# Part 5: Synthesis of habitat, diet and population results

## Discussion

### Dietary flexibility in relation to site habitat features and population parameters

Dietary analysis showed that the same three key prey items, *Melolontha melolontha, Aphodius sp.* (Coleoptera; Scarabaeidae) and moths (Lepidoptera), dominated the diets of bats at all eight sites, despite considerable variety in the availability of its preferred habitats around them at 1 and 3 km ranges from each roost. The large dung beetle, *Geotrupes sp.* was probably also important earlier and later in the year. This agrees with the findings of previous studies of UK roosts (Jones 1990, Ransome 1996), and also shows considerable agreement with those of Beck *et al* (1994) in Switzerland, and Pir (1994) in Belgium. Together the studies confirm that this bat is highly selective and conservative in its diet over a wide region and variable habitat circumstances. The overall importance of these key prey items (see table 1), the timing of the appearance of each item (see tables 2 and 3), and the levels each reached over the study period (see figures 2 (a) to (h)), however, varied significantly among sites, especially in the spring.

Timing differences seem to be the cause of many of the significant Tukey test results carried out on specific key prey during single weeks among sites (see table 2). For example if moths are considered from weeks 3 to 5, in week 3 the Woodchester colony ate significantly more than colonies at other sites, and Brockley more than Dean Hall, Stackpole and Slebech. In week 4, Woodchester, Dean Hall and Iford colonies ate significantly more than those at Mells, Stackpole and Slebech; and in week 5 Dean Hall, Iford and Mells colonies ate more than the one at Slebech. However, the lack of moths in the diet at Mells in weeks 3 and 4, coincided with the dominance of *Melolontha* during the same period. The colony at Mells had significantly more *Melolontha* in its diet than the one at Woodchester in week 3, and more than those at four other sites in week 4. In week 5, once *Melolontha* had virtually disappeared from the diet at Mells, moths rose dramatically to replace it. A similar situation was reported by Beck et al (1994) for the Castrisch colony in Switzerland. In week 5 Mells bats were consuming moths at similar levels to those at Dean Hall and Iford, and significantly more than those at Slebech.

Detailed comparisons of data sets, with confirmation from the Swiss findings, suggests that greater horseshoe bats prefer *Melolontha*, as long as they are abundant, to the moths which are flying at the same time. In the UK the moths flying concurrently with *Melolontha* are mainly medium-sized noctuids. Woodchester's habitat seems to produce low *Melolontha* numbers in recent years, since they did not appear in significant amounts in any of the diet studies carried out in 1986, 1995 (Ransome 1996) and in 1996 (this study).

Ransome (1996) has already shown that in August mothers feed selectively on moths whist their young, which are less than 45 days old, feed selectively upon *Aphodius* beetles and normally continue to do so if their numbers remain high. Since birth timing among colonies varied from 13th to 31st July (see table 4), it is impossible to make sensible comments on differences between moth and *Aphodius* consumption levels without allowing for birth timing differences. For example, the low level of *Aphodius* in the diet at Stackpole in week 8 relative to three other sites, including Slebech, occurred when moths were being consumed in quite large numbers. This situation probably reflects the late births there, which would mean that few young were foraging in week 8, rather than poor *Aphodius* availability. By week 9 the Stackpole colony was consuming much larger numbers of *Aphodius*. There are at least 3 possible explanations for this change. Either the moth supply fell to low levels after week 8, forcing the mothers to switch to *Aphodius*, or the *Aphodius* levels rose in week 9, or the young began to forage in significant numbers in week 9. Slebech, on the other hand, showed the lowest levels of moths in weeks 3, 4, 5 and 7, of all sites (Brixham was excluded due to lack of data), and similar late birth timing to Stackpole. Hence high levels of *Aphodius* eaten at Slebech in week 8 could not have been due to consumption by juveniles, since they were not old enough to forage. It must have been due either to a lack of moths, which is supported by its moth data, or high levels of *Aphodius* in the habitat, which is supported by the high levels of grazed pasture around the roost, as shown in table 11. With careful and detailed analyses, it may be possible to make some sense of many of the significant Tukey test results, but timing differences make comparisons very hazardous. Hence table 1, which summarises all data as total diets, is easier to relate to habitat differences as it eliminates the timing factors. The important relationships between high and low levels of specific prey will be considered site by site in part 6.

The three secondary prey items consumed, tipulids (Diptera: Tipulidae), caddis flies (Trichoptera), and ichneumonids (Hymenoptera; Ichneumonidae) of the *Ophion luteus* complex, were also eaten at all sites (see figure 3 (a) to (h)). There were marked differences in the overall proportions of each item consumed (see table 1), with significant trichopteran consumption only occurring in either spring or autumn at roosts close to extensive river and lake habitats, such as Slebech, Stackpole and Woodchester. Few trichopterans were recorded at Dean Hall and Brockley, which had two of the poorest freshwater rank scores (table 12). Conversely, however, bats at roosts close to abundant aquatic habitats, such as Iford, only ate caddis flies extensively in spring for one week, switching to tipulids briefly before key prey consumption took over. Also, ichneumonids were only consumed in large amounts around roosts likely to experience frequent cold snaps in summer. These can occur locally during periods of generally mild summer weather. They are caused by katabatic winds, which result from low temperatures developing on the slopes of steep-sided valleys, such as those near Woodchester, Iford and Dean Hall. These sites show the highest levels of ichneumonids overall, but their occurrence is highly erratic. (See figure 3 (c) (d) and (f) for week 9 especially; compare data with the flatter Welsh coastal sites 3 (a) and (b)).

Tipulids were especially eaten in large numbers, and for long periods at roosts in all lowland coastal regions where milder circumstances may permit more frequent flight by these dipterans. In addition higher rainfall in south-west Wales in summer and abundant short grassland in sheep-grazed fields should promote tipulid life-cycles. These data suggest that tipulids are preferred to both trichopterans, and ichneumonids, which are only eaten at times when other prey are unavailable under the influence of low climatic temperatures (Jones et al 1995, Ransome 1996) or phenological timing.

