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**Monitoring diets and
population changes of
greater horseshoe bats
in Gloucestershire
and Somerset**



Lowlands
Team

Roger D Ransome

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in Gloucestershire and Somerset**

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Summary

The objectives of this study were to:

1. Monitor and compare greater horseshoe bat diets at Brockley Hall Stables and Woodchester Mansion over the summer of 1998. Compare diets in 1998 with those in 1996 at the same two sites.
2. Monitor the growth performance of the young, population changes at these two sites and review historical data on population size to set current population levels in context. Compare these aspects with the Littledean Hall colony.
3. Investigate the relationship between the Brockley Hall Stables, the nearby Kings Wood mines, and surrounding hibernacula, through capture and marking studies.

Dietary studies at Woodchester and Brockley in 1998 showed that key prey levels at Woodchester were higher at 81%, than at Brockley, where it was 69%. It was a poor year for cockchafers, with few eaten at either site. Throughout the growth period of the young, however, diets at the two roosts were not significantly different.

Diet changes between 1996 and 1998 were similar, despite the differences in overall key prey consumption. Moth levels were lower at both sites in 1998 compared with 1996, and *Aphodius* beetle levels were much higher. The highest levels of *Aphodius* consumption were recorded at Woodchester, reaching virtually 100% in the first week of August in 1998. The dietary data confirms that the grazing agreements implemented in the Woodchester valley have been beneficial to the bats since consumption there was 40% of the overall diet. At Brockley *Aphodius* formed 30% of the overall diet. During most of the growth period of the young there were no significant dietary differences between the two roosts in 1998.

Secondary prey diet changes between 1996 and 1998 were marked. Few ichneumonids were eaten at either site in 1998, whereas they were abundant in 1996. Poor moth populations in 1997 and 1998 may explain this by reducing their supply of hosts. Tipulid consumption rose at both sites in the early weeks of summer 1998. Caddis fly levels were high in a few weeks, but only at Woodchester, where several lakes exist close to the roost.

Overall the dietary data further support the view expressed by Ransome (1997a) that differences in the abundance of selected prey determines consumption levels. In the absence of preferred key prey, or at low concentrations of them, bats switch to alternative secondary prey. Prey abundance differences in both prey types between the diets of two colonies may result from either habitat differences in foraging areas, variable land-management regimes such as grazed or non-grazed, or erratic climatic conditions operating during specific foraging bouts. In addition the population levels of some insects, such as cockchafers, show cyclical changes with infrequent peak years.

Dusk exit counts at all three roosts, with counts of young, allowed the estimation of total colony size at each roost, although complications exist at Brockley due to the split of bats between the Stables and nearby Kings Wood. In 1998 the Woodchester colony was estimated at 139 bats, Littledean Hall at 157, and Brockley/Kings Wood at 241. The occupancy levels varied at each site, and was highest at Littledean Hall, possibly due to having the most favourable habitat

circumstances. The roost sustenance zone around Brockley is believed to be the one most in need of improvement and safeguarding.

Since 1996, colony size has either increased or been stable at these roosts, but data are not complete. Woodchester studies from the late 1950's, when about 480 bats were present, shows that in 1984 there were 190 (40% of the 1950's figure), in 1988 there were 75 (16%), and currently 139 (29%). The introduction of an incubator, which has been used by the bats from 1994 onwards, seems to have provided an encouraging boost to recovery, which habitat and land-management changes implemented more recently should help to further accelerate.

The growth performance of young at the three roosts in 1998 showed, once again, that only female radius lengths were significantly different. Female young at the unheated Littledean Hall roost were significantly smaller at 55.2 mm mean radius length, than those born at the heated Brockley (mean 56.2 mm) and Woodchester roosts (mean 56.5 mm).

Growth of female young at Woodchester showed remarkable consistency over the three summers from 1996 to 1998, averaging 56.5 mm. This was despite significant changes in birth timing. At Littledean Hall in the same summers females averaged 55.9 in 1996 and 1997, but only 55.2 in 1998. These data were not significantly different, however.

Data for Brockley female bats were only available for 1997 and 1998. They averaged 56.2 mm for those years.

Kings Wood contains a series of small to medium-sized mines, some of which are used throughout the year. The Nursery Roost mine is used as a satellite maternity roost from the main roost at Brockley Stables, and is probably most used in spring and early summer. The various small mines are used as hibernacula, especially early and late in the hibernation period, probably because they are too small to provide good conditions for hibernation throughout a cold winter. Most appear to be type 3 hibernacula, occupied by one adult male and one or more adult female bats, but some are type 1 and 2 sites mainly used by clusters of first and second year bats. The sites are shared with small numbers of lesser horseshoe bats.

Young of the year leave Brockley in September, and some may move to Kings Wood to hibernate in their first winter. However, many travel to Cheddar Gorge, where they may occupy several type 1 hibernacula. Others reach Mells, Wookey Hole and Banwell hibernacula.

As Brockley-born bats age, they progressively use Cheddar Gorge caves less and less, moving first into type 2 sites, such as those at Banwell and Wookey, and later to type 3 sites. These are mainly within 20 km of the roost, but can be widely scattered over a considerable distance. One bat apparently regularly returns to one which is 43 km from Brockley.

The objectives of a UK monitoring system for greater horseshoe bats are suggested as being two-fold. Firstly it should detect and record changes in colony size at all important maternity roosts. Data from winter surveys should also be obtained as a check on the emergence of new nursery roosts, and the continued suitability of hibernacula conditions.

Secondly, by using a graded series of protocols, it should appropriately monitor diet and growth performance of the young at selected maternity roosts. This information may be necessary if problems occur at specific colonies.

Introduction

Recent research studies have shown the importance of diet and roost thermal conditions as factors which influence the growth of juvenile greater horseshoe bats, and the subsequent recruitment of female young to the adult population. Dietary information has been used to make habitat and land management recommendations to secure and enhance the long-term future of populations. These recommendations have been implemented as projects at specific roosts.

Further work is now required to strengthen our understanding of the effects of fluctuations in prey abundance and quality, and to ensure that key habitats are managed in a way that will buffer bat populations against climatic fluctuations.

In addition, data are required on the long-term performance of the colony centred on Brockley in northern Somerset, so that appropriate monitoring of the population associated with this SAC can be set in place. This should include some investigation of the way the bats use the Stable site, and the nearby Kings Wood roost, following extensive building alterations in the recent past.

Similarly, appropriate monitoring is needed at the Littledean Hall roost, which is within another SAC in the Forest of Dean, Gloucestershire. Finally, the Woodchester Mansion colony in Gloucestershire, although not within a SAC, has been the subject of extensive ecological research for 40 years. In recent years, land-management changes have been implemented in the Woodchester valley, and their impact requires assessment.

The two sites chosen for the complete study, Brockley and Woodchester, have both had an incubator installed in the maternity roost to improve the growth performance of the female young, with the aim of ultimately promoting population levels (Ransome 1989, 1998a). The Littledean Hall colony occupies an unheated roost, and so provides a control for growth of the young and population changes at the other two sites.

Part 1: Dietary monitoring during 1998

Methods

Dietary monitoring involved the collection and analysis of faecal samples collected during 11 selected weeks. The same methodology was used as previously (Ransome, 1997a) to generate estimates of the percentage volume of insect prey items consumed by foraging bats. However, the number of faecal pellets analysed per weekly sample was 12 instead of 16. This reduction was implemented since recalculation of previous data using the first 12 pellets produced very similar dietary estimates to those obtained from 16 pellets.

The dates selected for 1998 matched those used by Ransome (1997a), and were as follows:

- | | |
|---------------------------------------|------------------------------|
| (a) April 26; May 3; May 10 | Provided WEEK 1 & 2 SAMPLES |
| (b) May 24, May 31, June 7 | Provided WEEK 3 & 4 SAMPLES |
| (c) June 28, July 5, July 12 | Provided WEEK 5 & 6 SAMPLES |
| (d) July 26, August 2, August 9 | Provided WEEK 7 & 8 SAMPLES |
| (e) August 23, August 30, September 6 | Provided WEEK 9 & 10 SAMPLES |
| (f) September 27, October 4th. | Provided WEEK 11 SAMPLE |

These dates covered:

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

Juvenile growth occurred between periods (c) to (e) or weeks 5 to 10.

Summary

This procedure required 17 visits to each roost, divided into 6 sessions. Each of the five sessions required three visits, and generated two samples of one week, and one session (the last) generated one sample of one week. The samples covered the dietary changes from late April to early October. Ten of the samples were adjacent pairs, each of which allowed any short-term changes in dietary content to be detected.

Statistical treatment of data

Each raw datum obtained was the percentage of the faecal pellet by volume for a particular prey item. Data for specific prey items in each weekly 12 pellet sample were arcsine transformed in an attempt to normalise them (Whitaker 1988). However, in some cases normality was not achieved by this procedure. Because of this, t tests could not always be used in statistical comparisons of pairs of data sets. Hence nonparametric statistical tests (Kruskal-Wallis) were used on the arcsine-transformed data instead.

Working hypothesis previously used (Ransome 1996, 1997a) to explain dietary changes in this species

Greater horseshoe bats selectively feed on certain insects, specialising in certain scarabaeid beetles and large moths. The prey items eaten are virtually the same at maternity roosts throughout the UK, in spite of quite different surrounding habitat topography and proportions of woodland, grazed pasture, urban and aquatic areas.

Certain insect prey items (cockchafers, moths, *Aphodius*, *Geotrupes*) are preferred, or key prey, which form from 60 to 80% of the diet over a summer season. Other insects (tipulids, caddis flies, and ichneumonid parasites of moth larvae) are eaten when key prey are unavailable. They are termed secondary prey.

The relative proportions of the different prey consumed by bats at different roosts in the same year seem primarily to reflect:

- (a) differences in the phenology of specific prey items at different sites in the same season, probably under the influence of different climatic temperature exposure due to latitude, altitude or topographical features (different prey become available at different times);
- (b) differences in the abundance of specific prey items at different sites in the same season, probably under the influence of different habitat and/or land management regimes in foraging areas;
- (c) the ambient temperature conditions during specific foraging bouts. These are not only influenced by local weather at the time, but also by topographical effects which produce microclimates. (Below 12 °C key prey such as cockchafers and most moths are unable to fly, and hence are selectively removed from the air. Below 9 °C, *Aphodius* and tipulids cannot fly, leaving only caddis (trichopterans) and ichneumons available down to about 5 °C.;
- (d) differences in birth-timing of young bats at specific sites, since mothers prefer to eat moths, whilst the young prefer *Aphodius* beetles when they first fly at 30 days old. The young seem unable to catch moths until they are about 45 days old.

Diet at the Woodchester roost

Diet summary

The season in 1998 was characterised by a cold spring and early summer, with a wet and warm late summer. These conditions were predicted to delay births by reducing foraging opportunities during pregnancy (Ransome & McOwat 1994). They were also predicted to favour *Aphodius* populations rather than those of moths. In addition, the fields close to Woodchester Mansion were more intensively grazed by cattle and sheep in 1998 under a regime defined by a management agreement between English Nature and Ann Hardy, the grazier. Further habitat improvements were made with the co-operation of the National Trust, which owns most of the Woodchester valley. One change resulted in the removal of a nearby poplar plantation of some 2.7 hectares. It has been replaced by a gradually improving grazed grassland habitat in recent years, which should have further boosted local *Aphodius* populations. Currently the quality of

grazing in this cleared field is still poor, as a result of weed invasion, so stocking levels in 1998 were inevitably low.

A summary of the Woodchester bat's diet in 1998 is shown in Figure 1.

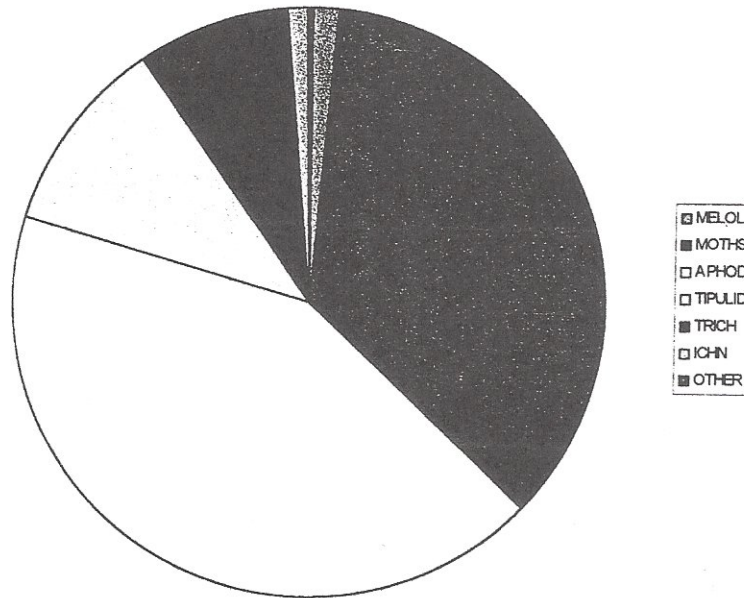


Figure 1

The key prey diet was dominated by high *Aphodius* (39.7%) and moth (33.3%) consumption, with low *Geotrupes* (6.2%) and very poor cockchafer (*Melolontha*) levels (1.4%). Overall the key prey formed 80.6 per cent of the 1998 diet, which is a very high figure. Secondary prey diet was split primarily between tipulids (10.4%) and caddis flies (7.7%), with very few ichneumons (1.1%).

Diet changes throughout the season

Figure 2a shows changes in key prey consumption by week of the study. *Geotrupes* levels fell rapidly at the end of April, and moths dominated the diet from late May to early July as usual. Cockchafers were hardly eaten at all. From late July, moth consumption fell markedly with a small rise later in the autumn. Significant *Aphodius* consumption started late in June and rose rapidly to nearly 100% in early August. Adult bats, including some late-pregnant and many lactating females, must have been feeding primarily upon them at this time. The mean birth date of 5th July (combined data for both sexes and all births) meant that most of the young would have started to feed in early August (during week 8).

