agricultural land, gardens, waste ground, open country, moorland where suitable plants grow. **Food plants:** dandelion (*Taraxacum officinale*), chickweed (*Stellaria media*), dock (*Rumex*), grasses and a wide range of herbaceous plants, - wild and cultivated. including dog violet (*Viola riviniana*) and primrose (*Primula vulgaris*), present in woodlands. **Life-history:** one generation per year; eggs laid in compact flat masses on underside of leaves in July and August. Hatch in August. Feed until mid-winter before diapausing, completing growth in spring. Eat leaves and stems. Active at night, sheltering in soil by day. Pupate in May in subterranean cocoons. Emerge in June or July and fly until late August; rarely September and October.

2) ***Noctua (=Euschesis) comes* (Hübner) (Lesser yellow underwing)**
Habitat: meadows, gardens, waste ground, hedgerows, open woodland, heaths. **Food plants**: as for *N. pronuba*, but also foxglove (*Digitalis purpurea*), heather (*Calluna vulgaris*), sallow (*Salix*), hawthorn (*Crataegus monogyna*), blackthorn (*Prunus spinosa*) and silver birch (*Betula pendula*). **Life-history**: one generation per year. Eggs laid in August and hatch in September. Larvae feed for a short time on low plants before diapausing over winter. In spring they become active and feed on low plants again, but also ascend tree trunks to feed on newly emerged foliage after bud-break. Mainly nocturnal activity shown. Pupate in underground cocoons in May, and adult moths normally fly from July to August.

3) ***Agrotis exclamationis* (L). (Heart and Dart)**
Habitat agricultural land, meadows, gardens, waste land and other places where suitable food plants grow. **Food plants:** dock (*Rumex*), plantain (*Plantago*), chickweed (*Stellaria media*), fat hen (*Chenopodium album*), turnip (*Brassica rapa*), sugar beet (*Beta vulgaris*), and many other herbaceous plants. **Life history**: one generation per year; eggs laid on leaves and stems in June, caterpillars hatch in July. They feed at night on roots, stems and leaves, hiding under soil by day. Fully grown by autumn; burrow into soil and diapause as larvae overwinter; pupate in spring and emerge as adults flying in June and July; sometimes in September as well.

4) ***Apamea (=Xylophasia) monoglypha* (Hufnagel) (Dark Arches)**
Habitat: meadows, moorlands and other grassy places. **Food plants**: cocksfoot (*Dactylis glomerata*), couch grass (*Agropyron repens*) and other grasses eaten, including their roots. **Life-history**: eggs laid in July; hatch in about ten days; caterpillars August-April/May. They feed at night at the base of stems. Pupate in May under soil. Emerge as adults flying from June to August; and sometimes also in September and October.

APPENDIX C: THE ECOLOGY OF *APHODIUS RUFIPES*

Aphodius is a very ancient genus, having been found in Baltic amber from the Lower Oligocene, 40 million years ago. Its distribution is virtually world-wide, as long as there are large grazers present. *A. rufipes* is known from Pleistocene deposits found at Isleworth, Middlesex, 43,000 years ago, and at Barton Court, Oxfordshire in late Roman times, 1,600 years BP (Cambefort, in Hanski and Cambefort 1991). Hence nocturnal *Aphodius* species have been potential prey items for bats over major time periods, and possibly since *Rhinolophus* evolved at least 35 million years ago.

Research findings relevant to comments made in Part 2.

Adult features:

1) Its relatively large size (93 mg live mass), and the fact that most of it is eaten (*pers. obs.*) means that between 50 and 70 beetles permit a full feed for one bat. In an hour a bat could easily catch and consume these numbers as this allows a detection, capture, handling and consumption time of 51 to 67 seconds/beetle caught, if they were freely available.

2) *A. rufipes* was the most sensitive to desiccation out of 8 species tested. Death provoked in 10 hrs at 0% RH and 20 °C. (Landin 1968).

3) Adults avoid temperatures <9 and >19 °C; preferred range is 14-17 °C. Cold stupor sets in below <6 °C, and convulsions & death >38 °C. Flight can occur above 9 °C. (Landin 1968), which is one of the lowest levels for the genus.

4) Normal flight direction is against the wind as it uses olfaction to find dung (Landin 1968). High winds are thought likely to suppress flight. Low winds assist in fresh dung location using the antennae and possibly maxillary palps (Landin 1968).

5) No activity was observed outside dung in heavy rain - possibly due to lack of olfaction clues (Landin 1968).
"It should be presupposed that extremely strong winds and continuous heavy precipitation constitute definite impediments to all activity, particularly flight, outside the droppings." (Landin 1968).

6) The membranous structure of the mouthparts of adults and the narrow channels of the mandibles force them to feed on fluids (Landin 1961). Hence fresh cow pats are a preferred diet. This is especially true in exposed habitats as dung dries rapidly. Less so in shaded habitats where horse dung is often used.

7) Eggs laid in dung; rarely in soil, in batches of about 5 (White 1960, Holter 1979). About 20-25 laid altogether (Schmidt 1935). Smaller Aphodius species are claimed to produce about 100 eggs per female (Holter 1979, Yasuda 1987). As ovaries

contain only 3-6 ovarioles, a period of recovery is needed between laying phases (Schmidt 1935). When females emerge from pupae they have immature ovaries (Madle 1934, White 1960) - need 1-6 weeks period to develop eggs and mate. A further period of 1-2 weeks or more elapses before females lay eggs (data from isolated females - Landin 1961).