The availability of different broad habitat types, (woodland, grazed pastures, arable, urban and aquatic), varied markedly within the 3 km diameter roost sustenance zone (Duvergé 1997) among sites, but bore no clear relationship to colony size. Larger colonies, estimated to have from 190 - 340 bats, with more than 40 young, exist in habitats with a wide range of woodland and permanent pasture levels. Linear regressions carried out on estimated colony size against 10 single factors, including both physical and habitat features, showed that the most important factor was grazed pasture at 3 km around the roost. This relationship was not significant however ($p = 0.28$). Similarly, multiple step-down linear regression failed to produce significant combinations of factors, with the best shown by topography with latitude, altitude and pasture close to the roost ($p = 0.408$, N.S.). The failure to obtain significant relationships between habitat factors within fixed radii of the roost and estimated colony size should not be too surprising. The concept of the RSZ as a circular area, which was developed following radio-tracking studies at inland roosts, has had to be revised in the light of further studies, both in the UK and in other European countries, as was discussed above in Part 4.

This study has shown that there is considerable stability of prey items over wide geographic regions, and the limited dietary differences detected among roosts are not easily related to major structural habitat differences within the 3 km RSZ. These can be explained if: (a) the distances commuted by bats to feeding grounds are variable, and adjusted in response to the insect densities encountered by bats searching for specific prey, (b) the various habitats specified above generate enough key prey and secondary prey items for the bats to feed upon, irrespective of their nature.

Of the two alternatives the first is more likely, as it is difficult to accept that arable, urban and aquatic habitats can generate even very low levels of scarabaeid dung beetles, or significant levels of moths at any time (see review in Ransome 1996). Furthermore, as mentioned above, the two radio tracking studies in Wales by Stebbings (1982) at Stackpole, and P.L. Duvergé (pers. comm.) at Slebech, show that bats may travel up to 8 and 14 km respectively to foraging areas. In Switzerland Beck et al (1994), followed up earlier work by Zahner (1984), and showed that greater horseshoe bats from the Castrisch roost, deep in an east-west running valley, restricted their foraging to the lower levels of the valley systems, and although foraging areas were mainly concentrated within 3 km of the roost, many areas were 5 or 6 km away in three arms radiating from the roost. They showed that mean distances to foraging areas were greatest in spring, when most bats foraged over 2.4 km from the roost, reduced in the summer, and was least in autumn, when most bats hunted at about 1.2 km from the roost.

Hence, as has already been argued, the percentage area of each structural habitat type available to foraging bats within the 3 km roost sustenance zone (RSZ) is only one of several important parameters which influence the dietary consumption of bats in a roost. Micro climatic temperatures are also crucial, and the RSZ seems to be within a radius of the roost which is both flexibly adjustable during a season, and is often asymmetrical as well. The latter effect could be due to the asymmetrical location of preferred habitat type, as has been shown by Duvergé (1996) for Brockley, or major topographical features restricting flight paths to certain directions, as was shown to occur in Switzerland by Zahner (1984). These factors must be crucial at the Brixham site, due to the restrictions imposed by three inhospitable habitats, viz. the sea, a wide river, and large urban areas over more than 320 degrees around the roost. Flight paths to the nearest significant foraging areas, which are likely to be at least 3 km from the roost, seem to be extremely limited, and probably occur mainly along coastal cliff faces. Hence the RSZ may involve a complex polygon. The shape of the RSZ affects mean commuting distances to foraging areas, increasing them markedly from circles to elongated polygons. The energy budgets of bats forced to fly further must be adversely affected relative to those travelling shorter distances, unless a superior diet is achieved. Without detailed radio tracking data from each site, it is impossible to achieve improved habitat parameters for linear regression analyses. The absence of such data will also hamper any serious attempts to safeguard key habitats for specific colonies.

**Key prey consumption levels and birth timing**

The observed difference in the timing of births among sites is statistically related to the consumption of high levels of key prey items, topographical rank order, and levels of woodland at the 3 km roost range. It may also be influenced by commuting distances to foraging sites. Linear regressions of 13 geophysical, habitat and dietary factors against birth timing showed that only percentage key prey ($p = 0.020$) and topographical rank order ($p = 0.045$) significantly negatively affected it. Earlier births occurred with high percentage key prey, and steep-sided valleys or slopes. However, woodland level at 3 km and pasture at 1 km were nearly significantly negatively related to birth time as well ($p = 0.066$, and 0.078 respectively), despite the problems discussed above.

Multiple step-down linear regressions of all 13 factors showed that the most significant combination of factors influencing birth timing together, are percentage key prey in the diet and woodland at the 3 km roost range ($F_{2,6} = 11.45$, $p = 0.039$, R sq = 88.4%, R sq adj = 80.7%).

The equation (number one) is:

Birth timing (July 1st = 1) = 63.9 - 0.189 % woodland - 0.552 % key prey

This equation explains over 80% of the variation shown among sites, as shown by the R sq values.

Woodland is thought to be important to greater horseshoe bats for several reasons. Deciduous woodland provides suitable habitat for abundant moth populations (see review by Ransome 1996), and it is the favoured habitat in spring and autumn (Beck et al 1994, Duvergé and Jones 1994) possibly because of elevated night-time temperatures in woods compared with nearby pasture land (Jones et al 1995). This may be especially critical in spring and early summer when mortality peaks. In summer, if adjacent to grazed pastures, woodland provides edges where bats can hunt for *Aphodius* beetles, since all radio tracking studies show that they will not hawk far from linear features. Whilst perch hunting, greater horseshoe bats require woodland edges, substantial hedgerows or large bushes to hang in. They prefer bare perches screened by overhanging umbrella-shaped leaves and branches as cover against predatory birds (Duvergé 1997). The value of linear landscape features to many foraging bats has previously been emphasised by Limpens and Kapteyn (1991), and the considerable advantages of the pasture-woodland ecosystem to many types of wildlife has been reviewed by Harding and Rose (1986) and its importance to conservation further emphasised by Kirby et al (1995). Many of the habitat features which are recommended to promote the recovery of greater horseshoe bats will, if implemented, also be of great value to many other plant and animal species.