Figure 2a

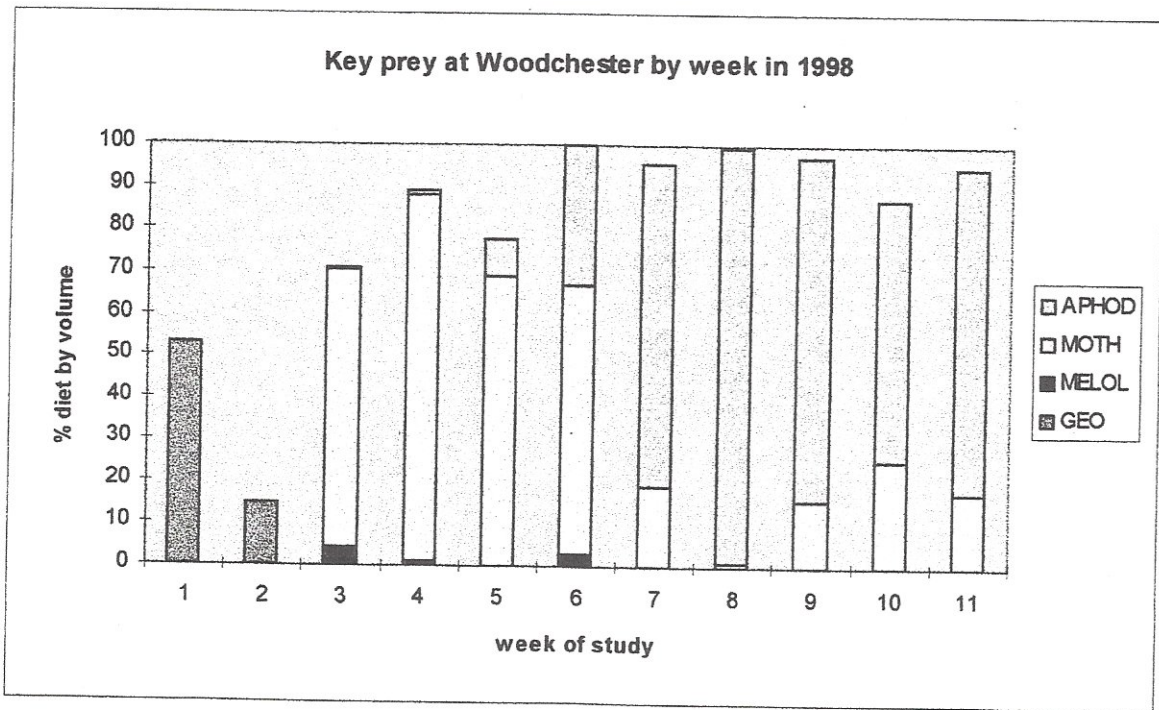
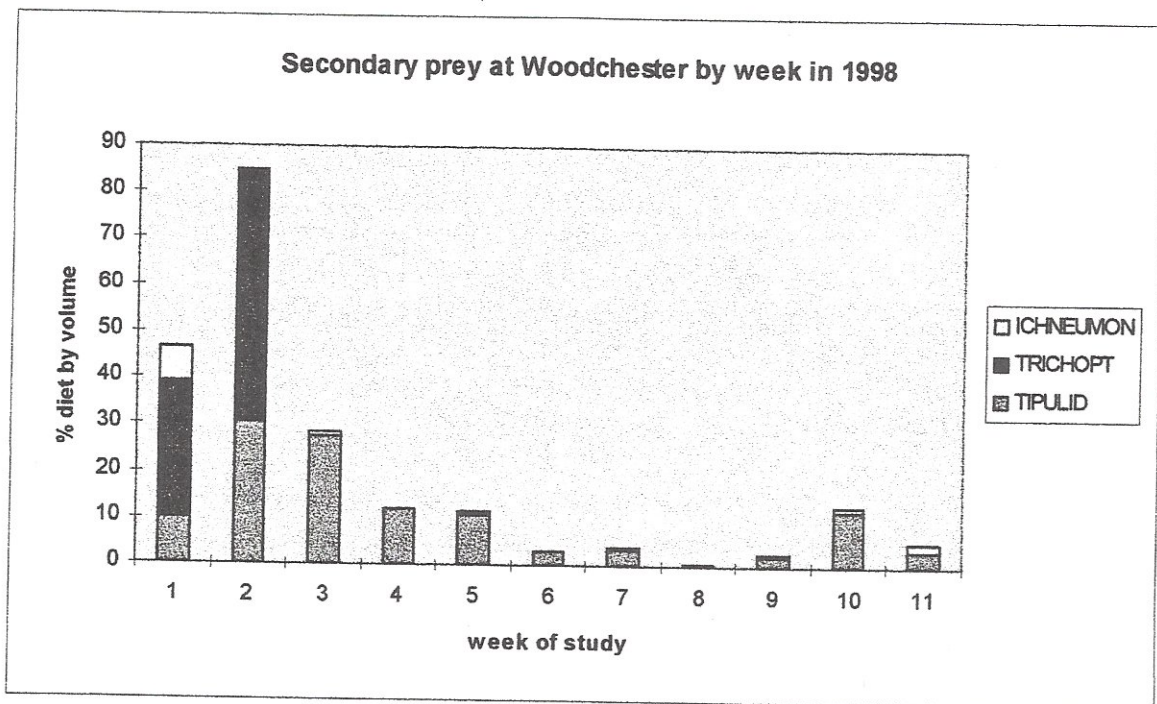


Figure 2b



Figures 2a, b

Figure 2b shows changes in secondary prey consumption by week of the study. Only in the first three weeks was consumption of all secondary prey above 10% of the diet. Caddis flies were mainly eaten in the first two weeks, which suffered from cold nights. Tipulids were also eaten during this period, and throughout the season in small amounts.

Diet at the Brockley roost

Diet summary

Brockley Stables experiences a similar climate to that at Woodchester Mansion, but is slightly warmer due to being more southerly and very close to the Bristol Channel. Although milder, it suffers from greater exposure to the prevailing south-westerly winds. It is not sheltered within a steep-sided valley as is Woodchester Mansion.

The 1998 Brockley climate was also predicted to favour *Aphodius* populations rather than those of moths. However, no habitat or land-management alterations have recently been implemented which may have further boosted *Aphodius* populations.

Figure 3 summarises the total diet for Brockley in 1998.

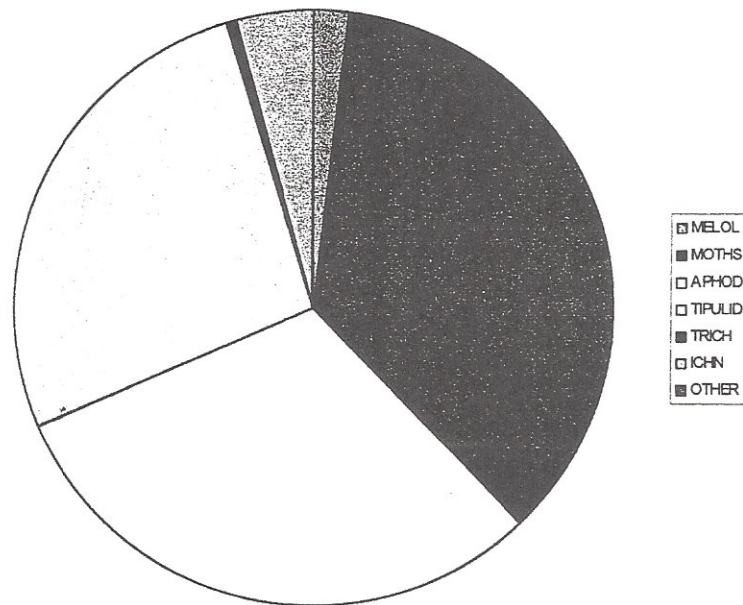


Figure 3

The key prey diet was mainly split between moths (35.3%) and *Aphodius* (30.0%), with very poor cockchafer (*Melolontha*) and *Geotrupes* levels (1.9 & 1.7% respectively). Overall the key prey formed 68.9 per cent of the diet, a much lower figure than at Woodchester. Secondary prey diet was dominated by tipulids (26.4 %), with some ichneumons (4.0 %), and very few caddis flies (0.7%).

Diet changes throughout the season

Figure 4a shows changes in key prey consumption by week of the study. Consumption of key prey virtually mirrored that at Woodchester with two minor differences. *Geotrupes* levels were lower at the end of April, Moth consumption did not fall quite as much, and showed a larger

increase later in the autumn than at Woodchester. Correspondingly, *Aphodius* consumption was lower, but followed a similar pattern. Adult bats must also have been feeding primarily upon them at this time. The mean birth date (combined data for both sexes and all births) of 7th July meant that most of the young would also have started to feed during week 8, as at Woodchester.

Figure 4a

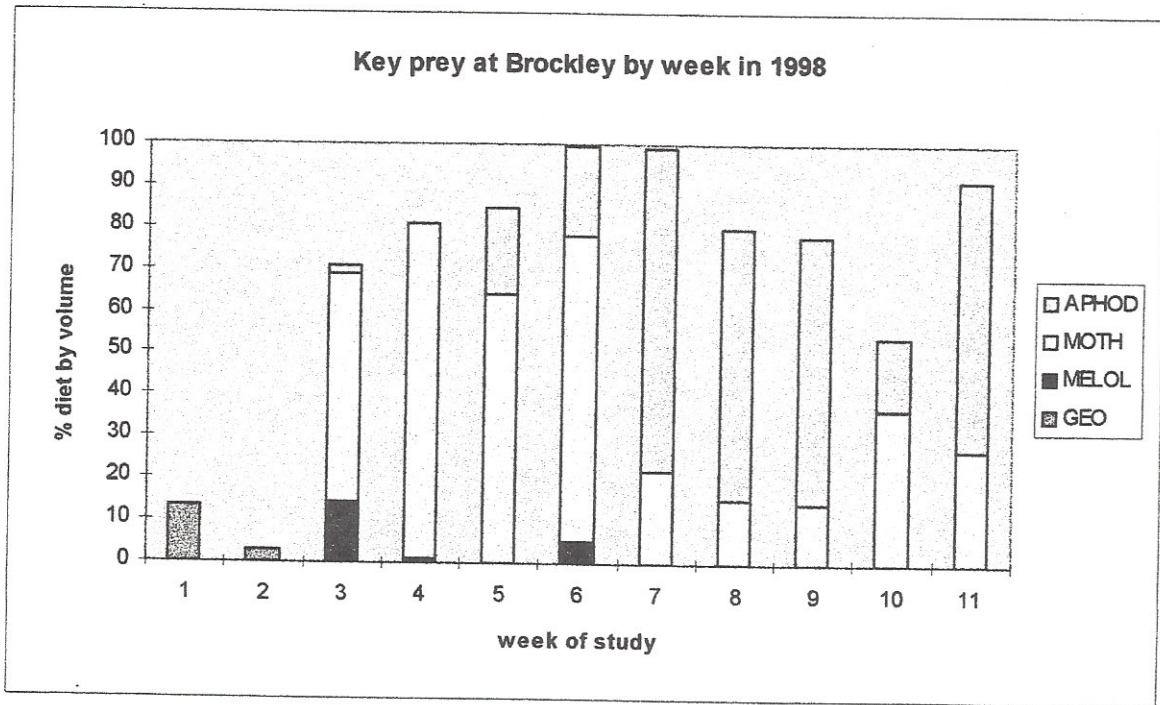


Figure 4b

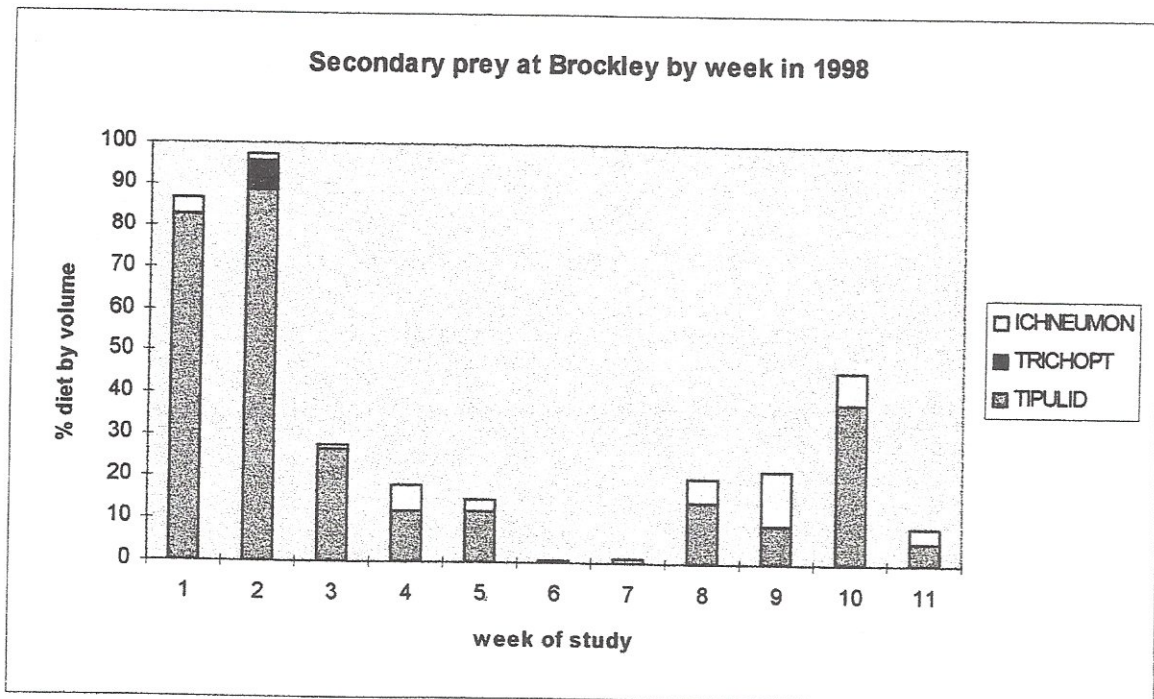


Figure 4b shows changes in secondary prey consumption by week of the study. In the first five weeks consumption of all secondary prey was above 10% of the diet, and above 85% for the first 2 weeks, when tipulids were mainly eaten. Some ichneumons were also eaten during this colder period, and in small amounts throughout the season, with larger amounts of tipulids. Caddis flies were hardly eaten at all.

Differences between the diets at the two roosts

The diet summaries for each roost in 1998 are shown in figures 1 and 3. Moth ($p=0.506$) and cockchafer ($p=0.663$) consumption levels were not significantly different at the two sites.

Woodchester showed significantly higher levels of the two dung beetle genera than Brockley (table 1). This may reflect the improved grazing regimes deliberately maintained near the Woodchester roost (see above). All other differences relate to secondary prey. The Woodchester roost is close to a series of large lakes, and the high consumption of caddis flies may reflect high availability at a time of poor alternative prey presence. Brockley's sustenance zone (Ransome 1996) lacks significant areas of lakes. In the absence of caddis flies, the Brockley bats consumed tipulids and ichneumons when key prey were unavailable.