8) As all dung rapidly dries out, especially in exposed positions (Landin 1961), points 5) and 6) above mean that adults are constantly forced to leave their dung supply and fly in search for fresh ones. Furthermore its nutritional value may deteriorate rapidly. Most adult *Aphodius* have left cow pats by the second day (Laurence 1956). This means they concentrate in regions with fresh pats and are repeatedly exposed to predation by bats. *Aphodius* females move longer distances and/or move more often than males (Hanski 1980a) and so disperse widely. Foraging greater horseshoe bats are known to follow cattle moved into new fields on the day the cattle are moved and feed on dung beetles attracted by the new dung (L. P. Duvergé *pers. comm.*). Maximum distance of attraction in the field is not known, but in experiments adults responded to dung from at least 40 cm in still air (Landin 1961). Landin refuted the claim of previous authors (such as Warnke 1931, 1934, and Madle 1934) who were of the opinion that their olfactory capabilities were very small. He argued that winds attract beetles from considerable distances, and stated that fresh dung placed in a field without other droppings would attract beetles within minutes. He also quoted a situation where fresh dung was placed on an isolated island 10 km from the nearest grazed island, and beetles arrived to feed on it. Furthermore Hanski attracted large numbers of *A. foetidus* to a dung trap in the centre of Oxford, several kilometres from the nearest cattle pastures.

9) Emigration rates from dung are density dependent at high densities (Landin 1961). Rates increase if they have < 25-70 times their volume of dung available per adult. An average cow pat of 1500 cm3 volume could support from 178 to 500 adults (max. = 63/pat observed by Holter 1975).

10) Denholm-Young quotes mean figures from 15 studies as follows. Grazing season = 188 days; average stock level (cattle) = 1.4 per ha; pats/cow/day = 11.9.

This translates into 16.7 pats/ha/day, and a maximum of 1052 adult beetles/ha/day. At 93 mg wet mass/adult this represents about 98 g/ha/day, or about 0.1 kg/ha/day of adult beetles. Adult bats eat about 3-4 g of wet mass of insect food/feed, or 6-8 g/bat/day. Juveniles eat from 0 to 3 g/bat/day between 29 and 45 days of age whilst they feed close to the roost at a distance of up to 1 km. This covers an area of 314 ha. If all the area was grazed pasture 0.1 x 314 = 31.4 kg of adult beetles could arrive at fresh pats per day. 100 pre-weaning young bats eating 3 g/day would consume 0.3 kg adult beetles/day if they ate no other food. This represents about 1% of available beetles if they were at maximum densities in the pats.

In practice stocking levels of 2-3 cows/ha can be maintained from mid July to late August in most years, so only 50% of the close surrounding habitat (157 ha) of a roost needs to be grazed pasture to keep predation levels at about 2%. There are allowances for lower levels than the maximum in the pats, since predation levels can probably reach 5%. Furthermore, since juveniles are normally born over a three week period, and since they steadily increase their foraging range after they are 30 days old, several hundred juveniles may be supported by these stocking levels.

If 157 ha of the land around a roost up to a distance of 1 km (50%) is grazed by cattle at 2-3/ha it means that 314-471 cattle should be kept to sustain a bat colony with 100 young. Smaller colonies may require lower stocking levels, but it is probably inadvisable to drop much below 100 cattle within the young's sustenance range (0.7 km). This is because low densities of fresh dung from grazers are much less attractive to colonising dung beetles than high ones, and population levels of adult beetles may fall disproportionately.

11) Adult greater horseshoe bats travel much further than pre-weaned young - up to 4 km; mean 2.84 + 0.91 km (Jones et al. 1995). At 3 km range they may feed over 2828 ha. If 50% of the area outside the young sustenance zone is grazed pasture (1257 ha) with 1.4 cows/ha and adult beetles = 0.1 kg/ha/day available it should generate 126 kg of adult beetles. A colony of 700 adults eating g/bat/day within this range would consume 5.6 kg beetles/day if they ate nothing else. This represents about 4.4 % of those in the area. Since fresh dung may attract beetles from a distance of many kilometres (see 8) above in Research Findings) the removal of a part of the local population by bat predation may promote immigration from further afield, if grazers are abundant there. Furthermore, in most years adult bats feed mainly on moths (Part 1) so the densities of cattle could be lower than 1.4 /ha without serious risk of shortages, especially as moths are only likely to be in short supply in cold wet summers. Such weather promotes the levels of *Aphodius rufipes*.

The key requirement may be the presence of abundant grazers, especially cattle and horses, within the 1 and 3 km radii. The most crucial for juvenile growth and survival, as well as helping reduce commuting distances for lactating females, will be 2-3 cows/ha in the 157 ha of grazing pastures which should be available (50% of 314 ha @ 1 km radius from roost). This area can support 314-471 cows for a short period between July and August, and up to 220 long-term.