Ransome (1996) recommended a target of 50% deciduous woodland within the 3 km RSZ, but several sites in the present study, including Iford, have large populations despite much lower woodland cover levels within the RSZ. Bright (1993) suggested that the reduction and fragmentation of large tracts of deciduous woodland habitat was responsible for the demise of the dormouse, *Muscardinus avellanarius*, in Britain, and that this factor would have contributed to declines in greater horseshoe bat populations. Whilst there is support for this view in Ransome (1996) and the present study, unlike dormice, greater horseshoe bats are not true woodland foragers. They concentrate their hunting at the edges of deciduous woods over most of the summer, especially during the most energetically demanding periods of late pregnancy (Racey and Speakman 1987), and lactation (Kunz 1987). These both occur at the time of year when moths are usually most abundant and reliable, as is confirmed by the present dietary study, despite the poor climate in 1996 (see figure 2 (a) to (h)). Consequently it is probably more important to provide a maximum length of woodland/grazed pasture edge close to roosts, rather than just large areas of dense woodland. Woodland edge length, for the same overall area, will be maximised by fragmenting it into many long thin strips, and minimised by concentrating it into a single large circle. Calculations of the capacity of different percentage into which areas of woodland to provide edge length showed that the number of equal-sized units it is fragmented has the greatest effect, with the shape of the units of secondary importance. However, at 50% woodland cover, the number of equal-sized units which can be created without overlaps is only three. If 25% woodland cover is present, it can be divided into ten equal-sized units without overlaps, and generate more edge length than the three units offered by 50% woodland. These situations, if they occur in the known RSZ of specific sites, may explain why large colonies can exist without extensive areas of woodland. I therefore believe that the previous figure of 50% woodland is too high, and it should be reduced to 40%, to allow many woodland blocks of varying sizes to be created in different topographical situations within the RSZ of woodland-deficient sites. They should always be adjacent to grazed pastures, preferably mainly by cattle.

Equation one showed that the higher the percentage of key prey in the diet the earlier births will be. However, since the percentage of key prey was calculated over the whole of weeks 2 - 10 of the study, much of which occurred after births had taken place, overall high levels of key prey consumption by a colony probably indicates that a generally high-quality habitat exists around the roost, and vice versa. However, if this is generally true, it does not apply consistently throughout the summer. Figure 2 (f), which shows key prey consumption for Iford, the site with the highest percentage key prey overall, shows that in week 9 serious dietary problems occurred. Figure 3 (f), shows that one of the most inferior secondary prey, ichneumonids, which are capable of flying below the lower critical flight temperature threshold for other prey, dominated the diet in that week. Week 9 was a period of cool weather, with a mean minimum night temperature of 9 °C at Dursley, near Woodchester. The following week, when the mean minimum temperature was 10.2 °C at Dursley, ichneumonids were replaced by tipulids as the main secondary prey.

The impact of climatic temperature on the percentage key prey in the diet was assessed at Woodchester over the study period. Regression of birth timing against the mean minimum temperature overnight produced the most significant positive relationship of the various daily temperatures recorded ($F_{1,10} = 19.83$, $p = 0.002$; R sq = 71.3%, and R sq adj = 67.7%)

This equation (number two) is:

$$\% \text{ key prey} = -19.5 + 9.87 \text{ mean minimum night temperature}$$

Hence the warmer the minimum overnight temperature, which tends to occur near dawn, the higher the level of key prey in the diet. The equation predicts that at 12.1 °C minimum overnight temperature the percentage key prey in the diet will be 100%. This is the temperature below which levels of flying moths become scarce. It also predicts that at about 2 °C minimum overnight temperature, no key prey will be in the diet, and all prey eaten will be secondary prey. These are likely to be eaten at dusk, as temperatures are normally much higher then.

Ransome and McOwat (1994) argued that a mean birth date of 15th July or earlier was necessary to support a viable population of this species in a region. It requires a mean temperature in April and May of at least 9.4 °C to do this. The first equation above, assuming a constant level of 40% woodland in the 3 km RSZ, predicts that at least 75% of the diet overall needed to consist of key prey to achieve this birth date in 1996. Since moths are the major key prey eaten prior to giving birth, the advantage of high levels of woodland may be in ensuring high levels of moths, which are mainly captured by bats hunting at woodland edges adjacent to pastures. This provision will, however, be to no avail if climatic temperatures are low, as shown by the second equation.

Hence low levels of woodland edge in the RSZ may become a serious limiting habitat factor affecting colony size under favourable climatic temperature conditions. The failure to detect significant linear regressions between percentage grazed pasture in the 1 and 3 km range RSZ and birth timing should not be a surprise, since apart from problems inherent in calculating the RSZ, grazed pasture generates mainly *Aphodius* and *Geotrupes* beetles at times which do not affect pregnancy length. As stated above, percentage pasture at 3 km was the factor which came closest to significance in regressions on estimated colony size, and there are many powerful arguments supporting the need for grazed pasture close to maternity roosts of greater horseshoe bats (Jones et al 1995, Ransome 1996).

Inferior insect availability at close foraging sites may force bats to travel further to find better ones. The extremely late births at Slebech and Stackpole coincided with high levels of secondary prey until the fourth or fifth week of the study (figures 2 and 3). Foraging areas at both sites are at much greater mean distances than at Brockley, Woodchester and Iford (Duvergé, 1997), where births were much earlier in 1996, and key prey items dominated the diets from the third week onwards. The more restricted data from Brixham, which showed the latest mean birth date of all sites from which data were available, essentially supports this hypothesis. It has already been argued that commuting distances from this roost are likely to be considerable for reasons of habitat structure, and the restricted dietary data available is very similar to that of Slebech, suggesting that levels of key prey there were also low in 1996. These points are important, since Brixham is in the most favourable climate of all sampled sites, whereas the two Welsh ones usually experience much poorer climate as stated in Part 4. Brixham, however, has its maternity colony in an underground roost, and this may be another seriously limiting factor, as roost temperatures are likely to be very low.

Overall these data support the hypothesis of Tuttle and Stevenson (1982), that distance to favourable foraging areas is an important factor affecting populations of bats. If local foraging areas fail to provide sufficient key prey, commuting distances are likely to increase as bats attempt to find superior foraging areas to enable them to give birth early in July. This follows since the present study shows that birth timing differences during the same year are mainly related to percentage key prey consumed, and is supported by data from Slebech and Stackpole. Birth timing is one of the key factors influencing population levels through its impact on juvenile growth and mortality, and mortality of the mothers (Ransome 1989, 1995). Hopefully the extremely late mean birth dates at the Welsh sites and Brixham in 1996 will not precipitate a population crash at each site as occurred after 1986. The mild autumn weather in 1996 may have been sufficient to prevent this from happening, or at least mitigate the impact of very late births.