Table 1. Significant differences in total prey consumption between the two maternity roosts during the 1998 season

Prey item	Roost with highest level	Kruskal-Wallis statistics (adjusted for ties)
<i>Aphodius</i>	Woodchester	H=4.60, n=108, p=0.032*
<i>Geotrupes</i>	Woodchester	H=7.55, n=36, p=0.006**
Tipulid	Brockley	H=8.37, n=132, p=0.004**
Caddis (Trichoptera)	Woodchester	H=17.49, n=24, p=0.000***
Ichneumons	Brockley	H=7.46, n=132, p=0.006**

* = significant difference; ** = highly significant difference; *** = very highly significant difference

Kruskal-Wallis statistical analyses carried out to compare prey consumption by each week of the study are summarised in table 2. These data largely repeat the results of the diet summaries, but they also provide details of the timing of significant differences already discussed. They concentrate in the early and later weeks of the season. The highly significant dietary differences only occurred in weeks 1 and 2.

Table 2. Significant differences in prey consumption between the two roosts by week of the study using Kruskal-Wallis tests

Week of study	Prey item (site with highest consumption)	Kruskal-Wallis statistics (adjusted for ties)
1	Tipulid (Brockley)	H=12.09, n=12, p=0.001**
1	Caddis flies (Woodchester)	H=9.13, n=12, p=0.003**
1	<i>Geotrupes</i> (Woodchester)	H=5.67, n=12, p=0.017*
2	Tipulid (Brockley)	H=10.37, n=12, p=0.001**
2	Caddis flies (Woodchester)	H=7.79, n=12, p=0.005**
5	<i>Aphodius</i> (Brockley)	H=5.95, n=12, p=0.015*
8	Moths (Brockley)	H=4.96, n=12, p=0.026*
8	<i>Aphodius</i> (Woodchester)	H=4.95, n=12, p=0.026*
10	<i>Aphodius</i> (Woodchester)	H=6.67, n=12, p=0.010*

* = significant difference; ** = highly significant difference

Two additional points are shown. First that moth consumption at Brockley was significantly greater than at Woodchester in week 8, and second that *Aphodius* consumption was also greater there in week 5. However, for most of the period from week 3 to 7 there were no significant differences detected by analysis of weekly samples between the diets at these two roosts. These weeks covered much of pregnancy and most of the early growth period of the young. Hence the diet quality during the key period of growth of the young (Ransome 1998a) at the two roosts was not significantly different. Later on the Brockley bats ate more moths, and the Woodchester bats ate more *Aphodius* beetles.

Overall the 1998 data mainly provide additional support for conclusion (b) above. Most of the prey items appeared in the diet at both roosts at the same time during the summer, and birth timing was similar at the two roosts. Hence phenological differences in the emergence timing of prey items were not important, nor the timing of initial foraging by the young. Differences between the roosts confirm the influence of habitat (aquatic habitat differences), especially upon the spring diet, and land management regimes (intense grazing regime favouring *Aphodius* at Woodchester) upon the diets of specific colonies in a given year.

Part 2: Diets in 1998 compared with 1996

Additional tentative conclusions (Ransome 1998b) to supplement previous studies carried out within the same year

The relative proportions of the different prey consumed by bats at the same roosts, and therefore in the same essential habitat surroundings, in different years seem likely to reflect:

- (a) differences between the gross population levels of key prey from year to year, and hence the availability of each to bats foraging during favourable weather (high ambient temperatures; low wind speed and rainfall)
- (b) the incidence of favourable foraging weather among different years, as it affects the number of times when bats have the opportunity to forage upon key prey whatever their population levels

Key prey population level changes appear to be at least partly determined by a factor, or factors, which operate in the preceding year for insects with annual life cycles, such as moths and *Aphodius*. One of the factors seems to be climate-induced, for example the impact of the drought which delayed the emergence of significant numbers of *Aphodius* in 1995 by more than a month. The same drought may also have reduced *Aphodius* populations levels in 1996, since low consumption by bats occurred at most of the five sites studied during that year. This was in spite of this prey emerging at its normal time of year. The factors, are likely to operate over the 4 previous years for insects with long life cycles such as cockchafers.

Significant differences between diets in 1996 and 1998 at the two roosts

Figure 5 shows diet summaries for the two roosts in the two years. Table 3 summarises the results of analyses carried out to compare the total diets for the two roosts by prey item. At Woodchester the total key prey consumption over the whole season was 76% in 1996 compared with 81% in 1998. At Brockley the 1996 figure was 78%, and 69% in 1998. Hence, overall, if key prey consumption provides dietary benefits to bats, the diet at Woodchester slightly improved between the two years, but at Brockley it deteriorated.

The greatest dietary differences between the two years occurred in the consumption of ichneumonids, and took place at both roosts. The fall in consumption between 1996 and 1998 was greatest at Woodchester, however. Ichneumons are believed to be the least preferred secondary prey, (Ransome 1996, 1997a) which is only taken at ambient temperatures below about 8°C. This level prevents the flight of most of its other prey. Hence low ichneumonid consumption may be due to either low populations of ichneumons; the higher availability of other preferred prey, or to higher minimum climatic temperatures in the 1998 season. In fact the minimum temperatures in both years were very similar during the sampling periods, so the first two hypotheses provide the more likely explanations. The yellow underwing moth (*Noctua pronuba*), is a major noctuid moth whose larvae are parasitised by ichneumonids of the *Ophion* complex. Captures of yellow underwing moths in light traps were very poor in 1997 and in 1998. Low population levels of resident moths are predicted to cause low ichneumonid populations.

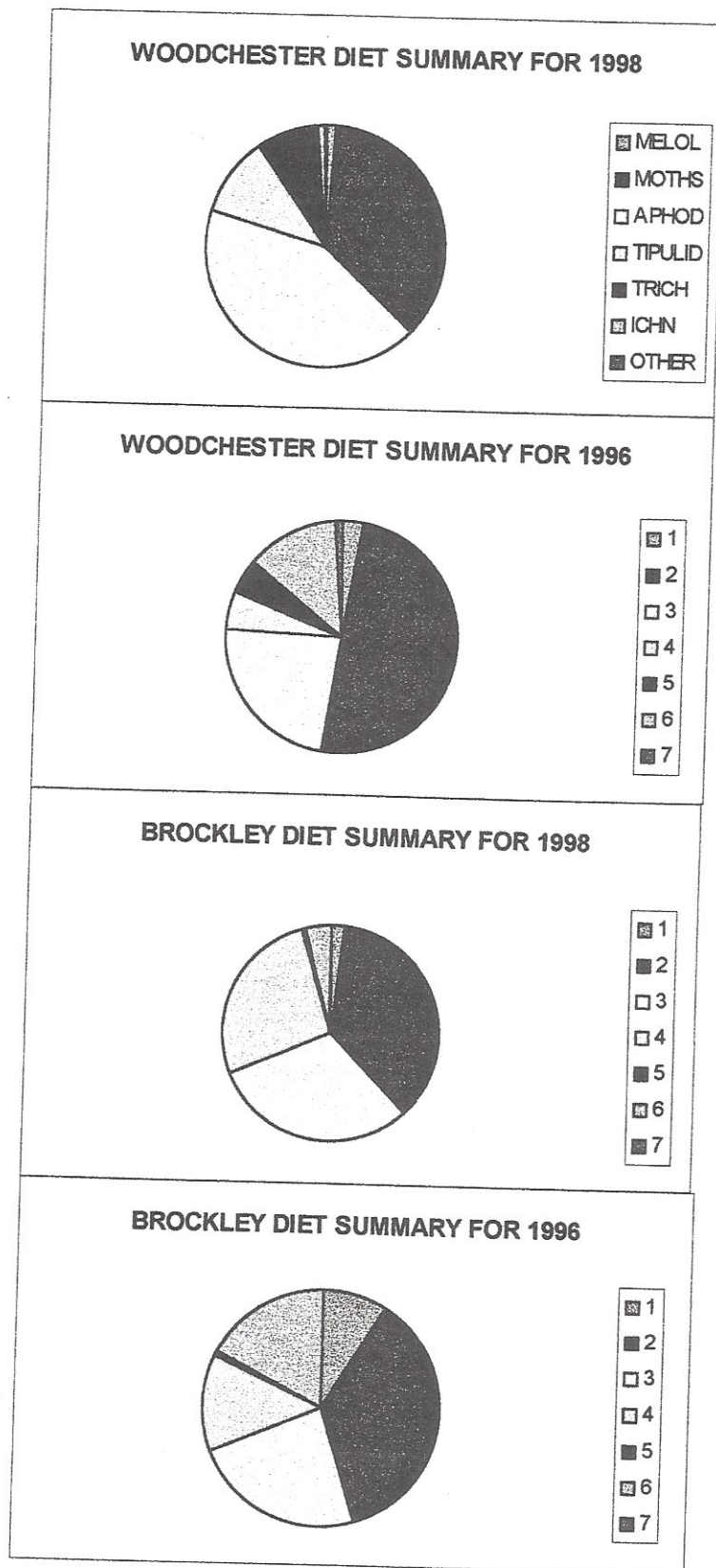


Figure 5

There was a rise in consumption of tipulids at both roosts in 1998 (table 3), even though the overall consumption was much greater at Brockley (Figure 5, table 1). Tipulids are favoured by damp grassland with short swards such as those maintained by sheep grazing. Higher consumption at both roosts may be a response to greater tipulid densities due to higher rainfall over the past two summers, combined with the sheep grazing regime recently instituted in the Woodchester valley, and consistently present near Brockley.

Table 3. Significant differences in overall diet between 1996 and 1998 of specific prey items

Roost	Prey item (year of highest level)	Kruskal-Wallis statistics (adjusted for ties)
Woodchester	<i>Aphodius</i> (1998)	H=4.63, n=96/108, p=0.031*
Woodchester	Tipulid (1998)	H=6.28, n=96/132, p=0.012*
Woodchester	Ichneumons (1996)	H=49.18, n=96/132, p=0.000***
Brockley	Tipulid (1998)	H=4.24, n=96/132, p=0.040*
Brockley	Ichneumons (1996)	H=13.88, n=96/132, p=0.000***

In column 3 the first figure for number of data (n) refers to 1996, and the second to 1998.

* = significant difference; *** = very highly significant difference

The only key prey difference between the overall diets over the two years was in *Aphodius* levels, and occurred only at Woodchester. Levels were higher in 1998 than in 1996. This further supports the view that grazing improvements implemented there have raised the availability of these beetles to foraging bats. From the high levels consumed (nearly 100%) in early August 1998, all bats were exclusively feeding on them at that time. *Aphodius* beetles must have been crucial towards the end of lactation by mothers, and to the growth of young in 1998, when moth consumption deteriorated rapidly in July.

Key prey consumption during lactation by mothers and growth of their young showed similar changes at the two roosts between the two years (tab. 4; compare rows 1 & 3; 2 & 4; 6 & 8; 9 & 11; 10 & 12). *Aphodius* levels were higher, and moth levels lower in 1998 than in 1996. However, the changes were greater at Woodchester (5 out of 6 analyses significant or highly significant) than at Brockley (2 out of 6 significant).

In summary it can be said that the dietary changes between 1996 and 1998 at the two roosts showed similar trends, despite the differences in overall key prey consumption. Among the key prey, moth levels declined, and *Aphodius* levels rose. Among the secondary prey, ichneumon levels greatly declined, and tipulid consumption rose. These changes are believed to be due to factors influencing the relative population densities of specific insect prey. Factors include natural ones such as climate (rainfall rather than temperature), and densities of host moth larvae, but also the grant-supported land management changes instituted at Woodchester.

Table 4. Key prey comparisons between 1996 and 1998 by roost during selected periods of lactation and growth of the young

Row number & Roost	Weeks of study	Prey item (year of highest level)	Kruskal-Wallis statistics (adjusted for ties)
1. Woodchester	5 to 10 (all lactation and growth)	<i>Aphodius</i> (1998)	H=8.90, n=72, p=0.003**
2. Woodchester	5 to 10	Moths (1996)	H=4.71, n=72 p=0.030*
3. Brockley	5 to 10	<i>Aphodius</i> (1998)	H=5.14, n=72, p=0.023*
4. Brockley	5 to 10	Moths (1996)	H=2.63, n=72, p=0.105
5. Woodchester	5 to 8 (most of lactation & early growth)	<i>Aphodius</i> (1998)	H=6.06, n=48, p=0.014*
6. Woodchester	5 to 8	Moths (1996)	H=9.63, n=48, p=0.002**
7. Brockley	5 to 8	<i>Aphodius</i>	H=0.08, n=48, p=0.772
8. Brockley	5 to 8	Moths (1996)	H=3.31, n=48, p=0.069
9. Woodchester	7 & 8 (later lactation & growth)	<i>Aphodius</i> (1998)	H=8.04, n=24, p=0.005**
10. Woodchester	7 & 8	Moths (1996)	H=10.51, n=24, p=0.001**
11. Brockley	7 & 8	<i>Aphodius</i> (1998)	H=5.27, n=24, p=0.022*
12. Brockley	7 & 8	Moths (1996)	H=3.37, n=24, p=0.066

Rows in bold type show significant differences in diet consumption between the two years. * = a significant difference; ** = highly significant difference.

In column 4, number of data (n) is identical for both years.

The 1996/1998 differences are best explained by major changes in the availability of cockchafers, ichneumonids, moths and *Aphodius* beetles to foraging bats. Data are consistent with conclusion (a) above.

Part 3: Population monitoring during 1998

Two types of monitoring were carried out at the two roosts. Dusk exit counts took place on the same dates as those selected for dietary monitoring, and the number of young left in the attic after the exit of the adults were counted on the same dates. The latter data were supplemented by additional counts made during growth studies.

Dusk counts at Woodchester

Dusk exit counts were made by the author within the corridors of Woodchester Mansion, the building in which the breeding attic exists (table 5). An ultrasonic receiver (narrow band), fitted with an earphone, was used to silently assist counts. Bats left the attic via a small doorway into a dark corridor and hung up on a rough patch of ceiling behind a protective grille. They were counted emerging through the grille as they passed across a large expanse of pale wall lit up by reflected light from the walls of the building across a courtyard, via a large window. Bats flew along the dark unlit corridors within the building for an unknown time before leaving to forage. After the end of the count, the attic was entered to collect dropping samples, count the number of young, and carry out growth studies as in Ransome (1997a & 1998a).

Table 5 Population data for Woodchester maternity roost in 1998

DATE in 1998	Total n bats exiting at dusk	n young left in roost after exit of adults
26 April	3	0
3 May	35	0
10 May	40	0
24 May	27	0
31 May	36	0
7 June	36	0
28 June	58	3
5 July	63	20 (+2 aborted)
12 July	56	28
26 July	73	25 (+1 dead)
2 August	88	11
9 August	80	4
23 August	77	0
30 August	67	0
6 September	52	0
27 September	16	0
4 October	9	0

Estimation of the number of births

Maximum number of young counted during these counts was 28. $28 \times 1.23^* = 34$ total (*Correction factor used by Ransome, 1997a.) Maximum number of young counted during all visits was 31. $31 \times 1.23 = 38$. As the total number of young ringed was 33, the correction factor used with the standardised counts provided the closest agreement with the actual number born.

