Part 3: Population parameters of the sites

Introduction

Ransome (1989) considered that there was no general agreement in the literature on what constitutes a bat population. The term has been used to mean the numbers of bats caught or counted in hibernacula, and also the numbers based on breeding sites. Ransome (1989) used the term 'population' to refer to bats occupying a series of hibernacula fairly close together, which are linked by regular movements, and 'colony' for those bats which originate from a specific maternity roost. If this terminology is used in this study, it means that 8 colonies of bats were studied.

Methods

There are a number of potential ways of estimating the total numbers of bats forming a colony, although currently there is no clear understanding between it and the parameters normally used. Ransome (1989), in an intensive ringing study of the Woodchester colony, in conjunction with regular winter captures at surrounding hibernacula whose bats derived almost entirely from it, was able to show that the total numbers of bats remained remarkably constant at about 180 bats over a 20 year period from 1965 to 1985. Despite this, the three parameters commonly used to estimate changing colony and population numbers, annual maximum exit counts from the maternity site, number of juveniles born, and numbers of bats in hibernacula, all showed considerable changes. Therefore all parameters commonly used are flawed as indicators of the underlying state of bat numbers. However, since alternative methods require long-term ringing studies, there were no other feasible alternatives available in this study. Hence exit counts of flying bats and numbers of juveniles born were used. In the absence of other data their use is justified on pragmatic grounds. Hopefully this study, which is based on a widespread sample of sites, will help clarify their usefulness as true colony size indicators.

Dusk exit counts

Volunteers visiting English sites were asked to visit their roost on the specified dates, with assistants if the site made multiple counts necessary. This was the case at Brixham, Mells and Iford, where the bats used two or more roost positions. Exit counts were started before dusk in good light before bats began to leave roosts, and continued for 5 minutes after the last exit was recorded. This gave the total number of bats flying out to forage at dusk or NBFD. Volunteers were asked to complete a standard sheet showing emergence patterns in 5 minute blocks of time throughout the count, and to record the weather conditions during emergence.

Data from the Welsh sites were provided by Tom McOwat and Peter Andrews. The former provided data on the numbers of young, and their precise birth dates, and the latter provided detailed data on the numbers of bats leaving the roosts on each evening. He used an infra-red beam counting apparatus linked to a computer, which was continuously operated throughout the summer. Dusk exit-count data for the relevant days of visual counts carried out at other sites were selected from the complete data set he kindly provided.

Counts of young after adult exits

From late June until the end of August according to the site studied, roosts contained varying numbers of juveniles. Experienced observers can easily recognise new-born young by their bright pink body and wings, so it is possible to indicate whether births are recent. Estimating the age of older juveniles is more difficult, unless a marking technique is used. This occurred at Stackpole and Slebech (by Tom McOwat) and at Woodchester (by RDR).

Volunteers were asked to count the numbers of juveniles left in the roost on each date, and comment on their state. Problems sometimes occurred in August at the time when juveniles first started to fly, due to their tendency to constantly return to the roost after exiting and vice versa. This behaviour can lead to confusion in obtaining total exit counts, and numbers of juveniles. Also, after age 20 days, the young begin to make serious flights around the roost, and even may fly out of the roost if an open exit is freely available during counts of the young. For this reason I recommend closing off exits during counting and dropping collection wherever it is feasible. Counts of non-foraging juveniles can be underestimated at this time, and the NBFD incorrectly boosted by such an effect, if another observer adds them to the totals.

At sites where previous studies involving roost entry had not taken place, volunteers were advised to use red-light torches to minimise disturbance to the young, and any occasional adults remaining in the roost.

From the data provided on juvenile numbers, the mean birth date was estimated for most sites. Births were spread over at least a 35 to 40 day period at most sites from which good data were obtained. Since juveniles normally start to forage from age 28 days onwards, and may carry out exploratory flights after age 23 days, this meant that the maximum number of young counted in the roosts in 1996 was not the total number of young born. Juveniles at certain sites (Stackpole, Slebech, Woodchester) were caught and marked or ringed, so mean birth date was accurately calculated. At other sites (Dean Hall and Iford) volunteers visited roosts more frequently than the specified dates, so their extra counts helped to make reliable estimates there. Data obtained from Woodchester was used to estimate total numbers of births and mean birth dates for Brixham and Iford. See table 4.