**Topography and micro climatic effects on key prey availability and birth timing**

The quality of the diet can be broadly assessed in this species if it is assumed that key prey provide a superior diet to that of secondary prey. Jones (1990) supported this assumption, arguing from a similar dietary study involving faecal pellets and culled remains at Brockley in 1988, that this species selectively feeds on large beetles and moths, which are culled to increase diet profitability.

The consumption of high levels of key prey items early in the spring is only possible if the phenology of the key prey makes them available. Many insects overwinter as larvae, pupae or imagos which may either be inactive due to diapause, or because of low ambient temperatures. Completion of the life-cycle, with the emergence of imagos from pupae (since all prey are holometabolous insects), is greatly influenced by climatic temperatures, which, although annually cyclical, can fluctuate dramatically and unpredictably. Local climatic temperatures around roosts, as described above in Part 4, are affected by the topography of the habitat within the RSZ, roost latitude, distance from the sea and its height above sea level. It has already be argued above that topography can have a major over-riding influence on the other factors if sunshine levels are high (see Part 4).

The temperature effect of prolonged sunshine upon steep valleys should assist in promoting the emergence of moths from their pupae early in the summer on south and south-west facing slopes. On a particular day, once adults are abundantly present, moth captures at light traps were shown by Jones et al (1995) to rise rapidly above 12 °C. This effect is due to the impact of temperature upon the flight capacity of many insects, including moths. At dusk following a sunny cool day, the warm slopes may allow moth flight to occur briefly whilst flatter regions are too cold to do so. However, after dusk, as slopes cool, katabatic winds may develop as dense cold air, especially over grassland, flows into the valley floor. These winds can produce lower temperatures than that above flat ground, and even ground frosts in late spring. As different insects have different flight temperature thresholds falling temperatures selectively remove prey items until between 8 and 4 °C the only available prey are ichneumonids. They are the smallest, and probably the least profitable prey item, although they may form large swarms in and near woodland throughout most of the year. This situation is most likely to occur at dawn in the summer, but can also occur at dusk in spring and autumn. In the flatter coastal regions, it is much less likely that temperatures will fall so low as often, as katabatic cooling does not occur, and proximity to the sea raises spring and autumn temperatures. Ichneumonid consumption is therefore generally very low in the coastal sites, even where woodland is abundant.

If both north and south-facing slopes occur close together in a region, any prey species should have its availability period extended in comparison to those of flat regions, via the temperature influences outlined above. This effect may be especially important in insects with a short emergence period, such as *Melolontha melolontha*, which are highly preferred prey to greater horseshoe bats. This hypothesis is supported by dietary data from Iford (fig. 2 (f)), which showed the longest dietary utilisation of *Melolontha* of all sites, and was highest in the topographical impact order. The effect could also help to explain why moths were consumed both earlier and later in the summer of 1996 at Woodchester and Dean Hall, than at Slebech.

A further effect of steep-sided valleys is the provision of shelter from high winds. Climatic data summarised over long periods (White and Smith 1982) show that south west Wales suffers from much higher mean wind speeds than the other regions, and also has a much flatter terrain. The spring of 1996 was much sunnier, and windier, with several extended periods of north-westerly winds which reduced temperatures across the whole of the UK in late May. Wind effects are likely to have had a greater impact on the Welsh sites than the English ones, particularly those within the most sheltered situations, such as Iford and Woodchester.

The climatic influence of topography upon insect phenology, and hence birth timing, is complicated by associated structural habitat effects due to topography. Steep-sided valleys are more likely to be associated with grazed permanent pasture adjacent to woodland, tree-lines or tall hedgerows, since ploughing is restricted by slope severity, and woodland is often restricted to the most severe slopes. Hence such valleys often provide excellent structural habitats for greater horseshoe bats, irrespective of the temperature microclimates they generate. Conversely, flat or gently undulating land is frequently used for other purposes such as arable crops, amenities, and urban development. All of these habitats have been shown to be avoided as foraging habitats by radio tracking studies.

## Summary hypothesis and general recommendations

### Hypothesis

It may be argued that using one year's dietary data to shed light upon the population level at a site is over ambitious and/or unacceptable. However, since the diet at Woodchester has been shown to be quite consistent over years (1986, 1995, 1996), despite major differences in the weather each year, and consequently in birth timing, there is justification for doing so. Furthermore the considerable diet similarities shown among widely dispersed sites, including parts of continental Europe, gives added confidence that the results are likely to be generally applicable during different years. Overall the data and arguments presented above, together with published radio tracking information, are compatible with the following hypothesis, which attempts to link up known bat foraging behaviour with habitat structure, habitat micro climate and population trends.

A greater horseshoe bat leaves its roost to search for key prey items in a known, and possibly traditional, foraging area which has very specific characteristics, and is generally within a 3 km range of the roost. Foraging areas normally involve lines or clumps of trees or bushes adjacent to grazed permanent pastures, such as woodland edges or fields traversed by thick, tall overhanging hedgerows with emergent trees (Beck et al 1994, Jones et al 1995, Duvergé 1997). Such habitats generate high densities of its key prey (moths and scarabaeid beetles), and its main secondary prey (tipulids and ichneumonids). It chooses foraging areas on sheltered warmer south or southwest-facing slopes, especially in early spring, but may use cooler north or northeast-facing slopes later on in summer, if key prey items continue to fly there. This is especially likely to happen during prolonged droughts. Normally it feeds on a single key prey item when it is sufficiently abundant and therefore profitable. The specific prey eaten depends upon the current climatic temperature operating during the foraging bout, which must be above certain critical limits to permit insect flight, as well as the phenology of the insect. If the current key prey item is not readily available during a foraging bout, it either eats a mixture of key prey, switches to more abundant secondary prey items if present, or feeds on mixtures of prey items. Alternatively it travels to other foraging areas, which may be at greater distances from the roost (up to 14 km away), where its preferred prey may be more abundant due to higher quality habitat (which includes more favourable temperature microclimates, as well as vegetation composition). If prey availability is scarce in all of its foraging areas, mixtures of up to four prey items are eaten during one foraging bout. In the absence of sufficient key prey items, tipulids, and then trichopterans seem to be preferred to ichneumonids, but trichopterans are only locally available near aquatic fresh-water habitats. Ichneumonids (of the *Ophion luteus* complex) form nocturnal swarms during most months of the year, but are only significantly eaten when other prey become unavailable as climatic temperatures fall below about 9° C. Consumption of small dipterans, some of which can fly at temperatures just above freezing, occurs as a last resort, and indicates severe dietary stress. Finally, at very low temperatures the bat is unable to feed, and it has to abandon feeding, and return to a cool roost where it becomes torpid in an attempt to avoid starvation. Once prolonged hibernation torpor becomes impossible in late May or early June (Ransome 1971, 1990), cold conditions which continue uninterrupted for several days may cause severe mortality, and a population crash, due to costly daily arousals which are not compensated for by successful foraging.