Numbers of adults present

The numbers of bats flying out to feed showed the typical pattern of changes at maternity roosts (Ransome 1997a), showing a minor plateau when only adults and subadults were present (mean = 33, n = 3) in late May and early June, and a rise to a second (major) plateau in late July and early August (mean = 80.3, n = 3). Poor weather in late April, and again in late May and early July, briefly depressed numbers. This may have been a response to restricted foraging success levels at those times.

Dusk counts at Brockley Stables and Kings Wood

Exit counts of bats leaving the attic roost of the Stables were made externally by David Clarke, with the aid of an ultrasonic receiver plus earphone (table 6). The opening which allows bat access to the attic faces due west, and the wall in which it is housed is painted white. In the absence of screening vegetation, the setting sun shines directly onto the exit hole. This effect is diminished by cloud cover, but not eliminated. The light conditions delay emergence timing, but permit accurate counts to be made.

Table 6. Population data for Brockley maternity roost in 1998

Date in 1998	Total n bats exiting at dusk	n young left in roost after exit of adults
26 April	3	0
3 May	14	0
10 May	22	0
24 May	10	0
31 May	6	0
7 June	9	0
28 June	58	10
5 July	59	28
12 July	57	28
26 July	42	12
2 August	84	22
9 August	88	10 (+ 1 dead)
23 August	87	-
30 August	34+	0
6 September	68	0
27 September	39	0
4 October	23	0

After the end of the count entry was made and work carried out as at Woodchester.

Only one evening count was made at the nursery roost in Kings Wood due to the difficulties of counting at the site. The bats occupy a location high in the roof of a disused ochre mine, which was excavated from a deep vertical rift leaving a thin surface cover perforated by open shafts. A large team of observers was needed, since bats left via many exit holes into dense deciduous

woodland. Although young bats could be counted in the roost after the exit of the adults, they were not accessible for growth or ringing studies. Consequently it was not possible to prove directly that young were being transferred between the two roosts by their mothers.

Calculations to estimate the total number of births

Maximum number of young counted was 28. $28 \times 1.23 = 34$ estimated total born. Maximum number of young counted during all visits was also 28. Total number of young ringed = 43, so the estimate is seriously too low. Furthermore 9 more unringed first-year bats were captured at Kings Wood and Brockley in October and November 1998. Only 15 from a cluster of 39 could be caught at Kings Wood, so several other first-year bats are likely to have been missed. Hence the minimum number born in the two sites during 1998 was 52 young. At least 60 births in total must have occurred, since nearly half of the young normally die before winter starts.

Numbers of adults and young present at the two roosts

On 11th July a count of bats leaving the various entrances to the Nursery Roost in Kings Wood from 21.10 to 21.30, totalled about 30 adults. Inside 15 young were counted. If these are added to the data on 12 July from Brockley, a total of about 87 adults and 43 young, (making 130 individuals) occupied the two roosts early in July. These counts were made well before all births had taken place, and possibly before all pregnant females had returned. However, a further 17 young and their mothers (if previously absent) would only raise the total to a maximum of 164, leaving at least 17 adults unaccounted for. These may well have been adult males which often occupy alternative summer roosts at this time of year.

The numbers of bats flying out to feed from Brockley Stables showed a variation on the pattern of changes seen at Woodchester and most breeding roosts (Ransome 1997a). The minor plateau (mean = 8.3, $n = 3$) in late May and early June was well below counts earlier in the season. A large increase to the major plateau in early August (mean = 86, $n = 2$) occurred before most young started to fly, showing that a major influx of older bats occurred suddenly at the end of July. These large fluctuations are presumed to be mainly due to switches between the Brockley and Kings Wood roosts, but may also have been due to an influx of pregnant females from the roost at Clapton Church (Jones, 1990). No counts took place at Clapton Church during 1998, but previously up to 36 bats have used the site.

In late May and early June the numbers fell markedly at Brockley, possibly due to poor weather seriously restricting foraging success levels, and an increasing need for the use of torpor in a cool roost. The underground roost at the Nursery Roost in Kings Wood may have provided more suitable conditions for this.

Dusk counts at Littledean Hall

Population and growth data from Littledean Hall were included in the monitoring program to provide a control for the two heated maternity roosts.

Dusk exit counts were made by David Priddis and his assistants from a car parked in the courtyard outside the large building in which the breeding attic occupies (table 7). An ultrasonic receiver, also fitted with an earphone, was used to assist counts. Bats left the extensive attic system via a

large opening into a dark sheltered section. They were counted emerging from it into the cover of an adjacent large tree.

Table 7. Population data for Littledean Hall maternity roost in 1998

DATE IN 1998	Total n bats exiting at dusk	n young left in roost after exit of adults
27 April	1	
10 May	52	0
24 May	50	0
31 May	48	0
7 June	71	0
28 June	98	4
5 July	115	18
12 July	120	24
26 July	120	23
2 August	123	14
9 August	123	4
23 August	123	0
30 August	127	0
6 September	103	0
27 September	68	0
4 October	12	0

After the end of the count, the attic was entered to collect dropping samples, count the number of young, and carry out growth studies on them as above.

Estimation of the number of births

Maximum number of young counted during these counts was 24. $24 \times 1.23 = 29.5$ total. Maximum number of young counted during all visits was also 24. The correction factor used with the standardised counts slightly underestimated the actual number born (known from ringing studies), which was 33.

Numbers of adults present

The number of bats flying out to feed showed a slightly modified typical pattern of changes at maternity roosts (Ransome 1997a). A minor plateau occurred when only adults and subadults were present (mean = 56.3, $n = 3$) in late May and early June, and was followed by a rise to a second, major plateau in late July and early August (mean = 122, $n = 3$). Poor weather in late April coincided with a virtual absence of bats from this unheated roost. However, the late May and early July, cool weather was not associated with a fall in numbers similar to that at Woodchester and Brockley.

Colony size estimation at the three maternity roosts

Ransome (1997a) used a formula to estimate total colony size in early August (page 29). The formula uses the peak exit count number in July (= the July Nbfd), before the young start to fly, and the number of young born. The latter is either obtained from captures during growth studies, or is estimated from counts as above. A ratio is calculated by dividing the July peak exit count by the number of young born. If the July ratio is below 2.2, an adjustment is made to it by adding 1. If it is above 2.5 it is used without adjustment.

The formula used to estimate total colony size in early August is:

$$(\text{July ratio} \times n \text{ young}) + n \text{ young} = \text{estimated colony size.}$$

Woodchester estimates

The ratio for Woodchester in 1998 was 73:33 or 2.212. This ratio is closest to option 6 in Table 8, and indicates that adult males were absent from the colony. Hence 1 has to be added to the ratio, making it 3.212. This is higher ratio than in 1996 & 1997, when it was 2.72 and 3.07 respectively. These ratios suggest that more non-breeding adult bats were present in 1998, than in the earlier years. Colony captures confirm that this was actually true (Ransome, unpublished data).

Table 8 Calculations to show the effect upon Nbfd: juvenile number ratios of the presence in the roost of different non-breeding age and sex groups (from Table 9, Ransome 1997a)

N breed. females (option)	N non-breed mat. females	Immatures 2& 3 years	Adult males	July ratio	August ratio
(1) 100	0	85	100	2.85	3.85
(2) 85	15	85	100	3.35	4.35
(3) 100	0	50	100	2.50	3.50
(4) 85	15	120	100	3.76	4.76
(5) 100	0	85	0	1.85	2.85
(6) 85	15	85	0	2.18	3.18
(7) 100	0	50	0	1.50	2.50
(8) 85	15	50	0	1.76	2.76
(9) 100	0	120	0	2.20	3.20

NB all calculations assume that all non-breeding sex and age groups specified remain in the roost during the entire period from July to a period in August when all young are foraging and all mothers are present. This does not occur in practice at roosts (see text), so August ratios shown are higher than those which are recorded, even though the specified groups may be present in July, or earlier. However, the calculations are meant to show the impact of different occupational scenarios on ratios, rather than provide accurate ratio predictions.

The varying numbers of immature bats reflect likely ranges occurring at roosts due to varying survival rates.

The 3.212 ratio produces an estimated total colony size of 139 bats in early August, with 106 adults and subadult bats alive in late July.

The mean number of bats flying out to feed during the 17 counts throughout the summer was 48.0, s.d. = 25.48. The peak total number of 99 on 2nd August was 71% of the estimated total colony size at that time, with the 88 bats flying out at dusk forming 63% of it.

Brockley/Kings Wood estimates

The peak July exit count: n young ratio for Brockley/Kings Wood in early July 1998 was 87:60 or 1.45. This ratio is below any option given in table 8 (Ransome 1997a), but is closest to option 7. It indicates that adult males were absent from the colony, and also some subadults. Hence more than 1 has to be added to the ratio, making it 2.45, plus an adjustment for missing subadults. This figure is well below the ratio at Brockley in 1996 of 3.02, which is close to the ratio for Woodchester in 1998. Since the Woodchester ratio had risen since 1996, is preferable to use 3.02, rather than an unknown figure above 2.45 as the ratio for Brockley/Kings Wood colony size estimation.

The estimated number of adults and subadults in the Brockley/Kings Wood colony in early August is about 181. Therefore the estimated total colony size, including young, early in August, is about 241.

The mean number of bats flying out to feed during the 17 counts made at Brockley Stables throughout the summer was 43.6, s.d. = 30.36. The peak total number of 106 on 2nd August formed 44% of the estimated colony total at that time, and the 88 bats flying out formed 37% of it.

By combining data from Brockley Stables and Kings Wood in July and adjusting them (see section 3.2 above) a maximum of 164 bats could be accounted for after all births had occurred. This total is 68% of the estimated combined total colony size, which is close to the Woodchester figure at a similar time.

Littledean Hall estimates

The peak July ratio for Littledean Hall in 1998 was 124:33 or 3.758. This ratio is closest to option 4 in Table 8, and suggests that adult males were present in the colony with significant numbers of subadults and non-breeding mature females.

This is a higher ratio than in 1996 and 1997, when it was 3.16 and 3.025 respectively. The presence of many more non-breeding adult bats in 1998, also occurred at Woodchester. However, no colony captures at this roost were made to confirm that this was actually true. The 1998 ratio with 33 births estimates total colony size at 157 bats in early August, with 124 adults and subadult bats alive in July.

The mean number of bats flying out at dusk was 84.6, s.d.= 42.02, n=16. On 2nd August 123 bats flew out to forage, and with the 14 young still left inside the attic, the roost held 87% of the estimated total alive. On 19th July a total of 147 bats were present before the last 4 babies had been born. This figure means that 96% of the total estimated to be alive at that time were in this roost, if these young are subtracted from the total.

Occupancy levels at different maternity roosts

Woodchester's estimate of 139 bats in early August is considerably below the 241 estimated for the Brockley/Kings Wood total. However, the maximum total counts for the two maternity roosts on 2nd August were only slightly lower at Woodchester (99) than at Brockley (106). These two roosts held 71 % and 44 % of the estimated total colony size respectively on that date. The combined Brockley plus Kings Wood estimate of 164 bats formed 68% of the estimated total colony (see above). Hence combining the two maternity roosts narrows the difference considerably. The data is consistent with bats from Brockley and Kings Wood maternity sites transferring throughout the season and varying the proportion each holds of the total colony. No such mass movements of bats occur at Woodchester.

At Littledean Hall the colony estimate of 157 is 18 higher than at Woodchester, but with an identical number of young born in 1998. Occupancy levels of adults from late June until late August are very high, with virtually all bats present in early August. This does not happen at Woodchester, nor at Brockley Stables.

Why are roosts occupied at different levels in the same summer season?

Many factors may potentially influence the proportion of bats from a colony occupying a specific roost on a particular date or time of year (table 9). Among them are:

Table 9. Some population statistics for maternity roosts studied during 1998

Maternity roost	mean n Nbfd	Estimated n adults in July (n young)	Estimated total colony n in August	mean n of adults flying in first plateau period (%)	mean n of total colony present in August (%)
Woodchester Mansion	48.0	104 (33)	137	36 (34)	80 (58.4)
Littledean Hall	84.6	124 (33)	157	50 (40.3)	124 (79.0)
Brockley Stables	43.6	181 (60+)	241	8 (4.4)	87 (36.1)
Brockley plus Kings Wood	?	181 (60+)	241	?	?

(a) disturbance levels at the roost (b) availability and suitability of alternative maternity roosts (c) the thermal regimes available in the roost (d) the quality of foraging within the roost sustenance zone (e) the phase of reproduction and hence the specific needs of individual bats (f) social and behavioural factors.

Data are only available for some of these aspects, so I will briefly consider just the first four possible factors.

Disturbance at the roost

There are two types of human disturbance which can occur at a site. First there is incidental disturbance which occurs when owners carry out activities during the normal use of their property. Secondly there is disturbance during studies, carried out under licence, to obtain data

for monitoring or research purposes. I will call this 'study disturbance'. Table 10 summarises the nature of disturbance levels at the various roosts.

Table 10. Summer disturbance levels affecting the maternity roosts

Roost	Incidental disturbance	Study disturbance
Woodchester Mansion	Regular visits by public to building on weekend open days (22 per summer); plus continuous occupancy by caretaker. Rules ensure quiet and no lights at dusk.	Long-term study site involving exit counts, dropping collections, growth studies of the young and captures of the whole colony for survival, matriline studies & radio-tracking.
Littledean Hall	Regular visits by public to a room below the roost attic throughout whole summer. Adjacent buildings occupied and courtyard with bat exit used as a car park.	More recent (1986+) study site as a control for Woodchester. Exit counts, dropping collections, and recent growth studies. Only one colony capture of adults within the roost (in September 1994). No radiotracking studies
Brockley Stables	Roost in the large attic of a substantial residential house converted from a previously unused stable block some 9 years ago. Within a walled estate occupied by many other properties, including regular vehicular access.	As for Littledean Hall, except that studies have only taken place since 1996 due to refusal of access by a previous owner. No colony captures of adults have been made.
Kings Wood	Located in a secluded wood, but a footpath runs close to the disused mine used as a nursery roost. Possible disturbance by walkers, but likely to be rare at dusk.	Used as a source of bats for radio-tracking studies in the early 1990's by mist-netting near entrances. Only a few exit counts and counts of young made since then.

It is impossible to quantify disturbance levels accurately, since most incidental disturbance is not observed. However, a rank can be drawn up without too much contention based upon known study disturbance levels plus likely incidental disturbance.