Results

Population parameter comparisons by site and season

At each site there were two peaks during the summer in the NBFD. The first occurred in July as mothers returned to give birth , and the other occurred in August as the young started to forage. This pattern is characteristic for this species (Ransome 1973). The number of juveniles counted in the roost, and the timing of births varied considerably among sites. A summary of the data for all sites is given in Table 4.

Table 4. Population parameters of the eight sites listed in order of decreasing latitude

Site	Max NBFD in July	Max NBFD in August	Number of juveniles	Estimated mean birth dated
Littledean Hall	114	126	36	(27) 14 July
Slebech	100	121	46	28 July
Woodchester	55	68	32 (26)	13 July
Stackpole	199	180	63	26 July
Brockley	99	112	49 (40)	15 July
Iford	159	180	92 (75)	19 July
Mells	69	156	68? (45+)	?
Berry Head	66	82	22 (18)	31 July

KEY: NBFD = number of bats flying out to forage at dusk.

NB Numbers of young in parentheses are maximum counts in the roost after exits by mothers, from data provided by observers. Total numbers of young born were known for Woodchester, Stackpole and Slebech from marking studies. Total numbers of young born were estimated from the maximum number of young counted in the roost x 1.23. This figure is the correction for Woodchester for 1995, where both figures were known from catches made. The Dean Hall estimate was by an experienced observer (D. Priddis).

Problems with counting due to colony shifts made it impossible to obtain reliable data for Mells. The figure of 45+ is a conservative minimum as 45 young were ringed there in November. Since it is exceptional for two thirds of the young to survive for 100 days, a more realistic figure is 68+ births.

The maximum NBFD in July and August on specified count dates varied markedly among sites, and seemed to bear no clear relationship to latitude, or to the numbers of young born at a site. If maximum NBFD in July is used as the best estimate of colony size, and Mells is omitted due to unreliable counts, then Woodchester has the smallest colony, followed by Brixham, Slebech, Dean Hall, Iford and Stackpole. If NBFD in August is used, the order remains the same, except that Iford and Stackpole have similar sized colonies. If number of young born is used, the order becomes Brixham, Woodchester, Dean Hall, Slebech, Brockley, Stackpole and Iford. Whilst the three parameters provide a reasonable level of consistency in the order of colony size, there are problems with the positions of certain sites. Which of the two pairs of Brixham and Woodchester, and Dean Hall and Brockley has the larger colony size? Should we pay more attention to exit counts or numbers of young born?

In an attempt to clarify important differences between the constitution of bats present in colonies among sites, data were transformed to produce a ratio between NBFD and total juvenile numbers born, as shown in table 5. Sites are again in order of decreasing latitude. The justification for using this ratio is given in the relevant part of the discussion.

These data show that the proportion of a colony formed by the number of births varies markedly among sites. This has important implications for the assessment of colony size.

Table 5. Peak exit number: birth number ratios from table 4

Site	Max NBFD in July/n births	Max NBFD in August/n births	Estimated mean birth date
Dean Hall	3.17	3.50	14 July
Slebech	2.17	2.63	28 July
Woodchester	1.72	2.13	13 July
Stackpole	3.16	2.86	26 July
Brockley	2.02	2.29	15 July
Iford	1.73	1.96	19 July
Mells	(1.01)	(2.29)	?
Brixham	3.00	3.73	31 July
Means (s.d.)	2.42 (0.61)	2.73 (0.63)	20.86 (6.83)

Means were calculated from all sites except for Mells, since data were unreliable due to counting difficulties. Each ratio is the relevant NBFD divided by the number of young born (actual or estimated). Mean birth dates are repeated to show that ratios do not significantly influence birth timing. Linear regression for mean birth date against NBFD in July; r = 0.405, n = 7, NS. Linear regression for mean birth date against NBFD in August; r = 0.450, n = 7, NS.

Changes in numbers of bats leaving to forage throughout the study period

Each site showed some differences in the timing of roost occupation and pattern of fluctuating numbers leaving to forage, but overall they were quite similar. As it would be very difficult to present all data for all sites completely, and very tedious to comprehend it, I calculated mean data for the six sites with complete and reliable data. The results are shown in table 6, which also includes percentages of the maximum NBFD, and the mean NBFD: mean birth number ratio. The mean number of births for the six sites was 53.