The longer the period that it remains in torpor, or that it is forced to feed upon less profitable prey, especially at distant foraging sites, the later mature females give birth, since it is rare for them to abort. The later births occur, especially if after 25th July, the greater the risk of subsequent mortality to both the mother and her young (Ransome 1995). Since it is the younger mature females which tend to give birth later in the summer (Ransome 1995) they suffer the greatest mortality levels. The loss of a cohort of young from a single summer is not a serious threat to colony size, if it occurs only spasmodically, but the death of many younger mature females in a single summer is potentially damaging to population levels for at least a ten year period (Ransome unpublished data). Its prevention should be a major thrust of conservation measures taken to ensure the survival of the species.

**Recommendations from the hypothesis**

This hypothesis suggests that land management measures taken to promote recovery of this species should concentrate on providing the best possible foraging habitat structure, which is ancient semi-natural woodland or substantial hedgerows, adjacent to permanent grazed pastures occupied primarily by cattle within the 3 km RSZ. These suggestions were previously made by Ransome (1996), and this study reinforces his habitat recommendations. However, much of central and northern Britain contains abundant areas of such habitat, and suitable roost sites probably occur within the range of at least some of them. Despite this the species does not manage to colonise these areas. Climatically the bats cannot do so for the reasons discussed. At higher latitudes the proportion of the habitat surrounding a roost which will be of continuous use to bats from spring to summer as foraging areas, is likely to decrease. Hence any topographical areas likely to promote locally-raised temperature climates should be selectively protected as foraging areas for this species. Priority of protection should be given to areas closest to roost sites, especially within 1 km of maternity roosts, and then up to 3 km range, but habitat protection should also include areas around hibernacula, especially those used as territorial breeding sites by males in spring and autumn. These sites can contain a substantial proportion of the older pregnant females up to late June (Ransome, unpublished data).

If potentially suitable topographical areas close to roosts have unsuitable habitats covering them, land managers should be encouraged by grant support systems to convert them to suitable habitat (pasture-woodland) as specified in Ransome (1996). If maternity sites lack substantial bodies of freshwater habitat close by, consideration should be given to its provision. In severe springs trichopterans probably provide a valuable secondary prey item which could be important in helping a colony to survive a severe cold late spring.

Overall recommendations concentrate on the generation of high quality habitat structure within the 3 km RSZ, but especially the 1 km young sustenance zone wherever feasible, to assist the growth and development of the young, and ensure their long-term survival potential. Essentially these recommendations add to those previously made (Ransome 1996), but the desirable level of deciduous woodland is reduced to 40%, as this level permits the development of numerous strips or small blocks of woodland adjacent to cattle-grazed permanent pastures. The latter habitat favours juvenile foraging on *Aphodius* beetles in the later phases of their growth. Such fragmented habitats provide very high levels of woodland/pasture edge lines, the preferred foraging areas for this species, and therefore should improve the numbers of potential foraging sites. The 40% level replaces the previous recommendation for 50% deciduous woodland. Woodland strip development, adjacent to grazed pastures, should be encouraged on the south or west-facing slopes near roosts, if they occur.

If fragmented woodland development to the 40% figure near roosts is not possible, major tree-lines or substantial overhanging hedges should be encouraged around cattle-grazed permanent pastures. If pastures are extensive, they should be sub-divided by tree-lines or tall hedges to provide many small fields, and/or field corners should be planted with deciduous trees as copses. Overhanging, umbrella-shaped cross sectional hedges should be encouraged, and the current manicured square or rectangular cross sectional hedges discouraged. Pasture-woodland habitats have been shown to support many other threatened or scarce plant and animal species, so the costs of protective measures taken to promote greater horseshoe bats can be partly justified by their likely benefits to wildlife in general.

Further afield than the 3 km RSZ, foraging areas which may be used by adult bats or potentially attractive to them, should be safeguarded and developed with similar habitat features of deciduous woodland adjacent to cattle-grazed pasture, particularly around known or potential hibernacula on south-facing slopes. Ideally radio-tracking studies should be carried out to determine the specific areas utilised as foraging areas by bats from specific roosts. They should then be safeguarded and improved as recommended. In the absence of such information, areas selected for improvement should concentrate on those with topographically suitable aspects, such as sheltered valleys with south or west-facing slopes as above.

# Part 6: Recommendations for land-management changes to improve population performance at each site

## Slebech

This is the second most northerly maternity site in the UK, but since it is at low altitude and quite close to the sea, it usually enjoys mild autumns and winters which should permit regular winter feeding (Ransome, 1968). However it has quite cold springs which are usually combined with strong winds. The lack of many sheltered valleys or extensive south-facing slopes makes prolonged exposure to winds, even with abundant sunshine, result in very late births during especially cold springs. Preliminary data from radio tracking studies in 1996 by Laurent Duvergé (pers. comm.) indicate that foraging areas are at the greatest distances so far recorded in the UK, and possibly elsewhere. Its key prey consumption was the poorest recorded from the seven sites, from which full data were obtained. This was despite its reasonable level of woodland around the roost, and its good level of grazed pastures.