The number of grazers in an area is crucial to the level of populations of dung beetles. In southern France in the mid nineteenth century, tens of thousands of sheep and goats used to be driven from the Garrigue to Mont Aigoual for the summer. Rural depopulation of grazers followed at the end of the century and intensified in the twentieth century. Many species of dung beetle became rare or extinct in this region, whereas in other regions where grazers did not decline, a rich fauna of dung beetles persisted (Lumaret and Kirk 1991). Similar losses of dung beetle populations are now occurring in northern Italy and Spain as grazers are removed.

12) To ensure against climatic disasters, a mixture of habitat types should be provided. These must include exposed cattle-grazed fields, preferably of different

topographical orientation (south and north-facing), surrounded by suitable hedges for perch-feeding, cattle-grazed parkland and/or grassy orchards, and deciduous woods or forests criss-crossed with woodland rides. The latter two habitats are particularly suitable for horse grazing.

Such a habitat range, suitably arranged in mosaics, should offer a large edge zone, and regions of woodland with a rich diversity of herb-layer plants. These woods should allow feeding in spring and autumn at critical marginal climatic temperature levels (Jones et al. 1995), and promote good supplies of maybugs (*Melolontha melolontha*) in May/June, and moths from June onwards. In mid to late summer adult bats usually feed on large moths whenever they are abundant, in preference to *Aphodius rufipes*. Juveniles appear to be unable to feed on moths until they are at least 40-45 days old, possibly because they are unable to compensate for Doppler-shifts in echolocation. Moths are much faster fliers than *Aphodius* beetles. Hence juveniles are critically dependent upon *Aphodius rufipes* (usually) or other small weak-flying insects.

13) Although different types of grassland have different dung insect faunas (eg Merritt and Anderson 1977), this factor is not so important to *Aphodius* sp. This is because almost the whole life cycle occurs within the dung.

Requirements of the larvae of *Aphodius rufipes.*

1) The average population of larvae of about 100 passes 40% of its pat through their gut (Holter 1975).

2) A single pat can have up to 9 *Aphodius* species adults and 1 *Geotrupes*, but only 3 larval species at any one time (Denholm-Young 1978). This is because adults can feed on a variety of fresh dung in many habitats, but adults are much more selective in both before laying eggs. Eggs are much less aggregated than adults (Holter 1979). Second instar larva needs from 200-400 times its volume of dung for optimal development, and 3rd instar larvae from 60-150 times (Landin 1961), or 2-3 cm^3 dung per 2nd instar larva, $5cm^3$ per half-grown 3rd instar larva. Densities of larvae can average 100 per cow pat, passing 40% of pat through their gut (Holter 1975). Larvae migrate vertically through the dung to obtain their preferred temperatures (Landin 1961) and so may compete for food supplies at high densities. If the densities of larvae exceed the requirements listed above, the larvae either force each other out of the dung, or bite each other to death (Landin 1961). This is especially likely to occur in the field as densities of all *Aphodius* species may reach several hundreds (Merritt 1974) or even thousands (Mohr 1943) per pat. Competition between species within dung in Landin's experiments gave no indication of one species being superior to another. Larger species, such as *A. rufipes* were not superior to smaller ones. However, in competition with dipterous larvae, Aphodius larvae are superior, since the former lack biting mandibles. High densities of dung beetles in dung are known to suppress populations of dipterans.

3) Larvae are more susceptible to desiccation than adults, and as they are unable to leave the pats before completing their larval life history, dehydration of the dung leads to major mortality. They have 3 larval instars and a pupa. The first larval instar is most vulnerable to desiccation. The third instar larva hibernates over winter within the pat in Sweden (Landin 1961) when desiccation is unlikely. It leaves the pat and pupates in the surface layers of the soil in spring. White (1960) states that adults also can hibernate in England.

4) Time needed for development is temperature dependent. In summer complete larval development can occur in 4 weeks (Landin 1961).
Landin's timings: Eggs hatch in 3-5 days; 1st instar = 2-4 days; 2nd instar = 3-8 days; 3rd instar = 3-5 weeks when hibernation starts. Third instar larvae must finish development before hibernating as it is incapable of feeding on dung in the spring. This may be due to dung quality deterioration over winter.

5) The pupae of *Aphodius* generally last from 1-4 weeks (Landin 1961, Holter 1975, Stevenson and Dindal 1985), but specific details for *A. rufipes* are not available. It may last much longer as adults do not usually start to fly until late May, or early June (Hanski 1979).

6) Larvae are capable of feeding on the coarser fibres of cattle dung because they have powerful sclerotised mandibles, and larger mouths than the adults (Landin 1961).

7) Dung characteristics allowing the completion of larval life history include:
(a) retention of enough water to prevent desiccation
(b) remaining within the thermal range (-4 to 46 °C, (Landin 1961)).

8) Larvae can develop in cow, horse or sheep dung. Landin (1961) experimentally tested adult *Aphodius* beetles' response to cow, horse and sheep dung. He found all species were attracted by all kinds of dung, but less so to horse dung with the exception of *A. rufipes*. This attraction may reflect the feeding requirements of the adults (see above), rather than their suitability for larval development. He felt that generally it was not the kind of dung that mattered, but the climatic conditions of the environment, particularly affecting the microclimatic conditions within the dung, which restrict dung beetles to a certain habitat.

9) Different types of grassland have different dung insect faunas (eg Merritt and Anderson 1977), but such differences are not so important to *Aphodius*, which breed within the dung. Hence *Aphodius* sp. are less affected by soil type and vegetation cover. These factors may exert small effects via their influence on dung desiccation rates.