The Woodchester colony is exposed to the greatest level of disturbance, followed by Littledean Hall, Brockley Stables and King's Wood.

Occupation levels were highest at Littledean Hall, then Woodchester and lowest at Brockley. Levels at Kings Wood were only assessed on one date, so the only comment which can be made is that it may contain bats from the colony not found at Brockley on a particular date. However, Clapton Church is also occupied by up to 36 pregnant females which seem to move into Brockley before giving birth in late June and July (Jones 1990). Overall, Kings Wood seems currently likely to contain only a low to medium proportion of the total colony in mid summer. Since 43 juveniles out of an estimated 60+ were ringed in Brockley Stables in 1998, most females used the Stable for birth and the early part of the growth of their young.

These considerations do not support the view that human disturbance determines occupancy levels at these three roost.

The availability and suitability of alternative maternity roosts

Of the three maternity colonies studied, only one uses alternative maternity roosts. This is the Brockley/Kings Wood colony. Ringing studies carried out at Brockley in the summers of 1987

and 1988 some ten years ago showed that young were being moved out of the roost on occasions, whenever the weather turned cold. The numbers of adults fell as well, only to recover with warmer weather. Such events have not been recorded at either Woodchester, or Littledean Hall once the females give birth. Furthermore, when Brockley Stables was converted from about 1989, the colony presumably moved into the Kings Wood roost for several years before they returned to the converted Brockley attic.

These considerations suggest that normally Brockley Stables is the preferred maternity roost between late July and September, and this preference is likely to have increased since the installation of an incubator there in 1997. Kings Wood is a secondary maternity roost which is utilised in poor weather, or when bats were excluded from the Brockley roost during building conversions. Non-breeding female bats and males may occupy it to varying degrees throughout the summer. There are probably no alternative suitable maternity roosts near either Woodchester or Littledean Hall, although non-breeding bats from both colonies must have one or more alternative summer roosts for use at certain times.

The choice of two maternity roosts, and three roosts during the pregnancy period, may be a benefit to the Brockley colony allowing the bats to choose among habitat types (e.g. woodland versus pastures) and to disperse and reduce their numbers in a given roost. The latter may reduce commuting distances to foraging sites. Alternatively it may be a response to high stress at the main Brockley roost. Possible stress factors include the lack of shaded exit conditions which delay emergence time (Jones *et al.*, 1995), or poor foraging conditions in the roost sustenance zone. The percentage key prey at Brockley was much lower than at Woodchester in 1998, and so provides support for this view.

The thermal regimes available in the roost

Two of the maternity roosts, Woodchester and Brockley, are currently provided with incubators, which maintain an ambient temperature of about 27 °C. The remainder of the roofspaces the bats occupy fluctuate with climatic conditions, especially temperature and solar radiation levels. At night temperatures fall quite rapidly, especially in the smaller attic at Woodchester.

The maternity roost at Littledean Hall currently has no incubator, so the colony does not have continuous access to a 27 °C region. Due to the enormous volume of the attic roofspace, conditions cool more slowly at night than in the unheated regions of the other two roosts.

The disused mine dome used as the nursery roost at Kings Wood has an unknown thermal regime, since it is out of reach. Being underground suggests that dome conditions will be cooler and much more stable than in the various roofspaces. However, a temperature of 27 °C or above could only develop in the presence of very large numbers of thermoregulating bats.

The widest choice of thermal conditions occurs at the Woodchester and Brockley roosts, especially if nearby cooler habitats are included. Littledean Hall lacks a region kept at 27 °C, which permits bats to minimise energy consumption whilst thermoregulating. In spite of this, the occupancy level there is the highest. The thermal regime present in these maternity roosts shows no clear relationship to occupancy levels.

The quality of foraging within the roost sustenance zone

Duvergé (1997) presented the results of his summer radio-tracking studies at the Brockley/Kings Wood, Woodchester and Iford colonies. He found that most adult bats foraged within 2.25 km of the roost. Since then, in studies at other sites in the UK, he has found bats flying much further, and in some cases, up to 14 km. He also showed that juvenile bats aged 30 days initially fed within 100 m of the roost. They stayed within 0.75 km of the roost for the first 5 nights of foraging, and were between 40 and 60 days old before they reached adult ranges. Similar data for Littledean Hall are lacking.

Ransome (1996) considered the detailed diets of these bats, and the habitats likely to generate the most insects the bats prefer. The 1 km and 3 km radii were used to define areas around a maternity roost called the juvenile and roost sustenance zones. In the light of further radio-tracking studies, the 3 km radius has subsequently been increased to 4 km. These areas are especially important to the female reproductive success, and hence bat populations, since mothers must forage over them. In spring pregnant females hunt mainly within or around deciduous woodland, whereas in summer and autumn they hunt over grazed pastures which either have substantial hedgerows, tree-lines, or woodland edges (Duvergé, 1997).

On the assumption that these distances also apply to bats from the Littledean Hall colony, we can compare the likely foraging quality of habitat at each site at different times of year. Table 11 summarises the data.

Table 11. Likely quality of foraging at different distances from the various roosts

Roost	Habitat up to 1km distance from entrance	Habitat beyond 1km up to 2.25km from the entrance	Habitat quality in spring & summer (overall ranking)
Woodchester	Mixed grazed pasture & deciduous/coniferous woodland within sheltered valley	Further similar habitat within other valleys, plus small urban areas; exposed flat hilly tops with arable crops	good in spring; good in summer (2)
Littledean Hall	Mostly grazed pasture & some woodland within sheltered valleys facing south east; some urban areas close by	Some urban (Cinderford). Lots of sheltered mixed woodland undergrazed by sheep all year round	very good in spring; very good in summer (1)
Brockley Stables	Urban habitat very close to roost; woodland & grazed pastures with hedgerows & tree-lines further away	Extensive grazing areas within hedgerows and more tree-lines; woodland & most urban development	poor in spring good in summer (4)
Kings Wood Nursery	Mostly deciduous woodland with surrounding grazed fields; little urban development	More extensive woodland and woodland/pasture edges; fringed by urban developments	very good in spring; poorer in summer (3)

Of the factors considered, these comparisons and rankings provide the best correlation with the observed occupancy levels. In addition, the probable population shifts between Brockley and Kings Wood coincide with the switch in habitat use by the bats. They move to the roost with the best predicted insect food supplies. The bats switched diet from tipulids to moths between weeks 2 and 3 of the diet study (figures. 2 & 4). Many tipulids emerge from close-grazed permanent pastures, especially damp ones, which currently occur extensively around Brockley Stables, whereas moths occur in greater numbers in deciduous woodland and taller grassland, which surrounds Kings Wood nursery roost. This view is supported by the reverse switch into the Stables late in July as moths declined in the diet, and *Aphodius*, generated by cattle and other grazers over pastures, rose dramatically.

Whilst these data do not conclusively show that habitat quality is the major determinant of occupancy levels (presumably via foraging success levels), this hypothesis is the most likely one to be correct. The improvement, retention, or creation of extensive areas of favourable foraging habitat around a maternity roost, at least up to the 4 km range, is therefore a very important conservation measure. In the current study, the Brockley Stables foraging habitat is probably the one most in need of safeguarding and improvement to ensure the long-term viability of the colony within the SAC.

Part 4: Population trends

Recent population trends

Comparable population counts for all three sites have only been made in 1996 and 1998. Furthermore no data for Kings Wood exists prior to this summer. Table 12 summarises the available data. The estimate for Brockley Stables in 1998 includes data from Kings Wood, which was not obtained in 1996. Hence colony size increase there could not be estimated. However, the other two roosts show an increase, and the rate seems to be greater at the heated roost. At Littledean Hall in 1998 it seems that some females which bred in 1996 and 1997, either failed to do so in 1998, or died after breeding. Both events commonly follow the first birth, as was shown by Ransome (1995). The high July peak ratio of 3.758 suggests the former is true. If this is correct, a significant increase in birth numbers should occur there in 1999.

Table 12. Changes in estimated colony size at the three maternity roosts since 1996

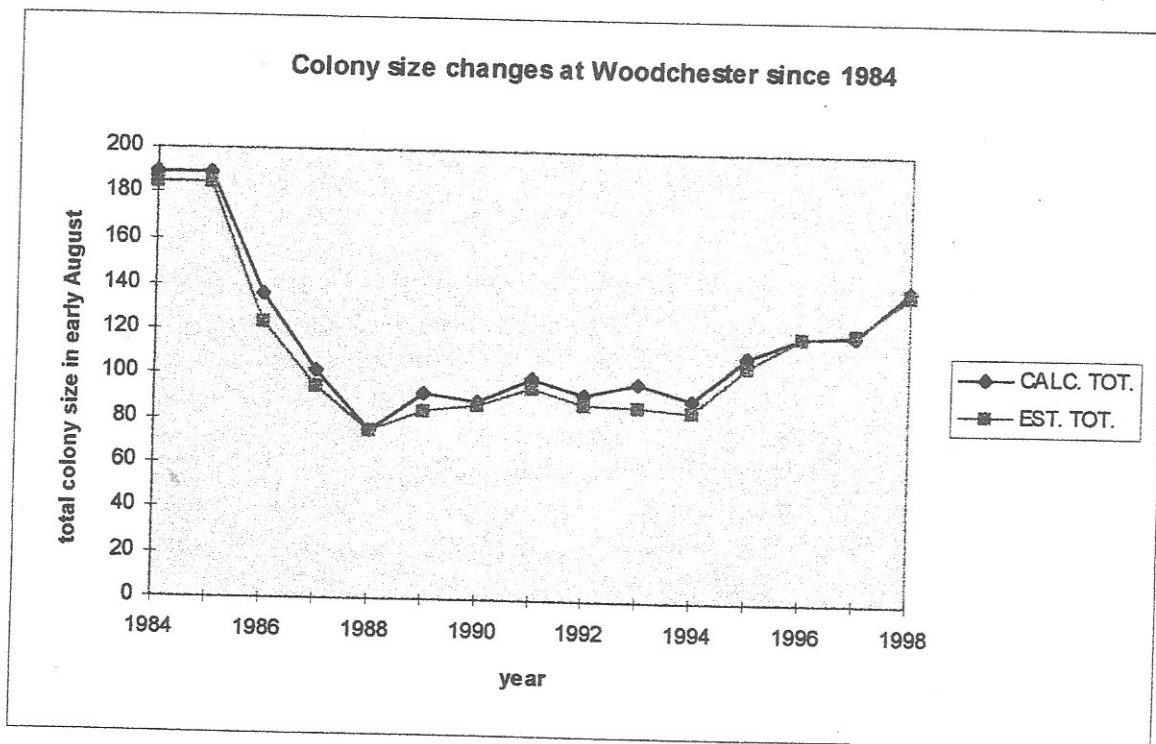
Maternity roost	Colony size estimate for 1996 (n young)	Colony size estimate for 1997 (n young)	Colony size estimate for 1998 (n young)	Change in colony size 1996-98
Woodchester Mansion	119 (32)	122 (30)	137 (33)	+18 (15.1%)
Brockley Stables	197+ (49)	? (30+)	241 (60+)	?
Littledean Hall	150 (36)	161 (40)	157 (33)	+ 7 (4.7%)

NB data from Brockley Stables were too incomplete and erratic to allow reliable estimates to be made.

Overall these data indicate that colony size is either stable or increasing at the three maternity roosts over the recent three-year period. The increasing July ratios at all roosts, suggest that many further subadult females are present, and will add to the breeding numbers and raise birth numbers still further over the next two years. This is known to be happening at Woodchester, where the population structure is known from captures.

Historical population changes at Woodchester Mansion

Ransome (1989) presented data on population changes from 1962 to 1986 in three study regions. One of these was the area around Stroud, which includes the Woodchester maternity roost and a series of hibernacula within a 32 km radius of it. The data in this study were obtained by actual captures of individual bats in these sites. One drawback to using data from captures, is that some individuals, especially adult males, can evade capture for many years. Hence the total known to be alive can only be a minimum figure. To overcome this problem Ransome (1997a) developed the formula which has been used in the present study to obtain estimates of colony size. Figure 6 shows changes in estimates from 1984 to 1998 using the two different methods of obtaining the numbers of young born. The calculated method uses data only from standardised exit counts in July, and subsequent counts of the young left in the roost. The estimated method uses data obtained from known numbers of young born as a result of ringing and growth studies.



The CAL. TOT. is the calculated total using the maximum numbers of young counted after exit counts multiplied by 1.23. The EST. TOT. is the estimated total obtained using the actual number of young born as shown by ringing studies. An incubator was provided in 1993, but only used by the bats from the summer of 1994.

Figure 6

There is close agreement between estimates obtained by the two methods. Where discrepancies occur, the calculated method slightly overestimates the numbers of young born, and so overestimates the total number. As expected, both estimates are higher than the minimum total number shown to be alive by Ransome (1989) for the overlapping years of data (168, 169, 119, 87 from 1984 to 1987, compared with 185, 185, 124, 95 in figure 6). However, the differences can be explained by the number of missing bats which were likely to be alive, as shown in table 4 in Ransome (1989). Hence we can be confident that the formula developed by Ransome (1997a), which uses a series of counts of young and adults flying out to feed, provides reliable data on colony size, as long as all young are born within a single roost. Complications occur if colony births are split between two or more roosts in a summer, as shown by data for Brockley in Part 3 above.

In the late 1950's the Woodchester colony produced 120 young, with up to 240 bats flying out to feed in late July. The estimated colony size then is about 480 bats. Much of the deciduous woodland in the Woodchester valley was then clear-felled. Following the population crash between 1962 and 1966, after a series of severe winters and cold springs, it fell to about 210, or 44% of the late 1950's level. Cattle grazing ceased in the fields close to the Mansion after 1963 as it became uneconomical in cold winters. During the 1970's and early 1980's about 190 bats were present, or 40% of the late 1950's level. It fell to 75 bats in 1988 (16%), after another series of cold winters and springs. Since then numbers have slowly risen to 139, or 29% of the 1950's level. The introduction of an incubator, which has been used by the bats from 1994 onwards,

seems to have provided an encouraging boost to recovery, which habitat and land-management changes implemented more recently should help to further accelerate.

Historical population changes at Brockley and Littledean Hall

Historical data for Brockley Hall is sparse, and erratically obtained, so no reliable estimates can be made. A small number of visits were made in the summer of 1987 and 1988 to ring the juveniles to follow their movements to hibernacula. Thirty four young were ringed in 1987, and forty two in 1988. In neither year were all young captured. About 100 adults flew out to forage at dusk in each year. These data are not markedly different from those of recent years. Colony size may have been quite stable for the last 10 years.