Table 6. Mean numbers of bats flying out to forage at dusk from 6 study sites through the study period

Date of count	Mean NBFD (s.d.)	% of max mean NBFD	Mean NBFD: mean birth n ratio
21-4-96	16.8 (11.2)	13.1	0.32
28-4-96	18.3 (10.7)	14.3	0.35
5-5-96	18.8 (15.8)	14.7	0.35
26-5-96	69.2 (43.3)	54.1	1.31
2-6-96	72.8 (43.6)	57.0	1.37
9-6-96	72.0 (34.2)	56.3	1.36
30-6-96	101.5 (38.4)	79.4	1.92
7-7-96	107.3 (43.4)	84.0	2.02
17-7-96	120.5 (46.7)	94.3	2.27
28-7-96	112.2 (41.9)	87.8	2.17
4.8.96	116.4 (43.3)	91.2	2.20

Date of count	Mean NBFD (s.d.)	% of max mean NBFD	Mean NBFD: mean birth n ratio
11-8-96	120.8 (43.5)	94.5	2.28
25-8-06	127.8 (38.7)	100.0	2.41
1-9-96	121.2 (48.6)	94.8	2.29
8-9-96	108.7 (42.3)	85.0	2.05
29-9-96	77.7 (40.3)	60.8	1.47

The two sites whose data were omitted from the samples were Brixham and Mells. This is because of counting difficulties.

Underlined % data occur during two periods of relative stability of bat numbers, or 'plateau' periods.

Underlined percentage data in table 6 occurred during two periods of relative stability of bat numbers, I refer to as 'plateau' periods. The first was in late May/early June, and the other from mid July to mid August. They may have a special significance as possible parameters relevant to assessment of colony size, and may provide key sampling periods in future attempts to monitor changes. Details of these two periods plateau periods by site are shown in tables 7 and 8.

The stability of numbers during the first plateau period varied among sites with the week of the study (table 7). Slebech, Dean Hall and Iford showed rises, Stackpole showed falls, and Woodchester was the most stable. The ratios obtained from the mean numbers were higher and more variable at the Welsh sites, but more consistent and lower at nearly 1:1 at the English sites.

Table 7. Numbers during the first'plateau' period at six sites

Site	NBFD 26-5-96	NBFD 2-6-96	NBFD 9-6-96	N young (estimated)	Ratio mean NBFD: young
Slebech	73	76	85	46	1.69
Stackpole	160	157	131	63	2.37
Dean Hall	34	36	42	(36)	1.04
Woodchester	32	29	31	32	0.96
Brockley	51	47	50	(49)	1.00
Iford	65	92	92	(92)	0.90

N young are in parantheses if they were estimated, either by the 1.23 conversion factor (Brockley, Iford), or by the volunteer concerned (Dean Hall).

The numbers were much more consistent during the second plateau period (table 8) than the first, despite the fact that it lasted for a much longer period. No clear trends are evident in any data set. At all sites the ratio is much higher than 1:1, but only Woodchester and Iford have similar ones.

Table 8. Numbers during the second 'plateau' period at six sites

Site	NBFD				mean NBFD (s.d.)	mean NBFD: n young ratio
	14 July	28 July	4 Aug	11 Aug		
Slebech	100	100	99	98	99.7 (0.5)	2.17
Stackpole	199	176	177	180	183 (9.4)	2.90
Dean Hall	116	114	126	120	119 (4.6)	3.31
Woodchester	55	50	45	60	52.5 (5.6)	1.64
Brockley	94	82	95	93	91 (5.2)	1.86
Iford	149	159	151	157	154 (4.1)	1.67

Discussion

Exit counts of flying bats

It is important to appreciate that the number of bats flying out to forage from a nursery roost fluctuates quite rapidly over the space of a few days, throughout the whole of the summer. This is clearly shown by data collected automatically on a daily basis by Peter Andrews from the Welsh sites, and similar data now being collected at Woodchester, using infra-red sensors and a computer logging system developed by Tim Chapman. Hence data collected by volunteers on specific dates are mere snapshots of a continuously changing, dynamic colony system. For example, in mid July the numbers at Stackpole varied from 198 to 160 over a 5 day period.