10) The abiotic environment in which the dung is dropped has a profound effect on the composition of its fauna (Mohr 1943) as it controls its desiccation rate and temperature range, and each *Aphodius* species has its own characteristic tolerance ranges (Landin 1961). So does seasonality since each species has its own period of

activity (Hanski 1980b, 1986, Holter 1982). Landin (1961) classified Aphodius into 3 groups as follows:

i. Eurytopic - wide range of habitats selected
ii. Oligotropic - reasonable range
iii. Stenotopic - narrow range. *A. rufipes* is eurytopic.

11) The key to successful completion of larval development is the retention of sufficient water within the dung (see comments on species survival above - points 3) and 9).

APPENDIX D: LIVESTOCK AND THE USE OF ANTHELMINTICS

Introduction

Grazing livestock may suffer from the activities of many parasites, including gutworms, lungworms, tapeworms, liver fluke and a range of ectoparasitic arthropods including ticks, lice, warble flies and blood-sucking insects. They may seriously affect the health and growth of livestock, and hence the financial return to farmers.

Chemicals which control one or more endoparasitic worm group are called anthelmintics. Some also control ectoparasites as well.

Notes on specific chemical groups used as anthelmintics

Source: 'Farmers Weekly' April 12 1991. Mainly derived from Joint Nature Conservation Committee leaflet 'Chemical Alternatives to Treatment of Cattle with Ivermectin'. D. McCracken (Dept. Agric. & Env. Sci. The University, Newcastle), & E Bignal (JNCC)

Key to abbreviations used for parasite groups:

GTW= gutworms; LGW= lungworms; TPW= tapeworms;
LVRF= liver fluke; EP= ectoparasites (including larvae of some insects which penetrate the body)

BENZIMIDAZOLES Effective against GTW, LGW, TPW, and some control of LVRF. Given by mouth; Oxfendazole can also be injected into rumen or used in pulse-release devices ('Autoworm' or 'Synthanic Multidose'). Usually administered at start of grazing season. Also fenbendazole ('Panacur^R, Hoechst'). Alternative to avermectins.

IMIDAZOTHIAZOLES Effective against GTW, LGW only. Given by mouth, injection and pour-on. 'Levamisole^R' preparations should not be given simultaneously with organophosphorous preparations, or for 14 days before or after treatment. Alternative to avermectins.

TETRAHYDROPYRIMIDINES Effective against GTW only. Morantel tartrate is currently sold as a slow-release device in cattle which is effective for 90 days ('Paratect^R Flex Bolus'). It gives no protection against lungworms, so a vaccination programme is needed in conjunction with it. Alternative to avermectins.

SALICYLANILIDES & SUBSTITUTED PHENOLS Effective against LVRF, and partially protects against GTW, TPW and EP.

SYNTHETIC PYRETHROIDS Effective against EP only. Applied as sprays, impregnated in ear tags against flies, or as a pour-on. Persist well on coat or skin, but not in tissue. Valuable against skin parasites e.g. lice, ticks some mites and nuisance flies. Low mammalian toxicity, but very poisonous to fish and crustaceans.

ORGANOPHOSPHATES Effective against GTW and EP only. Some, e.g. 'Coumaphos^R', used as powders for use against lice and fleas. Others, e.g. 'Chlorpyrifos^R', are used as sprays for tick control. Some can act systemically, via mouth or as a pour-on, to control warble fly larvae, lice and mites causing sarcoptic and chorioptic mange of cattle. Short-lived in animal tissues but last a reasonable time in the coat. Dangerous to operators using them, so needs special protective measures. Residues of 'Dichlorvos^R' in horse dung can have an adverse effect upon dung beetle fauna, and magpies have died after feeding on the backs of cattle treated for warble fly.

AVERMECTINS (fungal fermentation products) Effective against GTW, LGW and some EP e.g. sucking lice and warble fly. Can be administered as drench (pour-on), oral paste, subcutaneous injection or bolus. Has serious impact on dung fauna life cycles, especially those of cyclorhaphous flies and dung beetles. Includes 'Ivomec^R, MSD Agvet', 'Ivomec^R, SR bolus, MSD Agvet', 'Avomec^R, MSD Agvet' and 'Doramectin^R, Pfizer'.

MILBEMYCINS (fungal fermentation products) Effective against GTW, LGW and EP. Recently developed by Cyanamid of USA. Moxidectin tested by Strong and Wall (1994) on cattle and shown not to be toxic to dung fauna larvae. Includes'Cydectin^R Cyanamid'.

NB Whichever chemical is used, it is important to read instructions carefully in relation to the pest type controlled; class of stock recommended; limitation as to use; dose rate and the withholding period. Farmers should consult a vet to develop a control strategy designed for the farm which preferably does not rely too heavily on stock chemical treatment.

AVERMECTINS

These are compounds belonging to a family derived by fermentation from a naturally-occurring soil actinomycete, *Streptomyces avermitilis*. They were discovered in the mid 1970's. Synthetic derivatives are now available, such as avermectin B1, which has two homologes, $B1_a$ and $B1_b$. Ivermectin is a mixture of the two homologes, and is marketed and sold for use in cattle as 'Ivomec^R, MSD'.