The colony-size at Littledean Hall has only been known since 1987, from which time data has been collected by David Priddis. Since Ransome & McOwat (1994) showed that birth-timing and population changes are linked across large geographical regions, we expect the Littledean Hall colony to have experienced a similar population crash in the mid 1980's. The number of young born each summer at Littledean, and birth timing, are closely linked to those recorded at Woodchester, but the total number of adults using the former roost has always been greater. No marked changes in land-management regimes are known to have occurred around the Littledean roost, and since 1987 estimated total numbers have shown no marked trend. (mean = 150.7 bats; s.d. = 13.2, n = 11 years). The absence of an incubator within this roost may be a factor slowing further recovery, or the population may have already stabilised after a less severe fall in numbers than at Woodchester.

Part 5: Growth performance of young at selected roosts from 1996 to 1998

In a previous study (Ransome 1998a) single and step-down multiple regressions showed that early growth rate was the most important factor affecting the length of the radius achieved by both male and female young reared in unheated roosts. It explained 28% of male radius variation and 45% of female variation, and these levels were not affected by the heating regime experienced. When combined with the mother's radius length, the two factors explained 54% of the variation shown by male radius length, and 49% of female radius length variation. It was assumed that dietary factors were important in explaining the remaining variation. At unheated roosts, birth timing was a significant factor affecting the radius length of females, explaining about 14% of the variation. Later births led to smaller radius length. Heaters removed the influence of birth timing.

Early growth rate was defined as the growth rate between age 4 and 14 days after birth. In both sexes growth rate was also affected by the mother's radius length, birth date, and body condition, but their combined influence was greater in females (36% versus 32% respectively).

After heaters were installed at Woodchester, mean female radius length increased significantly from about 55.5 mm to about 56.5 mm. Although heaters raised the early growth rate for both sexes, only the ultimate radius length of females increased significantly after heaters were installed. This surprising result seems to be due to a reduction in the size of the mothers of males. Larger mothers are more likely to have female young.

Ransome (1998a) put forward the following hypothesis to explain these data:

The early growth rate of the young of both sexes is normally resource limited, probably via the quality and/or quantity of the mother's food consumption, and roost thermal regimes. The latter may be particularly important at night when mothers are foraging. Food consumption is influenced by factors such as climatic conditions during foraging, habitat quality within the roost sustenance zone, photoperiodic effects upon foraging opportunities, and the mother's foraging skills. Of these factors, climatic conditions can vary erratically among years; and influence both the quality and quantity of prey consumed (Ransome, 1996 & 1997a, 1997b). Habitat quality is likely to remain similar, or vary slowly among years; photoperiodic effects remain the same at the same time of year among years, and variation in a mother's foraging success among years is currently unknown. The latter may change slowly with her age.

Predictions from this hypothesis:

Among sites in the same year

- 1) the mean radius length of female young should be the same if roost thermal regimes, foraging conditions and climatic effects are similar.
- 2) mean radius length of female young should be different if one or more of these factors vary significantly.

Among years at the same sites

- 3) the mean female radius length at a specific maternity roost should stay the same in adjacent years under similar climate, foraging conditions, and roost thermal regimes
- 4) mean female radius length should rise if either climate, foraging conditions or roost thermal regimes improve, and especially so if all three do so
- 5) mean radius length should fall if one or more of these factors deteriorate.

NB As climate influences both roost thermal regimes and foraging conditions in unheated roosts, poor climate will be linked to poor roost conditions, and act together. In roosts with an incubator, only climate influences the foraging circumstances.

Table 13. Summary of growth achieved by females at maternity roosts in 1998

Roost	Female mean radius length, s.d.,n	Female mean digit 5 length, s.d.,n	ANOVA for radius length (3 roosts)	ANOVA for digit 5 length (3 roosts)
Woodchester Mansion	56.50 ± 0.766, 14	73.04 ± 1.083, 14	F = 6.35, P=0.005	F = 1.37, P=0.268
Brockley Stables	56.35 ± 0.878, 10	72.25 ± 1.486, 10	highly significant	not significant
Littledean Hall	55.20 ± 1.162, 10	72.21 ± 1.712, 10		

ANOVA for radius length followed by Tukey tests showed that female radius length was significantly different between Woodchester and Littledean Hall, and between Brockley and Littledean Hall. Only the roost at Littledean Hall was without an incubator during 1998.

Table 14. Summary of growth achieved by males at roosts in 1998

Roost	Male mean radius length, s.d., n (mm)	Male mean digit 5 length, s.d., n (mm)	ANOVA for radius length (3 roosts)	ANOVA for digit 5 length (3 roosts)
Woodchester Mansion	55.00 ± 1.097, 14	70.77 ± 1.615, 14	F = 0.32, P=0.729	F = 0.19, P=0.830
Brockley Stables	54.69 ± 1.431, 11	70.91 ± 1.924, 11	not significant	not significant
Littledean Hall	55.137 ± 1.349, 8	71.23 ± 1.371, 8		

Growth during the 1998 season

Data presented in tables 13 and 14 confirm the findings of Ransome (1998a), and agree with predictions 1 and 2 above. The only significant difference in the growth of young at the three roosts occurred in the radius length of female young, and was associated with the presence or absence of an incubator in the roost. Climatic effects influencing foraging and roost thermal regimes are likely to have been very similar at all roosts, since they are close to each other. Significant diet differences between the Woodchester and Brockley colonies during 1998 mainly involved weeks 1 and 2 of the study (table 2). Differences later on, during the growth period of the young, only involved the relative consumption levels of *Aphodius* beetles and moths.

No dietary analyses of the dropping samples collected from Littledean Hall in 1998 were carried out, but in 1996 Woodchester and Littledean Hall colonies showed very similar diets (Ransome 1997a).

Growth in 1996 and 1997 compared with the 1998 season

Data shown in Tables 15 and 16 support prediction 3 above, where data are available. Radius growth shows no significant changes in either sex over the three summers, at both Woodchester and Littledean Hall. This is despite considerable changes in the mean birth dates among the three years at Woodchester. Birth dates are normally synchronised in a given year by spring thermal climate (Ransome and McOwat, 1994), so it is very likely that birth dates were similar in the same years to those at Woodchester. Late births are associated with poor growth and survival in unheated roosts (Ransome 1989). However, since heaters remove the impact of birth date upon growth of the young (Ransome 1998a), the consistent radius data at Woodchester and Brockley are expected. At Littledean Hall mean female radius growth was expected to be poorest in 1996 (latest mean birth date) and best in 1997 (earliest mean birth date). In fact there were no significant differences among the three years, and the mean for 1998 was the lowest.

Table 15. Female growth by maternity roost and year

Roost (aspect)	1996 season mean, s.d., n	1997 season mean, s.d., n	1998 season mean, s.d. n	ANOVA statistics
Woodchester Mansion (radius length mm)	56.38 ± 1.029, 12	56.56 ± 0.987, 14	56.50 ± 0.766, 14	F = 0.12 P = 0.891
Brockley Stables (radius length mm)	no data	56.26 ± 0.858, 10	56.35 ± 0.878, 10	F = 0.05 P = 0.819
Littledean Hall (radius length (mm))	55.88 ± 0.727, 8	55.85 ± 1.076, 10	55.20 ± 1.162, 10	F = 1.34 P = 0.281
Woodchester Mansion (digit 5 length mm)	72.72 ± 1.222, 12	72.76 ± 1.252, 14	73.043 ± 1.083, 14	F = 0.30 P = 0.744
Brockley Stables (digit 5 length mm)	no data	72.69 ± 0.953 10	72.25 ± 1.486, 10	F = 0.62 P = 0.441
Littledean Hall (digit 5 length mm)	72.30 ± 1.214, 8	72.11 ± 1.256, 10	72.21 ± 1.712, 10	F = 0.04 P = 0.961
Woodchester Mansion (birth date)	41.7 ± 6.72, 12	29.5 ± 9.09, 14	33.9 ± 7.02, 14	F = 9.04 P = 0.001
Brockley Stables (birth date)	no data	34.7 ± 3.83, 10	36.4 ± 3.05, 5	F = 0.74 P = 0.405
Littledean Hall (birth date)	no data	36.5 ± 13.87, 10	39.0 ± 8.15 9	F = 0.22 P = 0.643

Significant differences among means are indicated by bold type. Birth date is number of days after 1st of June. July 4th = 34.

Table 16. Male growth by maternity roost and year

Roost (aspect)	1996 season mean, s.d., n	1997 season mean, s.d., n	1998 season mean, s.d. n	ANOVA statistics
Woodchester Mansion (radius length mm)	55.32 ± 1.203, 11	55.55 ± 1.355, 11	55.00 ± 1.097, 14	F = 0.64 P = 0.534
Brockley Stables (radius length mm)	no data	55.10 ± 0.721, 3	54.69 ± 1.431, 11	F = 0.21 P = 0.654
Littledean Hall (radius length (mm))	55.17 ± 1.160, 20	54.87 ± 1.446, 9	55.14 ± 1.349, 8	F = 0.18 P = 0.837
Woodchester Mansion (digit 5 length mm)	71.15 ± 1.659, 11	71.19 ± 1.861, 11	70.77 ± 1.615, 14	F = 0.23 P = 0.793
Brockley Stables (digit 5 length mm)	no data	72.23 ± 0.751 3	70.92 ± 1.916, 11	F = 1.29 P = 0.278
Littledean Hall (digit 5 length mm)	71.06 ± 1.446, 20	71.34 ± 1.531, 9	71.23 ± 1.371, 8	F = 0.13 P = 0.880
Woodchester Mansion (birth date)	45.9 ± 8.04, 11	29.7 ± 8.01, 11	37.0 ± 6.67, 14	F = 12.79 P = 0.000
Brockley Stables (birth date)	no data	35.7 ± 8.33, 3	35.44 ± 10.51, 9	F = 0.00 P = 0.974
Littledean Hall (birth date)	no data	39.7 ± 11.74, 9	38.12 ± 7.70 8	F = 0.10 P = 0.757

Significant differences among means are indicated by bold type.

The growth of juveniles occurs between weeks 5 and 10. In 1996 lactating females showed a high consumption of moths, whereas in 1998 they mainly ate *Aphodius* beetles (table 4). Juvenile radius growth of females showed virtually no differences at Woodchester between these years (table 14). Hence the relative proportions of these two key prey consumed by lactating mothers seems to have no important growth implications for their young, at least in heated roosts. At Littledean Hall in 1998, female radius length was smaller in 1998 than in 1996, but the differences were not significant. Possibly dietary differences are more important to bats occupying unheated roosts, where they are under greater stress, or quantity is more important than quality.

These data do not tell us whether juvenile bats would grow as well if *Aphodius* beetles were scarce, and moths abundant. Their growth may well be hampered, since young less than 45 days old seem to be unable to feed on moths, and tipulid populations do not peak until September (Ransome 1996).

The quantity of prey consumed was not assessed at any roost, however, so its effect remains unknown.

Part 6: Historical winter records from Kings Wood

Nomenclature and descriptions of subterranean roosts at Kings Wood

Eleven separate disused mine systems occur in Kings Wood. Some entrances are very small and located within dense woodland, where they are difficult to locate. The mines are not extensive, and most have only limited regions of darkness. They are distributed as two main complexes of 5 and 6 as shown in figure 7. The western complex consists of 5 mines. The eastern complex includes the main Nursery Roost and 5 other mines.

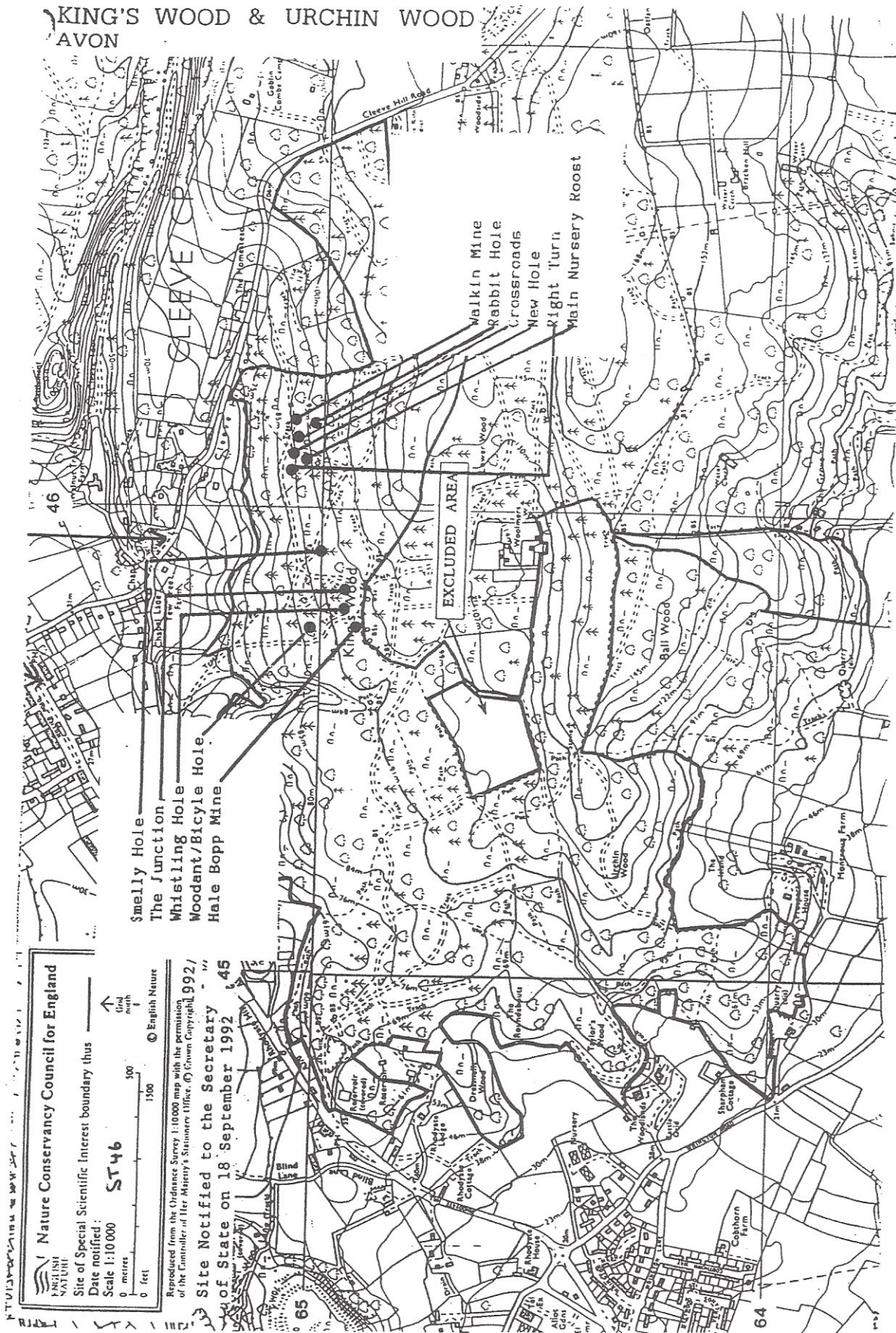
Table 17 describes the general physical structure of each mine.