Overall the diet at Slebech showed poor levels of moths, and ichneumonids, but high levels of tipulids and trichopterans. The low levels of moths are believed to reflect cool conditions during the prolonged spring period, and again in the late summer, in the absence of local south-facing slopes, rather than insufficient woodland. The lack of ichneumonids probably indicates that, although too cold for extended moth availability, conditions were mild enough to allow bats to feed on tipulids and trichopterans, rather than ichneumonids. Only good trichopteran consumption reflects high habitat availability (freshwater). The failure of high levels of grazed pastures to be reflected in the overall levels of *Aphodius* was surprising, but they were significantly higher at Slebech than Stackpole in week 8. Possibly differences among all sites was affected by the absence of data from mid September when most juveniles would have been foraging.

### Overall assessment and recommendations

This site is in quite favourable habitat circumstances, although its topography is poor. The lack of shelter from the high winds is a problem, but primarily its population suffers from severe climatic stress due to latitude. Since it has good levels of woodland and pasture, and climatic factors are beyond immediate human control, it is difficult to see how improvements can be made, other than within the roost. Possibly a thorough review of whatever favourable topographical features exist within the 3 km range, and the conversion of such places to suitable habitat combinations (woodland/grazed pasture), would ensure the continued survival of this colony. Any such slopes, close to the roost, which are utilised as foraging areas at present, should of course be fully protected and their habitat enhanced if suboptimal.

## Stackpole

This is the fourth most northerly maternity site in the UK, but since it is at very low altitude and very close to the sea, it usually enjoys mild autumns and winters which should permit winter feeding as at Slebech. Climatically it is similar to Slebech, but probably suffers even more from the effect of strong winds as its terrain is even flatter, and it has less woodland beyond the 1 km range. Consequently it also has very late births during especially cold springs as in 1986 and 1996. Data from preliminary radio tracking studies by Stebbings (1982) showed that many foraging areas are at distances up to 8 km from the roost. Its key prey consumption was the second poorest recorded from the seven sites, from which full data were obtained. This site has a good level of woodland and lakes close to the roost, but woodland is very sparse at greater distances, and a reasonable level of grazed pastures within a 3 km range of the roost.

The diet here, as at Slebech, was high in tipulids and trichopterans, and was also low in moths and ichneumonids. The explanations are the same. In addition the levels of *Aphodius* were lower than at Slebech and most other sites, presumably because of poorer cattle-grazing regimes.

**Overall assessment and recommendations**

This colony, like its close neighbour at Slebech, is in favourable habitat circumstances close to the roost, but is deficient in woodland beyond 1 km. Its topography is very poor. The lack of shelter from the high winds is an even greater problem than at Slebech, but its climatic stress should be lower, due to its lower latitude. Additional levels of woodland up to 3 km from the roost, and additional cattle-grazed pasture especially close to the roost, should help to secure the colony against the effect of severe cold springs. Woodland strips, preferably on any south-facing slopes available, should provide some shelter from the winds, and provide greater moth supplies. The grazing by cattle should improve conditions for the young, and promote their growth and survival.

As at Slebech, any south-facing slopes, close to the roost, which are utilised as foraging areas at present, should of course be fully protected and their habitat enhanced if suboptimal.

## Dean Hall

This is the most northerly maternity site in the UK, and it is at the highest altitude of the sites studied. Although it is not close to the sea, it is close to the Severn Estuary and its south or south east-facing slopes. Hence, although colder than the Welsh sites, it may enjoy milder autumns and winters than Woodchester. Although it has quite cold springs, winds are less severe than in west Wales, and the presence of many sheltered slopes gives it some immunity from winds, especially the coldest ones from the north east. With abundant sunshine, early births occurred in the cold spring of 1996, helped by very favourable habitat, especially at the 3 km range, with substantial amounts of ancient natural deciduous woodland interspersed with sheep or cattle-grazed pastures and many woodland glades. Deer and sheep wander freely in the forest beyond the 3 km range providing many short-cropped open glades. Close to the roost, a herd of cattle has recently been removed from fields. No radio tracking studies to determine foraging areas have been attempted so far, but the habitat structure is very favourable. The site is within the Forest of Dean, which contains four major horseshoe bat breeding roosts of national importance. Dean Hall is one of them, and the other three are lesser horseshoe roosts. Its key prey consumption was among the best recorded from the seven sites, from which full data were obtained.

Overall the diet here showed the best level of *Geotrupes* and high levels of moths, reflecting the generally favourable habitat conditions, especially high woodland levels at the 3 km range. Surprisingly there were low levels of *Aphodius* during the weeks (2 to 10) of the overall prey consumption. In week 11 it had significantly more *Aphodius* in the diet than either

Woodchester or Brixham. This may be the result of the recent removal of a large herd of cows from fields close to the roost. By late September the young would have been flying at adult distances, and be capable of finding *Aphodius* further afield. The diet was also poor in trichopterans, which is to be expected as few extensive freshwater habitats are close to the roost.

**Assessment and recommendations**

This colony is in very favourable habitat circumstances between 1 and 3 km from the roost, but is deficient in woodland close to it, and the recent loss of cattle nearby is a possible threat to the growth of the young. Its topography is very good, providing shelter from the high winds, and its slopes compensating to some extent for the climatic stress due to its high latitude. The provision of some additional woodland strips close to the roost is recommended, but the restoration of cattle in the pasture adjacent to the roost should be the first priority. These should help to secure the colony against the effect of extended cold springs, which have severely reduced the colony size in the past. It will always be one of the most vulnerable due to its high latitude. Hence, as elsewhere, any south-facing slopes, close to the roost, which are utilised as foraging areas at present, should of course be fully protected and their habitat enhanced if suboptimal. Radio tracking studies should be attempted to identify foraging areas if possible.

## Woodchester

This roost is the third most northerly maternity site in the UK, and it is at the second highest altitude of the sites studied, in a steep-sided valley running from east to west. Like Dean Hall, although it is not close to the sea, it is near the Severn Estuary, but it is on the opposite side of the river, and is close to its northwest-facing slopes. Hence, it is usually one of the coldest sites, together with Dean Hall. Although it has cold springs, winds are much less severe than in west Wales, and having many sheltered slopes nearby gives it considerable immunity from winds, especially those from the north east. With abundant sunshine, as at Dean Hall, early births occurred in the cold spring of 1996, helped by very favourable habitat, especially at the 1 km range, with substantial amounts of ancient natural deciduous woodland interspersed with some sheep or cattle-grazed pastures, and a series of substantial lakes which allow trichopterans to be eaten in spring and autumn. Radio tracking studies to determine foraging areas by Duvergé (1997) showed commuting distances were low, mainly within 2.5 km range of the roost. This may partly be due to the small number of adults using the roost through the summer. The habitat structure is very favourable close to the roost, but there is less woodland available at greater distances. The Woodchester valley is currently mostly owned by the National Trust, and is close to several NT-owned commons which are cattle-grazed throughout the summer and early autumn. Its key prey consumption was also among the best recorded from the seven sites, from which full data were obtained, although *Melolontha* were deficient in the diet.