Control programmes for treatment using ivermectin were given in Part 2.

Control of infections in young animals may require several treatments, or use of a pulse-release bolus. This strategy allows young cattle to graze the same pasture early in the grazing season until pasture contamination with infective larvae becomes high. They are then treated with an anthelmintic to remove existing burdens and transferred to a parasitologically 'clean' pasture; the so-called 'dose and move' strategy.

Some farmers do not treat until a clinical problem occurs, and a therapeutic treatment is then required to prevent cattle losses. Whichever program is adopted, a strategic treatment at the end of the period of transmission is commonly recommended ro remove burdens acquired late in the grazing season. On some farms this may be the only treatment administered in a year. The avermectins and some of the benzimidazoles can be very valuable at this time because of their good efficacy against *Ostertagia ostertagi* adults and larvae. Avermectins also remove several potentially damaging ectoparasites, including lice, mange mites and warbles (Ryan & Guerro, 1987).

Treatment of second season animals may also be undertaken, but at reduced frequency. Adult dairy or beef cattle are rarely needed to be treated. In horses a bi-monthly treatment schedule during the period of risk has proved effective in helping prevent adverse effects of the main target parasites including large and small strongyles and stomach bots.

METHODS OF ADMINISTRATION OF IVERMECTIN TO LIVESTOCK

Ivermectin can be used to treat livestock in four possible formulations. These are listed in the following table, with details of the livestock concerned, and the nature of the ivermectin medium used.

Table 1: Source Steel, 1993

Ivermectin formulations for livestock; dose rate is 200 μg/kg except where indicated

Admin. route	Species	Ivermectin. conc. (%, w.v)	Formulation
Subcutaneous	Cattle,Sheep	1	non-aqu. soln.
Oral Drench	Cattle	0.4	"
	Sheep,Goats	0.08	Aqu. micelle
	Horses	1	"
Oral Paste	Cattle	0.15	N/A
	Horses	1.87	
Topical (pour-on) 500 ug/kg	Cattle	0.5	N/A
Intrarum. bolus 40 ug/kg/day for 120 days	Cattle	0.5	Osmotic pump

Ctle = cattle
Topical (pour-on) = 500 μg/kg
Intraruminal bolus for cattle uses an osmotic pump (lasts 120 days).
Non-aqueous solution = 60% propylene glycol: 40% glycerol formal (v/v) for cattle injections & 100% propylene glycol for cattle oral drenches. For sheep, goats and horses the oral drench is an aqueous micellar solution of ivermectin which is formed with a surface-active agent, polyoxyethylene sorbitan monooleate, and cosolvents, glycerol formal and benzyl alcohol.

Does the formulation used and its method of administration matter?

Steel (1993) states that the biological half-life of ivermectin in plasma is similar in cattle (2.8 days) and sheep (2.7 days), but because of a larger volume of distribution, plasma clearance is more rapid in sheep. However, injection of a (tritium labelled) subcutaneous formulation of ivermectin prolongs plasma residence time and persistence of residues in liver and fat. Increasing the organic solvent content of subcutaneous formulations slows the release of drug from the injection site and thereby prolongs its presence in the bloodstream. (Lo et al, 1985: half life 2.0 days with aqueous micelle; 3.7 days in mixed aqueous micelle/glycerol formal 50:50 v/v; 8.3 days non-aqueous propylene glycol-glycerol formal 60:40 v/v.) Because ivermectin and its metabolites are mainly excreted in bile, residues continue to appear in faeces for substantially longer after subcutaneous injection compared with oral dosing. At least 98% of the ivermectin dose is excreted via the dung no matter what administration route is used (Halley et al., 1989; Chiu et al., 1990).

Pour-on applications and aqueous based injectable formulations in cattle may therefore reduce the impact of ivermectin treatment on dung fauna (Sommer *et al.*, 1992) compared with organic solvent-based ones. Binding of avermectins to digesta particulates during gut transit may potentially lower drug bioavailability and also contribute to faecal residues. Further research on formulation and dosage strategies is advocated to increase bioavailability at the gastrointestinal site of action, so that both dose rate and faecal residues can be reduced.

REPORT OF THE UNITED STATES DRUG ADMINISTRATION (Bloom and Matheson, 1993; small part only.)

Chemicals introduced into the environment tend to distribute within and between environmental compartments (air, water, soil, and biota). This distribution pattern will, in large part, determine whether or not organisms present in a compartment will be exposed to levels of chemicals sufficient to cause adverse effects.

Certain physical or chemical properties can be used to predict a chemical's potential for distribution among compartments. Ivermectin's very low vapour pressure indicates that it is unlikely to enter the atmosphere. It has low water solubility (<4 mg/l), but the K_{ow} value indicates a moderate affinity for lipid-like material.

Tests to find the ability of ivermectin to distribute between soil and water were conducted. A soil sorption/desorption test, a soil column leaching test and a soil thin-layer chromatography test all confirmed that avermectin compounds appear to bind very strongly to a wide variety of soil types. The distribution adsorption coefficient, expressed on the basis of organic carbon in the soil (K_{oc}) for ivermectin has been reported to be between 12600 & 15700. These values show very strong binding to soil. Ivermectin appears to be very immobile and would not be expected to readily transfer into the aquatic environment from animal-waste contaminated soils. Ivermectin in aquatic systems would be expected to bind tightly to sediment or particulates.