Table 17 Description of the main mines in Kings Wood

Disused Mine Name (complex)	Rough description of mine
Walkin (East)	Small horizontal system with one entrance.
Rabbit Hole (East)	Small system with one entrance which slopes downwards. Fairly stagnant.
Crossroads (East)	Vertical ladder drop into single entrance. Small & stagnant.
New Hole (East)	Small horizontal system with one entrance.
Right turn (East)	Medium sized system with 2 small entrances, a central pit, and a short stagnant end part. Ventilated, but some resistance to cold weather.
Main Nursery Roost (East)	Largest: long rift system with several horizontal entrances. Far end has a very high domed chamber used as a nursery. Too cold in severe winters.
Smelly Hole (West)	Deep open criss-cross rift system which is difficult to access. Cold in winter.
The Junction (West)	Has 3 entrances opening into a long rift which has 4 changes of direction. Well ventilated so too cold in severe winters.
Whistling Hole (West)	Lengthy complex slit with several entrances which drops to different levels. Filled with rubbish in places.
Woodant/Bicycle Hole (West)	Complex rift system which also contains dumped rubbish. Open to the light in many places. Temperature varies in different parts.
Hale Bopp (West)	Small; single entrance; beneath a path. Roof could collapse without conservation work

Due to the small size and structure of most of the mines, and the number of multiple entrances involved, few of them seem capable of sustaining suitable temperatures for hibernation throughout a severe winter climate. However, in spring and autumn, the likely high levels of air circulation occurring make several of them potentially very good transitional hibernacula.

KING'S WOOD & URCHIN WOOD
AVON



Nature Conservancy Council for England
 ENGLISH NATURE
 Site of Special Scientific Interest boundary thus
 Date notified: ST46
 Scale 1:10000
 0 metres / 0 feet
 Grid north
 English Nature

Reproduced from the Ordnance Survey 1:10000 map with the permission of the Controller of Her Majesty's Stationery Office. © Crown Copyright, 1992.
 Site Notified to the Secretary of State on 18 September 1992

Figure 7

Summary of historical winter censuses

Surveys have been carried out since 1989 by David Clarke and his assistants. He developed the nomenclature used, as the different mines were discovered. Since all mines were not known until several years had elapsed, the surveys were not consistently carried out at all sites. Table 18 summarises the census data obtained.

Table 18. Historical horseshoe bat occupation by specific mine at Kings Wood

Disused Mine Name (complex)	Greater horseshoe statistics: mean; standard deviation; n visits; range	Lesser horseshoe statistics: mean; standard deviation; n visits; range
Walkin (East)	0.462; 0.776; 13; 0-2	0.308; 0.630; 13 0-2
Rabbit Hole (East)	0.769; 1.363; 13 0-4	1.385; 0.870; 13 0-3
Crossroads (East)	1.417; 1.929; 12 0-5	1.083; 1.084; 12 0-3
New Hole (East)	1.83; 2.791; 12 0-10	0.833; 0.577; 12 0-2
Right turn (East)	8.36; 7.762; 11 1-26	0.727; 0.905; 11 0-2
Main Nursery Roost (East)	19.33; 21.93; 9 0-64	0.444; 1.014; 9 0-3
Smelly Hole (West)	0.833; 0.937; 12 0-3	0.750; 0.866; 12 0-2
The Junction (West)	0.727; 1.009; 11 0-3	0.272; 0.467; 11 0-1
Whistling Hole (West)	0.417; 0.900; 12 0-3	0.545; 0.934; 11 0-3
Woodant/Bicycle Hole (West)	2.455; 2.622; 11 0-9	0.545; 0.934; 11 0-3
Hale Bopp (West)	0.600; 0.548; 5 0-1	0.800; 1.304; 5 0-3

Initially no ringing studies were carried out at the site at the request of English Nature, but some recaptures of bats ringed elsewhere were carried out. More recently, with a need to understand the growth performance of the Brockley bats, and the relationship between Brockley and the hibernacula used by the colony, including the Kings Wood mines, ringing studies of greater horseshoe bats commenced. However, the high rift within the Nursery roost has made capture of the whole clusters there impossible. There is therefore no accurate information about the sex, age and reproductive status of the greater horseshoe bats occupying the various mines. The majority of recaptures of ringed bats involved older, mature animals. However, these provide strongly biased data which cannot reflect the true status of the bats.

Most mines were occupied by small numbers of greater and lesser horseshoe bats from October to April, with a frequent absence of bats in mid winter. Usually only one or two of each species

was present. If ringed, the greater horseshoe bats were often mature males or females, suggesting that some mines are being used as male breeding territories.

Other mines, particularly the Main Nursery Roost, Right Turn and to a lesser extent Bicycle/Woodant Hole, can contain much larger numbers of greater horseshoe bats. Numbers tend to be highest in October and April, when clusters of up to 64 bats may occur if they congregate into a single mine. The Nursery Roost is occupied by greater horseshoe bats during the summer as described above.

Limited captures of these larger groups of bats show that first and second year bats are most frequent, with a few older ones. These bats either originated from Brockley Stables, where they were ringed as juveniles, or from captures within hibernacula in the Mendip Hills, such as the caves of Cheddar Gorge.

The relationship between Brockley and Kings Wood roosts

Part 3 above contains an in-depth discussion of this aspect. Available evidence suggests that Brockley Stables is the preferred maternity roost in July and August, possibly due to a superior thermal regime, and/or foraging circumstances during lactation. Kings Wood mines, especially the Nursery Roost Mine, provides an insurance against cold spring weather, and may permit colony fragmentation, possibly under food stress conditions. However, Brockley has close access to extensive areas of permanent pastures grazed by cattle and other grazers, which supply *Aphodius* beetles for juveniles to start feeding upon, as they are weaned.

Movements between Brockley/Kings Wood and surrounding winter hibernacula

The number of movements of ringed bats recorded as taking place depends upon several factors. They include:

- 1) the number of bats actually moving
- 2) the proportion of bats which are ringed before movements take place
- 3) the frequency and timing of survey visits to the other roosts the bats visit, if they are made at all.

NB 100 bats from a given Maternity Roost can visit Cave A to hibernate, and return to the given roost undetected the following summer if either:

- none are ringed before they leave the maternity roost
- or: no visit to Cave A occurs after ringing
- or: the visit to Cave A occurs before the bats arrive, or after they have left it
- or: no colony captures at the maternity roost occur in subsequent summers.

A sensible ringing programme to detect the proportion of a breeding population which uses certain hibernacula, and return to the natal maternity roost, would involve the following protocol. First all young would be ringed at the maternity roost over a period of several years, and the whole colony would be caught annually in early August. Second, visits to all surrounding

hibernacula (caves, mines tunnels etc.) up to a distance of at least 40 km radius would be thoroughly searched for ringed bats. These searching visits would be made on at least three occasions each winter (in early, mid and late winter). Thirdly they would be repeated for many years to detect any long term movements into other hibernacula. This protocol would only fail to reflect a true picture of where the bats hibernate if significant unknown hibernacula existed. However, it is very demanding, time-consuming and expensive. It has not been properly carried out at the Brockley Stables maternity roost.

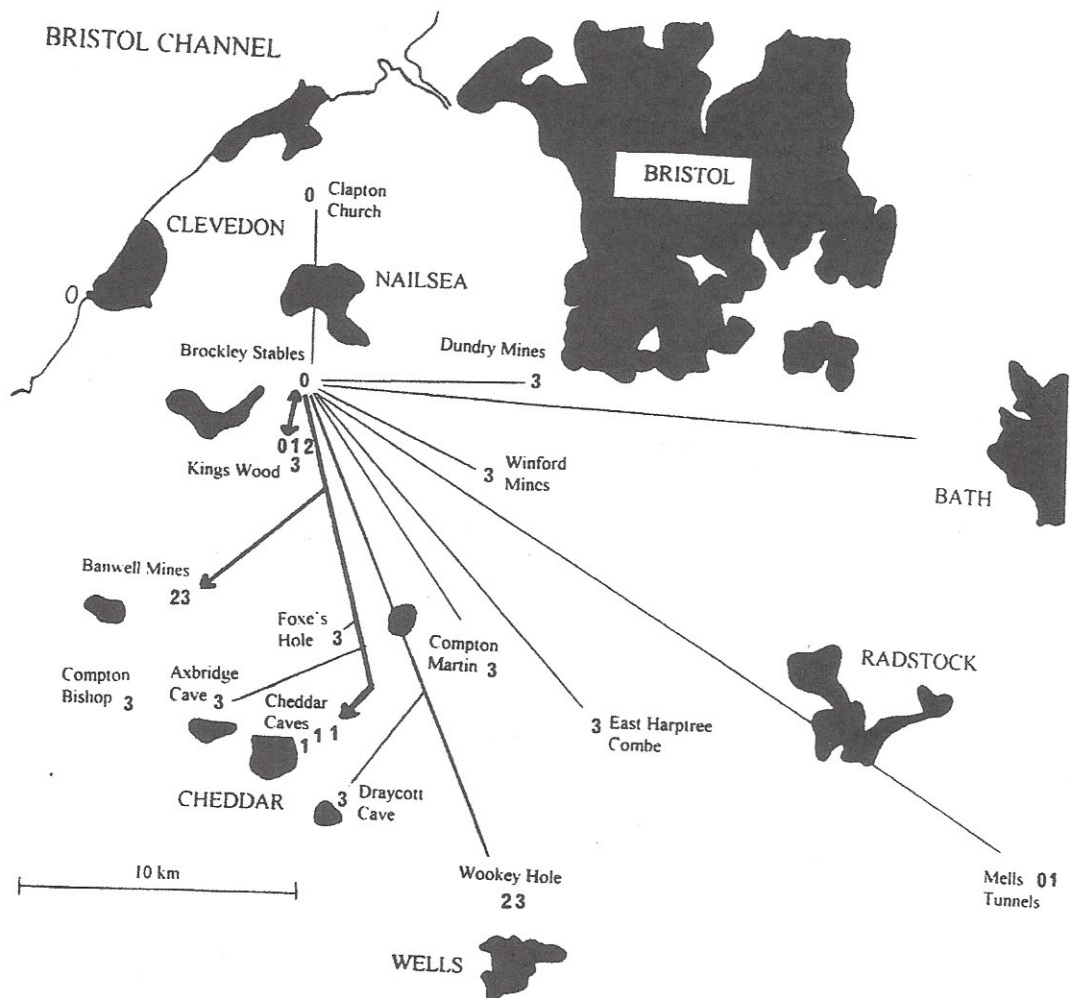
During the summers of 1987 and 1988, before the Stables were converted, and again in 1997 and 1998, cohorts of young were ringed. Unfortunately probably only from 60 to 76% of the young born have been ringed in a given summer. Captures of the whole colony in August, or at any other time in summer, have not taken place. Furthermore, only in the case of the two early years has enough time elapsed to discover the long term movements of individuals as they age.

Figure 8 is a map showing the relationships between Brockley, Kings Wood, Clapton Church and various hibernacula known to be used by the colony. Visits to surrounding hibernacula have not been consistently made. Wookey Hole, Cheddar Caves and the disused mines at Banwell have been visited three times each winter in late October, late January and early April over several decades. Winford Mine, Dundry, Compton Martin, East Harptree, the Combe Down Mine complex, Winsley and Mells tunnels have either been visited bi-annually by Bob Cropper, or annually in January or February by the author. These considerations need to be born in mind when considering the numbers of recorded movements shown in Tables 19 to 21.

Ransome (1991) described three types of hibernacula, defined by the age structure of the greater horseshoe bats found in them. Type 1 sites contain mainly first-year bats of both sexes, with good numbers of immature second-year, and some third-year bats. Type 2 sites contain few first-year bats, but many second and third-year ones, with surplus adult males which build up after many years of mild winters. Each type 3 site is occupied by a single mature male and up to 8 mature female bats. Often the site is small, and provides little protection against cold mid-winter weather. If so, it is mainly used in autumn and spring. Larger ones may be occupied all through the hibernation period, if they provide suitable temperature and air-flow regimes (Ransome 1968, 1971). Both sexes show high fidelity to these sites over many years, and they seem to be partly used as mating territories. They may also be roosts in which much of pregnancy takes place.

Table 19 shows that most first-year bats from Brockley move to Cheddar Gorge in their first winter, where several type 1 caves occur (Figure 8, thick line). They mix freely with bats born at another large maternity roost, which is assumed to be close to the Gorge (Ransome 1998a). Using limited data from three summers, Brockley-born bats are estimated to form about 20 to 33% of the first-year bats found at Cheddar in a particular winter. A few other first-year bats travel to the Gorge from maternity roosts at Mells and occasionally Iford each winter. Nearly all of the first-year bats from Brockley arrive at Cheddar by the end of October, so they are caught on the first winter visit.

Banwell mines consist of one large type 2 site, plus several type 3 sites. Few first-year bats normally spend the winter there (table 19). If they do use Banwell, often they are not captured there until the January visit, and they have left by early April. October capture of any significant clusters found there are dominated by mature males. Their numbers can build up after a long series of mild winters, and if insufficient type 3 sites are available, the surplus males congregate together at Banwell. This has not happened since the 1985/6 population crash (Ransome 1989).



Map showing movements of greater horseshoe bats from Brockley Stables Nursery Roost to other sites

Key: 0 = Nursery Roost; 1 = Type 1 hibernaculum; 2 = Type 2 hibernaculum; 3 = Type three hibernaculum (see text for definitions).

Figure 8

Table 19. Numbers of recorded movements of young bats ringed at Brockley to hibernacula in their first winter

Year cohort was ringed (n young ringed)	Minimum number alive	Number of movements to Kings Wood	Number of movements to Cheddar Caves	Number of movements to Banwell Mines	Number of movements to other sites (name)
1987 (34)	19	0	10	4	1 (Mells) 2 (Wookey)
1988 (42)	12	0	8	0	1 (Mells)
1997 (30)	14	1	9	1	0
1998 (42)	20	6	7	1	0

Exceptionally, first-year bats travel long distances to other sites, such as Wookey Hole and Mells. Wookey is another type 2 site, with several small type 3 sites nearby. At Mells they are found hibernating in a tunnel with bats from the local maternity roost. They carry out these movements either in autumn, or early in the winter. Similar behaviour occurs at Woodchester, where one or two unringed first-year bats often arrive in late September or early October and stay for a few weeks. They rarely return in subsequent years, and are assumed to return to their natal maternity roost.