Despite this situation, the numbers of bats flying out to forage at dusk (NBFD) on the selected dates over much longer periods (1-3 weeks) show similar trends at each site. Data for each date should be regarded as a random sample taken from among the short-term fluctuations, and is unlikely to represent extreme data points. Early in the season, numbers are generally low, and vary erratically in response to fluctuating climatic temperatures and their probable effect upon food supplies (Ransome 1973). This situation is commonly seen at the maternity roosts of other bat species (e.g. Rydell 1989a). As the season progresses, and rising night temperatures promote insect availability to foraging bats, numbers usually rise in May. More young from the previous summer, pregnant mothers, older immature bats of both sexes, and adult males all return. This is followed by a period of relatively stable numbers, referred to as the first 'plateau', which occurs in late May and early June (tables 6 & 7). As June progresses, the first plateau is followed by a period of rapid rise in numbers, which peaks at about the mean birth date at Woodchester, and is due to the return of most of the breeding females in late pregnancy (Ransome, unpublished data). As their numbers rise, the total number is compensated for by a loss of all adult males, and also older immature males at Woodchester, producing a roost containing primarily mothers, their young, and immature females in their second and third summers. From mid July to mid August, total numbers stay relatively stable again, producing the second plateau. At some sites numbers may even fall slightly, before they sharply rise again to a brief peak as most of the juveniles begin to forage. This period is usually in early to mid August, but in 1996, due to the late cold spring, it was delayed until late August, and even early September at some sites. Soon afterwards, by mid September, NBFD falls rapidly at most sites, due to the departure of both mothers and older immature bats, until only small numbers remain into October.

However, at some sites such as the Welsh ones, Dean Hall, Mells and Iford, numbers remain very high, even into November. At Dean Hall, good numbers of older immature bats, mothers and adult males have been shown to remain in the roost late in one September (D.J. Priddis & R. D. Ransome, pers. obs.) and at Mells they regularly occur even until late October and early November (D. Cottle & R. D. Ransome, pers.obs.). This is in contrast to Woodchester, where almost all bats in the roost are juveniles by mid September, and very few of these remain into October.

Juvenile counts within the roost

Female greater horseshoe bats have single births, usually annually, but may occasionally miss breeding in a given summer. Normally they breed at age 2 years (earlier breeders) or 3 years or older (later breeders) at Woodchester (Ransome 1995). Earlier breeders breed at 96% of their opportunities, and later breeders at 85% of their opportunities.

When young are born they are left within the roost by their mothers at her next foraging flight. Mothers make no attempt to hide their young, which are usually left in favoured warm spots, especially as they age, forming creches. This behaviour usually makes it relatively easy to count them, unless the roost is very high, with corners which are out of view. Mothers usually adhere to the same region of the roost to deposit their young, but fluctuating temperature conditions can cause movements to new areas, or even alternative roosts. This was a difficulty at Mells and to some extent at Brixham in the summer of 1995, and similar problems have occurred at Brockley in earlier years.

Exit count: number of juvenile ratios

Data presented in table 4, showed no clear relationships between maximum NBFD levels in July and August, numbers of young born, and latitude. Data were therefore transformed to ratios as shown in table 5, to compare the population structure during the two plateau periods among sites, in view of the differences in the age and sex groups noted above between some sites, at certain times of the summer.

Since greater horseshoe bats always have single births, the NBFD: birth number ratio should be 1: 1 in July if only breeding females occupy a roost. If the ratio becomes 2:1, in July or August, before the young start to forage, then an equal number of non-breeding bats must occupy the roost with the breeders. If the ratio reaches 3: 1 in July, then twice as many non-breeders must be present as breeding females. Hence the NBFD: juvenile number ratio provides an estimate of the proportion of non-breeding bats present at the time of the count, **providing that all breeding females are present in the roost**. This proviso is only usually true for the period from mid or late July to mid or late August. (Ransome unpublished data), so only the ratios obtained during this period, which includes the second plateau period, should be used to indicate the levels of non-breeding bats. Ratios are not seriously affected by the start of foraging by juveniles, since non-breeding bats leave as the juveniles begin to forage. This must be true, or the second plateau of exit numbers would not occur.