ACTUAL EFFECTS OF IVERMECTIN INTRODUCED TO THE ENVIRONMENT

Halley *et al.* (1993) gave the following summary of abamectin B1 and ivermectin effects following research in the Merck Laboratories in New Jersey. Numerous environmental fate and effects studies have been carried out and reviewed. Both are immobile in soil, rapidly photodegraded in water (half-life 0.5 dys in summer) and as thin films on surfaces (half-life <1 dy), and aerobically degraded in soil (ivermectin in soil/faeces mixture = 7-14 dys half-life; avermectin B1a = 2-8 weeks) to less bioactive compounds. Abamectin is not taken up from the soil by plants, nor is it concentrated by fish. *Daphnia magna* is the fresh water species found to be most sensitive to ivermectin & avermectin (LC50 values of 0.025 & 0.34 ppb respectively). fish (e.g. rainbow trout) are less sensitive (LC50 values of 3.0 & 3.2 ppb respectively). In the presence of sediments, toxicity towards *Daphnia* is significantly reduced. Neither chemical has any significant antibacterial or antifungal activity. They display little toxicity to earthworms (LC50 values of 315 ppm & 28 ppm in soil for iverm. & abamect. resp.) or avians (abamamectin dietary LC50 values for bobwhite quail & mallard of 3102 ppm & 383 ppm resp.) and no phytotoxicity. Residues of the avermectins in faeces of livestock affect some dung-associated insects, especially their larval forms. This does not delay degradation of naturally formed cattle pats under field conditions, however, in some cases, delays have been observed with artificially formed pats. Based on usage patterns, the availability of residue-free dung and insect mobility, overall effects on dung-associated insects will be limited. As they undergo rapid degradation in light and soil, and bind tightly to soil and sediment, they will not accumulate and will not undergo translocation in the environment, minimising any environmental impact on non-target organisms resulting from their use.

DUNG DEGRADATION

Wall & Strong (1987) & Strong & Wall (1988), using data from cattle dosed at 40 ug/day with continuous intraruminal dosing, concluded that degradation of manure pats was prolonged and populations of dung-degrading insects in pats were decreased. The sustained release formulation was estimated (Strong and Wall, 1988) to lead to concentrations of 400 or 500 ug/kg ivermectin in the faeces. This compares with a peak of 80 ug/kg between day 3-7 post dose with pour-on; decreasing to 13 ug/kg at day 42. Also treatments with pour-on or injections are a maximum three times per year, compared with 120 days for bolus.

Ivermectin is therefore not likely to be a problem in the wider environment. It is its failure to degrade within dung, and its impact on the dung fauna which are causes for ecological concern, especially with the use of a bolus.

AVERMECTINS AND THEIR EFFECTS ON DUNG INSECT FAUNA

1) VIEW OF A. B. FORBES, 1993, REPRESENTING MERCK SHARP AND DOHME.

How much avermectin is used world-wide?

The answer to this question is pertinant since the amount used will influence the levels of possible environmental damage worldwide.

Forbes used these figures: 1.3 billion cattle world-wide; An average cow treated is about 200 kg mass (allowing for the smaller size of those actually treated); assumed all avermectin sold in 1991 was used, and that each cow was treated once, then 15% of the world's cattle were treated. The figure falls if some were treated more than once in the year. In North America. where about 111 million cattle exist, about half receive no anthelmintic treatments at all. Just over half of the remainder (about 25%) were treated with avermectins, with an average dose rate of 1-1.3 per animal/year. Younger cattle are treated more often than adults. If seasonal sales reflect usage, 40% of the sales of avermectins occur in the fourth quarter of the year, coinciding with large intakes into feedlots, calf weaning, and movement to winter grazing. World-wide the sales show a similar pattern; a peak in 4th quarter; a secondary peak in the second quarter. The secondary peak not only reflects sales in the southern hemisphere, but also use in young stock in the early grazing season, particularly in Europe.

Forbes consideration of the ecological impact of avermectins

Daily faecal production by cattle is about 6% of body mass (Marsh & Campling, 1970). Forbes estimates for a typical herd: young stock contribute about 20% to total dung deposited by a beef herd, and <5% by a dairy herd. Treatment of young animals would result in only a small proportion of their faeces containing residues, thus further reducing the potential for any effects. Seasonal treatment patterns show that many ivermectin treatments occur when the insect dung fauna are reduced and inactive e.g. during temperate winters and subtropical dry seasons. This would further reduce the potential of avermectin residues to affect local pasture ecology (Ridsdill-Smith, 1988). Grazing milking herds provide further sources of dung free of faecal residues of avermectins.

Many members of the insect dung fauna colonise dung from species other than cattle (Halffter & Matthews, 1966; Fincher et al, 1970; Skidmore, 1991), and hence the untreated other animals supply further food supplies. Treatments are rarely administered simultaneously to all cattle on the same farm, so alternatives exist. Adjacent farms are likely to be out of phase in their treatments.

Although the number of treatments of horses is potentially greater per year, the oral formulation of ivermectin used does not result in persistent excretion and faecal residues. Activity is not normally detected later than 72 hrs after administration (Ewert et al, 1990; Herd et al, 1990). Horses produce dung at a rate of 3% of body mass/day (Rossdale, 1976) ie a 600 kg horse would produce 18 kg dung/day or 6.57 tonne/year. If it were treated 3 times during a grazing season, no more than 5% would contain residues.