A cohort dwindles away as the years pass. The numbers reaching the Mendip hibernacula depend upon the mean birth date (Ransome 1989), declining with later births. Furthermore, the long-term survival of cohorts also depends upon mean birth date. If it is after the 17th July, a cohort usually becomes extinct within 10 years. This effect can be seen in figure 3 of Ransome (1989), and also tables 20 and 21 of this study. (Compare the loss of bats in column 2 of table 21 from the cohorts born early in 1987 and 1989, with that born late in 1990.)

Table 20. Numbers of recorded movements of second year and older bats from Brockley to winter hibernacula

Year cohort was ringed (n young ringed)	minimum number alive in following years	Number of movements to Kings Wood	Number of movements to Cheddar Caves	Number of movements to Banwell Mines	Number of movements to other sites
1987 (34)	11, 8, 7, 7, 6, 4, 3	1, 1, 0, 1, 0, 0, 0	9, 3, 1, 1, 1, 0, 0	1, 1, 1, 2, 3, 2, 1	3, 2, 2, 1, 2, 1, 2
1988 (42)	12, 7, 5, 2, 2, 0	5, 2, 0, 0, 0	6, 5, 2, 2, 0	0, 0, 0, 0, 0	0, 1, 1, 0, 0

NB the numbers in each cell are in year sequence from age two years. For example there were at least 8 third-year bats alive from the 34 juveniles ringed in 1987. Of these, 1 was found at Kings Wood, 3 at Cheddar, 1 at Banwell, and 2 at other sites. Some bats (very few) were recorded at 2 sites in the same winter. 'Other sites' include Mells, Combe Down in Bath, and Coaley in Gloucestershire. These involve the longest movements recorded.

Table 21. Total numbers of recorded movements of bats from Brockley and Kings Wood to winter hibernacula

Year cohort was ringed (n young ringed at Brockley)	minimum number alive (proved by capture)	Number of bats at Kings Wood	Number of movements to Cheddar Caves	Number of movements to Banwell Mines	Number of movements to other sites
1987 (41)	26, 18, 15, 11, 8, 7, 5, 4	0, 1, 7, 4, 1, 0, 0, 0	17, 10, 3, 1, 1, 1, 0	4, 3, 3, 2, 2, 3, 2, 1	4, 4, 2, 2, 2, 2, 2, 3
1988 (54)	24, 24, 18, 6, 5, 1, 0	2, 9, 7, 2, 2, 0, 0	16, 6, 5, 2, 0, 0, 0	1, 2, 3, 0, 0, 0, 0	2, 2, 4, 1, 0, 1, 0
1989 (0)	19, 17, 12, 6, 4, 2, 0	11, 8, 6, 1, 0, 0	18, 8, 3, 1, 0, 0	1, 2, 3, 1, 1, 1, 0	0, 3, 1, 2, 2, 1, 0
1990 (0)	12, 8, 5, 2, 0, 0	4, 5, 2, 0, 0, 0	9, 4, 0, 0, 0, 0	4, 2, 1, 0, 0, 0	0, 0, 0, 2, 0, 0
All years combined (% of those known to be alive)	81, 67, 47, 23, 17, 10,	17, 18, 22, 2, 2, 0 (21, 27, 47, 9, 22)	60, 28, 11, 4, 1, 1, (74, 42, 23, 17, 6, 10)	10, 9, 10, 3, 3, 4 (12, 13, 21, 13, 18, 40)	6, 9, 7, 7, 4, 5 (7, 13, 15, 30, 24, 50)

NB the numbers in each cell are in year sequence as in table 19, except the first number in each cell refers to first-year bats. Actual proof that bats originated from the Brockley/Kings Wood maternity roosts only existed for cohorts born and ringed at Brockley in 1987 and 1988. Those born in 1989 and 1990 were not ringed as juveniles within the maternity roost. Only bats that were subsequently found in Kings Wood mines in their first, or later, years were used in this table. They were assumed to have been born at the Brockley/Kings Wood maternity roost. This procedure is likely to underestimate the number of Brockley bats reaching hibernacula. The low numbers of first-year bats at the start of the second column for these years supports this view.

As bats age, they move from type 1 sites, into type 2, and finally into type 3 after sexual maturity. This effect can be seen by comparing data in the sixth row of table 20 in the present study. The percentage of Brockley-born bats known to be alive falls from 74% at Cheddar (mostly type 1) to 10% over 6 years; rises from 12% to 40% at Banwell, and from 7% to 50% at the other sites. The latter are many, and widely dispersed (see figure 8). The most unusual being a rift mine near Coaley in Gloucestershire, which is 43 km to the north-east of Brockley, and too far away to be included in figure 8 (as is Combe Down at Bath). This is the minimum distance involved, using a straight line which would pass through the centre of Bristol. The female bat which made this movement spent her first two winters at Cheddar, which is 13 km to the south-east of Brockley. The following October she moved to Coaley as a third-year, early breeding, mature female Ransome (1995). She is now in her 12th year, having bred every year since. However, although she hibernates only about 2 km from the Woodchester maternity roost, she has never bred there. Presumably she returns to Brockley each summer where she was born and ringed in 1987. If so, she has clocked up a minimum total of 817 km in 9.5 return journeys so far.

Data for Kings Wood is both sparse, averaging once per year, and erratically obtained, as previously explained. Movements between Brockley Stables and Kings Wood mines are therefore considerably under-recorded because of this. As previously stated, most Kings Wood mines probably provide very good thermal and air-flow conditions for hibernation in autumn and spring, and throughout mild winters. However in cold winters, the small capacity of most mines, and/or their multiple entrances, temperatures are likely to fall below those selected by horseshoe bats

(Ransome, 1968, 1971), and force them to move elsewhere. This probably accounts for the low numbers in many winter censuses (table 18).

Summary

The most feasible movement scenario is as follows.

Cohorts of young born early in the summer at either Brockley or Kings Wood, have a long period in the autumn to complete their growth and learn the locations of the more distant hibernacula. In late September and October they move to them, showing a preference for two of the three type 1 sites in Cheddar Gorge (Ransome 1968, Cave C = Gough's' Old Cave; Cave E = Canyon Cave), rather than the inferior ones in Kings Wood. The majority of these first-year bats spend the whole winter in the Gorge, where they are frequently captured on all three annual hibernation visits. In mild weather they mainly occupy Gough's Old Cave, and in colder weather they move to Canyon Cave. In exceptionally cold weather they use Whitespot Cave.

Cohorts born late, and the later-born individuals of early-born cohorts, may have insufficient time to learn the locations of the more distant hibernacula. They use the ones in Kings Wood, especially the Nursery Roost and Right Turn mines which are type 1 sites, unless cold weather forces them out in mid winter. If this happens, some move to the more stable conditions found the type 2 Banwell mine, which is closer to Kings Wood (9.5 km) than Cheddar (12 km).

As the bats age, they progressively use the Cheddar type 1 hibernacula less frequently. They use both Banwell and Kings Wood type 2 and 3 sites, or other type 3 sites both closer and further afield. Eventually they occupy the same type 3 sites consistently over many winters. One territorial male and several females are regularly found together in a specific site.

Part 7: What type of monitoring system is needed to support the conservation of greater horseshoe bats in the UK?

Setting up an effective UK monitoring system is an important step in promoting the recovery of any endangered species. I believe its objectives should be:

- 1) to detect and accurately assess significant population trends within the current range of the species
- 2) to determine the most likely causes of any population trends observed, so that action may be taken by appropriate agencies to oppose harmful effects, and promote favourable ones.

The most likely natural factors which may cause significant population changes involve either the climate, or the habitat within the roost sustenance zone around maternity roosts. Both of these factors are able to influence the food quality and quantity accessible to foraging bats, and so can alter their reproductive performance. Over time they may change population levels.

There needs to be a balance between the collection of sufficient data under an agreed protocol (which must provide important and reliable data), and the need to limit harmful disturbance to the bats. If we err too greatly in restricting data collection, monitoring may become merely a simple counting exercise. Counts of adults and young inside maternity roosts can only provide limited data, especially if carried out on only one or two occasions each summer. Furthermore, even if they do show up trends, they cannot explain the cause(s). In short, a monitoring protocol which rests entirely upon counts fails the second objective. It precludes effective subsequent action by any agency.

Control mechanism for colony size by heating regime

It is not sensible to set up a monitoring system without first considering what limiting factors influence the size of a colony. Combining the results of the present study with previous findings, I believe that the following model explains colony size changes, and indicates aspects which need to be monitored. The laws of limiting factors apply to population control.

Maternity colonies within unheated roosts, which have fluctuating thermal conditions, but are surrounded by good foraging habitat, should generate cohorts of female young annually which have a mean radius of about 55.5 mm at maturity. The birth sex ratio is 1:1, and enough female young are born and able to survive long enough to breed to maintain a stable population. If the spring climate deteriorates, birth timing is delayed, and mean female radius length falls as more stunted females are produced. These have low survival rates, possibly partly due to a lack of time in which to learn the locations of important hibernacula. Those that do survive and eventually give birth, often after prolonged years of immaturity, have young whose sex ratio favours males. The situation is reversed if birth timing is earlier after a warm spring. Colony size at unheated roosts tends to rise and fall according to the relative frequency of warm and cold spring weather conditions, but overall it reflects the mean climatic circumstances. Colony size is smaller at higher latitudes, if foraging conditions within the roost sustenance zones are both similar, and stable.

Colony size is expected to vary independently of latitude if foraging conditions are different or changing. Roosts with high quality roost sustenance zones will sustain larger colonies than those with poor ones.

Female young born within roosts provided with an incubator show a mean radius length of about 56.5 mm, at least in the initial years after installation. This reflects improved, less-stressful growth overall. It results in a higher proportion of the female young surviving to reproductive age, and a rise in the proportion of female young born to these larger females when they give birth. Therefore the colony increases in response to these two underlying causes. Female radius length should remain stable at about 56.5 mm until the colony size approaches the foraging carrying-capacity of the roost sustenance zone. Female radius length is independent of birth timing, and spring climate, as long as habitat and land-management circumstances remain constant. As the carrying capacity of the roost sustenance zone is reached, the mean female radius length is predicted to slowly decline to 55.5 mm, and stabilise colony size again.

If this model is correct, a colony provided with an incubator, as a measure to improve its thermal regime, will show an increased colony size, whatever its former level. It is predicted to be more resistant to harmful climatic changes than a colony without an incubator.

A colony which is in serious danger of a major climate-induced population crash, as happened after several years of cold springs in the early 1960's and 1980's, is predicted to show the following features. Firstly female cohorts with an increasingly smaller mean radius length. Secondly a biased birth sex ratio in favour of males. Thirdly increasingly late birth timing. Fourthly a deterioration in both the quantity and quality of insect prey. Fifthly, significant juvenile mortality within the roost, especially of older juveniles.

What data should be collected in a monitoring protocol?

The model above requires five types of data collection during monitoring for it to be properly tested. They are as follows:

- (a) daily local climatic data from late April to early October each year
- (b) annual data on any significant habitat and/or land management changes implemented since the previous year
- (c) exit counts, counts of young, and juvenile mortality within a specific roost under a standard protocol
- (d) dropping sample collection under a standard protocol
- (e) radius measurement of young of the year either in the roost in early September, or within known associated hibernacula (ringing may, or may not be necessary)

Climatic data can be obtained from regional meteorological offices, or local recorders. Habitat data changes needs annual surveys and discussions with land managers. Counts require trained observers, prepared to visit roosts on specified, agreed dates, who would also be able to collect dropping samples. Radius measurements require well-trained, experienced licensed personnel, and may only be feasible at certain roosts.

In addition, winter surveys of associated type 1, 2 and 3 hibernacula should be carried out in October, January and April. These surveys should confirm population trends seen at maternity roosts, as well as permit the conservation state of the hibernaculum to be monitored. They may also indicate the existence of new maternity colonies. If young of the year are sampled at type 1 sites, their growth performance and birth sex ratios may be assessed without disturbance at maternity roosts. Before this can be usefully attempted, the association of specific maternity roosts with specific type 1 hibernacula need to be determined by ringing cohorts and tracing their movements. It may not always be a simple association..

Standard protocols

All known significant maternity roosts throughout the UK should be monitored annually. As it is unlikely that sufficient trained observers will be available to cover all of these sites, a graded level of monitoring is suggested.

Grade 1: full monitoring protocol from April to October, as at Brockley Stables and Woodchester Mansion in the current study, for all roosts within SACs. The young may or may not be ringed (e.g. to determine growth performance or specific maternity roost/hibernacula associations). Dropping collections should be made and analysed for at least three years per site to discover natural variability and/or the impact of any land-management agreements instituted. Attempts should be made to assess birth sex ratios, juvenile mortality and female radius length for the young of the year to monitor growth performance, where such data collection is feasible.

Grade 2: reduced monitoring protocol. Counts (exit & young) and dropping collections made only throughout July and early August, on 6 specified dates which match those for grade 1 sites. Assessment of birth sex ratios, juvenile mortality and female growth performance if possible. The 5 dropping samples obtained should be dried and stored. Analysis may only be necessary if the colony shows a decline, if growth problems are detected, or if high juvenile mortality occurs.

Grade 3: minimum monitoring protocol. Counts (exit & young), and dropping collections on 3 specified dates which match grade 1 sites. The 2 dropping samples obtained to be dried and stored as in the grade 2 protocol. Assessment of female growth performance within known hibernacula, if possible.

Comments

The grade 1 and 2 monitoring protocols should provide reliable numerical data annually from which colony size and mean birth date can be calculated. Trends over time can be compared among roosts, and any anomalies can be further investigated by the analysis of stored dropping samples. If birth sex ratios and female growth performance are assessed at sufficient roosts, the model can be tested, and possibly further refined.

The grade 3 monitoring protocol should provide some useful data, but they will be less reliable than those from grade 1 and 2. Peak July exit flights and juvenile numbers are unlikely to coincide with these limited monitoring visits, and it will be impossible to calculate mean birth date. The data generated is unlikely to be accurate enough to be confident that small changes among years are really happening. Dietary analyses carried out on 2 samples collected over several weeks may not show up important diet switches, which are often short-lived.

It is recommended that all significant UK roosts should experience grade 1 monitoring for at least one year, to provide baseline data on diet in relation to the roost sustenance zone habitat. Woodchester should continue to be monitored at grade 1 level in each year to provide important control data for comparison with other roosts, which may be monitored at grade 1, 2 or 3 level according to available resources.

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