Overall the diet here showed one of the best levels of *Aphodius* and high levels of moths, reflecting the very favourable habitat conditions, especially high woodland levels close to the roost at 1 km range for moths, and cattle grazing close to the roost . Moths were consumed here very early in the spring, at high levels and continued late in the summer. Ichneumonids were eaten in large numbers, significantly more than at several other sites in weeks 2 and 10, probably due to the topographical effects of the valley. The diet was also quite high in trichopterans, which reflected the abundance of lakes close to the roost.

**Assessment and recommendations**

This colony is in very favourable habitat circumstances between 1 and 3 km from the roost, but is slightly deficient in woodland further away. The reintroduction of cattle nearby under grazing agreements between English Nature and the Woodchester Mansion Trust, is an advantage to the growth and survival of the young. Its topography is very good, providing shelter from the high winds, and its slopes compensate to some extent for the climatic stress due to its high latitude. Some additional pastures close to the roost on the south-facing slopes are currently being developed by the National Trust, to further enhance habitat structure and microclimates. The loss of a large herd of cattle above the valley last year was a retrograde event, which could have harmful consequences in the future as the population recovers. Severe springs have severely reduced the colony size in the past, as at Dean Hall, and it will always be one of the most vulnerable due to its high latitude. However, as most of the foraging areas close to the roost are NT owned, many of them should enjoy long-term protection. Radio tracking studies have identified many foraging areas, and those on other land should be safeguarded by grant aid mechanisms.

## Brockley

This is located at a middle latitude, and its altitude is very low. It is close to the sea/estuary of the Bristol Channel. Consequently it normally enjoys a milder climate than Dean Hall and Woodchester, especially during the critical spring period. Although it has milder springs, winds are probably more severe than at the Gloucestershire sites, but less so than in west Wales. It has many sheltered south and west-facing slopes nearby which are well-wooded with ancient semi-natural deciduous or mixed woodland, interspersed with grazed pastures occupied mainly by cattle and horses. It therefore has very favourable habitat, especially at the 3 km range. The only useful habitat which is locally missing is a significant level of freshwater, but as its climate is generally mild, this is probably not a serious deficiency.

Radio tracking studies to determine foraging areas by Duvergé (1997) showed commuting distances were low, as at Woodchester, and mainly within 2.5 km range of the roost. Its key prey consumption was also among the best recorded from the seven sites, from which full data were obtained, and *Melolontha* levels were very high, together one of the best levels of *Aphodius*. reflecting the very favourable grazing habitat conditions. The high woodland levels close to the roost at 3 km range, might have been expected to result in high levels of moths. However, *Melolontha* may have been eaten in preference to moths in some of the early weeks, and this may be the reason for average levels being consumed overall. Ichneumonids were eaten in quite large numbers, significantly more than at the other coastal sites, probably due to the cooling effects of katabatic winds on the slopes. The diet was also very low in trichopterans, which reflected the lack of freshwater habitats near foraging areas.

**Assessment and recommendations**

This colony is in very favourable habitat circumstances between 1 and 3 km from the roost, apart from an absence of freshwater habitats. It is slightly deficient in woodland close to the roost. Cattle, which are in good numbers near the roost, together with other grazers, should provide abundant *Aphodius* to promote the growth and survival of the young. Its topography is good, providing some shelter from the high winds, and its slopes enhancing the relatively mild conditions are due to its favourable latitude and coastal proximity. Some additional cover close to the roost opposite the exit hole would promote earlier foraging flights. Severe springs, in combination with the temporary loss of the roost attic during building works have reduced the colony size in the past, but conditions are now much improved, and the colony should grow steadily over the next few years. However, creeping urbanisation around the roost should be opposed as a long-term threat to foraging habitats. Radio tracking studies have identified foraging areas, which should be safeguarded by grant aid mechanisms where they are not presently covered.

## Iford

This is located at a middle latitude, at a similar level to Brockley, but its altitude is slightly higher, and it is deep within a valley system which radiates out in a complex manner between a series of hills at the south-western edge of the Cotswolds. The hills reach nearly 300 metres height between the valleys, and the slopes are very severe. It is an inland site which normally enjoys a milder climate than Dean Hall and Woodchester, especially during the critical spring period, and it has many, very well-sheltered south and west-facing slopes nearby. The more distant ones are well-wooded with ancient semi-natural deciduous or mixed woodland, interspersed with grazed pastures occupied mainly by cattle, deer and horses. Within the 3 km range woodland is rather more sparse, but it is well provided with permanent cattle and horse-grazed pastures. Much of the woodland within the 3 km range consists of narrow strips, but it also has substantial suitable hedgerows. There is abundant freshwater available, including the River Avon which flows adjacent to the roost. Further afield there is an extensive canal system.

Radio tracking studies to determine foraging areas by Duvergé (1997) showed commuting distances were the lowest of the three sites he studied, although the number of bats tracked was low. Its key prey consumption was very close to the best recorded (at Mells) from the seven sites, from which full data were obtained.

*Melolontha* levels, though not very high in any one week, persisted for a very long period and so were quite high overall. Moths were very high, especially in view of the low level of woodland at the 1 and 3 km range, but adults may have travelled further to more abundant woodland just outside it. The low level of *Aphodius* was surprising in view of the favourable grazing regimes around the roost. Possibly the early births (mean = 19th July), which would have resulted in most of the young first flying about the 19th August, meant that the peak *Aphodius* consumption period was missed. On the other hand, in week 9 when *Aphodius* consumption should still have been high, ichneumonids dominated the diet for one week only, reflecting a cold period which could have prevented the flight of *Aphodius* locally. Overall ichneumonids were important in the diet. The abundant freshwater habitats close to the roost was not reflected in high consumption of trichopterans except in one week. During other weeks the bats at Iford ate tipulids or key prey in preference to trichopterans.