Forbes conclusions

Any potential ecological impact resulting from the use of avermectins in large animals world-wide should be limited by the dilution effects of untreated animals, lack of synchrony of treatments, the timing of treatments often not coinciding with the main dung insect breeding seasons, treatment of housed or penned animals and the limited period of time after treatment when sensitive dung feeding insects are at risk. Gross effects on dung degradation or pasture availability have not been observed following the use of avermectins under commercial conditions which have been in operation for 10 years or more, and on experimental farms for 15 years. Improved health and performance resulting from control programs utilising avermectins in cattle and horses could not be expected to be sustained if pasture ecology and quality were adversely affected by their use.

2) VIEW OF INDEPENDENT DUNG FAUNA ECOLOGISTS

Strong (1992) reviewed the available evidence on the impact of ivermectins on dung insects, and McCracken (1993) considered the potential of ivermectins to affect all types of wildlife.

STUDIES OF COLEOPTERA AND DIPTERA FEEDING ON DUNG

Toxicity to adult beetles entering contaminated dung appears to be low, but studies have shown effects do occur. The age of individuals may be important e.g. *Copris hispanus* and *Onitis belial* adults die if they are newly emerged in the dung of cows injected 1-5 days earlier, but can survive if they are a few days older (Wardhaugh & Rodriguez-Menendez, 1988; Houlding et al., 1991). Possibly permeability of the cuticle changes in early life result in this effect, but the full mechanism is not known.

Larval stages are much more sensitive, possibly due to their more permeable cuticle, e.g. *Onitis gazella* larvae cannot survive in dung deposited up to 21 days post-treatment (Roncalli, 1989), and it is about 8 weeks after treatment that larvae of *O. binodis* can develop normally. Larval *Copris hispanus* cannot complete development until 16 days after injection (Wardhaugh & Rodriguez-Menendez, 1988). Similarly *Aphodius* larvae die in dung collected 1-2 days after injection (Madsen et al., 1990). Numbers of *Aphodius* larvae were markedly depressed in dung voided by cattle fitted with a bolus releasing 40 μg/kg/day (Wall & Strong, 1987).

Ivermectin in cattle dung does not deter colonising insects (Strong and Wall, 1988, 1994), and may even be more attractive to burying beetles than control dung (Wardhaugh and Mahon, 1991, Holter *et al.*, 1993). Wardhaugh and Mahon also showed that adult departure rates from the treated dung were slower. These effects were noted for dung up to 25 days after injection. Similar effects were noted for sheep, but the attractive period was much reduced.

Diptera are also affected, but Cyclorrhapha much more than Nematocera. Annelid densities do not seem to be affected by avermectin treatment (e.g. Wall & Strong, 1987), possibly because soil contact accelerates degradation.

Larval insects treated with sub-lethal doses of avermectins often fail to grow at the normal rate; be unable to shed their skins, or metamorphose into a pupa. All of these events would be expected if there is an anti-feeding effect, or if neuromuscular paralysis occurred. A failure to pupate is not, however, entirely explained by an inability to feed and accumulate tissues and reserves. Some dipterous larvae will not pupate normally after ivermectin contact, even though they have ceased feeding before contact.

Studies in Australia by Wardhaugh *et al.* (1993) showed dung from ivermectin-drenched sheep caused significant mortality to newly-emerged larvae of the bushfly *Musca vetustissima* for up to 1 week after treatment. Those drenched with a mixture of levamisole and oxfendazole also resulted in larval mortality, but the effect was limited to the first 48 hrs after treatment. Flies reared to adult stage on dung collected up to 32 days post-drenching were tested for evidence of fluctuating asymmetry as an indication of developmental stress. None was found for either drench treatment, but ivermectin residues may directly affect wing size. In contrast Strong and James (1993) found very low levels of ivermectin exposure (0.0005 ppm) to larvae caused wing abnormalities in *Scatophaga stercoraria*, as well as larval mortality at higher levels. (EC50 values for 24 and 48h exposure of 0.051 ppm and 0.036 ppm (wet weight) respectively.) In addition to the significantly higher level of fluctuating asymmetry, 23% of the treated insects developed new veins and cells in their wings. They drew attention to the practice of failing to observe the full impact of sub lethal effects, which can be as serious as those of acute toxicity.

Wardhaugh *et al.* (1993) also found that the introduced dung beetle *Euoniticellus fulvus* was sensitive to ivermectin residues in sheep dung. In the first day after drenching, dung caused mortality among newly emerged beetles and delayed the reproductive development of survivors. However, beetles in which the reproductive development was impaired regained their capacity following transfer to non-toxic dung. Day 1 caused no mortality among sexually-mature adults, but there was a significant reduction in their fecundity. Dung collected 2-10 days post-drenching had no effects on either the survival or reproductive development of adult beetles, regardless of age. Residues in dung collected 1-2 days post-drenching caused 100% mortality in beetle larvae, but by day 5 there was no evidence of acute toxicity.