### Assessment and recommendations

This colony is in apparently quite unfavourable habitat regarding woodland between 1 and 3 km from the roost, although it has abundant freshwater habitats. It is deficient in woodland close to the roost, but has favourable grazing regimes at 1 and 3 km range. Cattle and horses are present close to the roost in good numbers. Its topography is excellent, providing outstanding shelter from high winds, and its slopes enhance the relatively mild conditions due to its favourable latitude. Some additional cover close to the roost is needed to promote earlier foraging flights and security against bird predators which continue to be a problem. More woodland strips close to the roost should be encouraged, and linked up by linear corridors of substantial hedgerows to provide cover. This is one of the largest maternity colonies in the region, and this seems to be due to its consistently early births, possibly aided by close proximity to good hibernacula (Ransome unpublished data). However, creeping urbanisation around the roost is becoming a problem, and is likely to continue. Further development should be opposed as a long-term threat to foraging habitats. Radio tracking studies have identified some foraging areas, but more studies are needed to provide data for opposition to planning applications.

## Mells

This is located close to Iford, at a middle latitude, but at a higher altitude. It is on the edge of a weak rolling valley system which runs from east to west. The slopes are not severe. It is an inland site which normally enjoys a milder climate than Dean Hall and Woodchester, especially during the critical spring period. The habitat close to the roost is generally quite well-sheltered, and well-wooded, with shallow south-facing slopes close by. The more distant ones are only sparsely covered with ancient semi-natural deciduous or mixed woodland present mainly as thin strips along riverine habitat. There are abundant grazed pastures occupied by cattle, sheep and horses, often in small fields with extensive hedgerows. As at Iford there is abundant freshwater available, including the River Mells which flows very close to the roost, which has lakes not far upstream. No radio tracking studies to determine foraging areas have been carried out. Its key prey consumption was the best recorded from the seven sites, for which full data were obtained, just ahead of Iford.

*Melolontha* levels were very high, and significantly more than other sites in two weeks, possibly due to extensive areas of short-grazed grass in its habitat. Moths, on the other hand were not very high, either reflecting the low level of woodland at the 1 and especially the 3 km range, and beyond, or the preference for abundant *Melolontha*. The high levels of *Aphodius* reflected the very favourable grazing regimes around the roost. The abundant freshwater habitats close to the roost were reflected in high consumption of trichopterans in the first two weeks, before key prey became available.

### Assessment and recommendations

This colony, like Iford, is also in apparently unfavourable habitat regarding woodland between 1 and 3 km from the roost, although it also has abundant freshwater habitats. It is deficient in woodland, especially away from the roost, but has favourable grazing regimes at 1 and 3 km range, and substantial hedgerows with emergent trees which may compensate for the lack of woodland. Cattle nearby are in good numbers, as are other grazers. Its topography is reasonable, providing good shelter from high winds, and its slopes enhance the relatively mild conditions due to its favourable latitude, but less so than at Iford.

This is another large maternity colony, although counts are so difficult here that the size is still unclear. Birth timing has not been easy to assess either, as the mothers keep moving their young between various underground sites, following the loss of their maternity roost building in a fire. The foraging habitats are unknown as no radio tracking studies have been attempted. Additional woodland strips should be encouraged especially beyond the 1 km range up to 3 km from the roost, linked by linear corridors as for Iford.

## Brixham

This is the most southerly maternity site in the study, and it is at very low altitude, close to the sea. The roost is the only long term underground maternity site in the study, and consists of two adjacent caves within a bowl-shaped rocky quarry, very close to the open sea of the English Channel. The quarry is at the tip of a peninsula at Berry Head which projects well out to sea, resulting in very mild autumns and winters. Being coastal, it is similar to the Welsh sites, but as it is much further south, its springs are even milder. Winds are more severe than at inland sites, and although the quarry provides shelter on emergence, bats have to fly up over the quarry ridge to forage at distant sites. The immediate habitat around the roost consists of steep cliffs, with permanent short-grazed pasture, mainly by sheep, and some sparse, wind-stunted woodland. Further away, up to the 3 km range, most of the land is urbanised. The most likely foraging areas are beyond this distance, and may only be accessible by commuting routes along, or close to the cliff edges. No radio tracking studies to determine foraging areas have been attempted so far, but as the habitat structure is extremely unfavourable, it would be a very interesting site to investigate.

Young were born later here than anywhere else in the study, and the estimated population is the lowest, with the smallest number of births. Dietary data for weeks 4 and 5 were not obtained, as the cold weather in those weeks (early June and early July) caused the bats to abandon their normal roost positions in the caves. Consequently dietary data for this site were incomplete, and the key prey consumption level could not be assessed over weeks 2 to 10.

*Melolontha* levels were very high, and significantly more than other sites in two weeks, possibly due to extensive areas of short-grazed grass in its habitat. Moths, on the other hand were not very high. This may reflect the low level of woodland at the 1 and especially the 3 km range, and beyond, or the selection of *Melolontha* instead. The low level of *Aphodius* in week 11 reflects the poor grazing regime around the roost, especially the absence of cattle. The lack of freshwater habitats close to the roost was reflected in fairly low consumption of trichopterans in the first three weeks, before key prey became available.

### Assessment and recommendations

This colony is surrounded by the most unfavourable habitat conditions of all sites studied, between 1 and 3 km from the roost. The bulk of these areas are unlikely or impossible foraging areas. It is deficient in woodland, and lacks significant cattle grazing, although sheep-grazed permanent pastures exist within the 1 km range. The short turf produced by sheep grazing may be responsible for high *Melolontha* levels and hence dietary consumption.

Its topography is poor at providing good shelter from high winds, but its favourable latitude and proximity to the sea results in a very mild climate, which is its only positive attribute.

This is one of the smallest maternity colonies, due to its poor habitat structure, and the likely long commuting distances to foraging areas. It also has an underground roost, which adds to thermal stress levels on breeding females because ambient roost temperatures are low. The foraging habitats are unknown as no radio tracking studies have been attempted. They are urgently required to enable their protection before it is too late. It would probably benefit most from close cattle-grazing around or near the quarry, together with additional woodland if trees capable of growing successfully in such exposed circumstances can be found. Any further urban developments on the peninsular will aggravate an already precarious colony, and should be opposed.