BALANCING THE CONFLICT OVER THE USE OF IVERMECTIN

Avermectins clearly are valuable broad-spectrum anthelmintics which can help veterinary practitioners and farmers to maintain healthy, profitable livestock. After drench and injection administration methods the dung initially produced by livestock is ecotoxic to the dung beetle and cyclorhaphous dipteran fauna by interferring with the adult beetle's capacity to reproduce, and the capacity of larvae of both groups to feed, grow and develop (Strong *et al.*, submitted), rather than by any obvious 'knockdown' effect. Such an effect would be more easily detected, and may have delayed or prevented licensing approval in various countries. After a maximum of about 10 days following drench and injection treatment, further dung excreted shows much lower ecotoxicity, though we cannot yet rule out further sub-lethal effects, such as minor deformities which may prove to have a genetic basis. Ecotoxicity may further be reduced if the drug was injected as aqueous micelles, rather than in organic solution.

As Forbes (1993) has argued, the percentage of cattle treated world-wide is probably less than 15%. With the asynchronous use which happens over much of the regions in which it is employed, it should be no surprise that its environmental impact has been limited so far. However, its use is likely to increase, especially in countries like Australia (Wardhaugh *et al.* 1993). Also, until recently approval has only been for drench, injection and paste formulations. We are now faced with a much more worrying trend. This is the use of sustained-release bolus formulations which are now being licensed.

SUSTAINED INTRARUMINAL RELEASE

An intraruminal sustained-release bolus for cattle utilising an osmotic pump has been in progress for several years and is now available. It is designed to deliver a minimum of 40 µg/kg/day over 120 days. Pope et al. (1985) showed that this delivery system achieved steady-state concentrations in plasma within 7-14 days and a systemic availability of 40%. From this study it was predicted that at 40 µg/kg/day mean steady state levels of approx. 20 ng ivermectin/ml plasma would result. However, in trials calves given this dose showed mean plasma levels of only <5.5 ng/ml plasma (Baggott et al., 1986). The reasons for the difference is not known, but may be due to the presence of a substantial mixed gastrointestinal nematode infection in the calves used. Abomasal parasitism may reduce the systemic availability of anthelmintics (Marriner et al., 1985), whereas intestinal parasitism appears to have no significant effect (McKellar et al., 1991). It may be that higher doses are therefore necessary to achieve parasite control, and even higher levels will be added to the environment.

Strong *et al.* (submitted) have recently tested the effects of ivermectin and fenbendazole sustained-release boluses on cattle. Their results, from blind tests using dung collected 21 days after dosing, showed that both types of treated dung, and control dung were equally attractive to adult *Aphodius* dung beetles, with a slight tendency towards treated dung being more attractive. Development of larval beetles was normal in both control and fenbendazole treated dung, but was prevented from progressing past the first instar by ivermectin. Dung degradation was also noticibly inhibited by ivermectin.

The pressure to switch from pour-on, paste or injection administration to bolus sustained release devices is likely to rise as it reduces the number of handling events of livestock needed. This saves manpower and therefore costs.

This suggests that total avermectin losses from livestock to the environment will rise in many countries in the near future. Since all dung from a bolus-treated animal is likely to be ecotoxic to dung fauna, and they last for 120 days, this could pose a serious threat to foods webs based on dung fauna. This is not the only problem which is likely to arise. Prolonged exposure to ivermectin is predicted to hasten the development of resistant worms and other parasites.

IMPROVED STRATEGIES IN THE USE OF ANTHELMINTICS

Herd (1993) agreed with the views of Waller (1993) that the total reliance on anthelmintics to control nematode parasites is no longer tenable. In the USA the situation is even less tenable because of trends for ivermectin over-use, a lack of effective monitoring of its effects on the host, parasite and the environment. There is an obvious need for better use of existing anthelmintics, and better dissemination of reliable information to vets. and livestock owners. The consequences of drug abuse and short-sighted sales tactics that make no effort to conserve anthelmintic efficacy have been seen already in the development of resistance to ivermectin by sheep and goat nematodes in the USA and other countries. Herd summarised a number of epidemialogic approaches to parasite control for horses, cattle and sheep in northern USA to control worms effectively.

The approaches reduced costs, labour and drug-related problems. They were explained in a series of papers published over more than a decade. They include strategies, such as pasture hygiene, which is designed to minimise resistance, encystment and ecotoxicity; others, such as spring treatments, may require some manipulation to avoid ecotoxicity. They have been used on a limited basis so far, but are urgently needed now.

Waller (1993) of CSIRO in Australia, summarised the future of livestock health practices in his abstract which is as follows.

Farmers world-wide have come to expect, and rely almost exclusively on, broad-spectrum anthelmintics to control nematode parasites among their livestock. However, the threats of resistance, residues and ecotoxicity are of increasing concern to the future of chemotherapy. It is imperative that sustainable parasite control schemes be developed and implemented which will integrate a range of techniques to minimise anthelmintic use and still maintain high levels of profitability of the farming enterprise. At present, these need to focus on the better use of existing drugs to maximise their effectiveness and minimise the selection for resistance and impact on the environment. New drugs should also be used according to these principles. In future it is expected that other non-chemotherapeutic options will become available, e.g. helminth vaccines, resistant hosts, biological control using fungi (e.g. Grønvold *et al.* 1993), and nematode growth regulators, which will revolutionise the current thinking on nematode parasite control of livestock.

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