Table 5 shows that the mean ratio for 7 sites in July, when NBFD peaked, was 2.42, but that among sites it ranged from 1.72 at Woodchester to 3.17 at Dean Hall. Hence there are major differences in the colony sex and reproductive structure among sites at that time. Woodchester, Iford, Brockley and Slebech showed low levels of non-breeding bats in July, and Dean Hall, Stackpole and Brixham showed high levels. Both groups show variable mean birth dates, so differences in sex and reproductive structure have no clear impact on birth timing in the same season.

At peak NBFD levels in August, when the young are foraging, we expect the ratio to rise as they add to counts, and this is actually what happens to the mean levels. It should theoretically rise suddenly by 1 at all sites if no other bats leave the roost, and if all juveniles start foraging simultaneously. Neither is the case (Ransome pers. obs.), however, so the ratio only rises by 0.31 overall. To a variable extent according to site, non-breeding bats vacate their maternity roost at the time that juveniles gradually become serious foragers, increasing their foraging range as they do so (Jones et al, 1995). At Stackpole, the ratio actually fell between July and August peak numbers, showing that this loss was a major event. It rose by 0.73 at Brixham, where losses must have been much less important.

The lowest August peak ratios, as in July, were at Woodchester, Iford, and Brockley, with Slebech just below the average level. The highest ratios again occurred at Dean Hall and Brixham, with Stackpole just above average level, close to Slebech. This suggests that whatever factor, or factors, cause the ratio differences among sites, it (or they) operates over at least a single summer. The ratio differences among sites seem not to be related to mean birth date, geographic location, or latitude.

Non-breeding bats present in a roost may produce both benefits and costs to breeding female bats. Their presence should benefit reproduction by elevating roost ambient temperatures. Higher roost temperatures lower the considerable costs of thermoregulation during stressful phases, such as late pregnancy and lactation (Stones 1965, Stones and Wiebers, 1965, 1967, Racey and Speakman 1987), and promote the growth of the young (Tuttle 1975, Ransome unpublished data). However, by exiting to forage from the same roost, non-breeding bats may compete for the use of foraging areas within the roost sustenance zone of breeding bats, and later their young. If the number of suitable foraging areas close to the roost is limited, breeders may be forced to travel longer distances to forage, and so increase their commuting costs. However, breeders may enjoy preferential access to favoured foraging areas, such as by aggressive defence, as has been shown by Rydell (1986b) for *Eptesicus nilssoni.*

A cost/benefit analysis of these competing behaviours has not as yet been successfully carried out, but the analysis is likely to be influenced by the total numbers of foraging areas available locally, relative to the numbers in the colony. Data concerning numbers of foraging areas and roost temperature differences are currently not available from most of these roosts. However, although we do not have good data on the total numbers of foraging areas, radio tracking studies carried out by Stebbings (1982) at Stackpole, and Duvergé (1997, pers. comm.) for the other sites, show that mean distances to foraging sites are considerably shorter at Iford, Brockley and Woodchester (about 2-3 km), where ratios are lowest, compared with Stackpole (about 8 km), and Slebech (about 14 km) where ratios are higher. This lends some support for the hypothesis that low ratios reduce commuting range and vice versa. However, Slebech did not show very high ratios, despite having the greatest commuting distance known so far from the UK. As it suffers from one of the most severe climates in the study, the proportion of its surrounding habitat which is suitable for foraging may be quite low, even though structurally much of it appears to provide suitable foraging areas. This point will be developed in Part 4.

The NBFD: number of young ratio is not fixed at a given site over long periods. Studies at Woodchester (Ransome 1989) showed that the mean maximum August level (recorded after most of the young were foraging) for blocks of five year periods, from 1962-66, 1967-1971, 1972-76, 1977-81, 1982-1986, were 1.96, 1.98, 2.26, 2.67 and 2.28 respectively. These periods covered major changes in the demographic structure of the colony, despite considerable stability of total population size from 1967 to 1985 of about 180 bats. Low ratios, about 2.0, occurred in the years during and after population crashes (1963-5; and 1985-6), and higher levels were reached in the late 1970s following a series of mild winters and several warm summers. The number of juveniles born showed declines from a mean of 65 in the late 1960s, to 61 in the early 1970s, 52 in the late 1970s, to 43 in the early 1980's. From 1987- 91, following the 1986 crash, the ratio was 2.14, and from 1992-1996 it was 2.08. These data suggest that the ratio changes with demographic structure, particularly the proportion of juveniles which survive to maturity, and the numbers of adult males.

High juvenile survival generates many immature bats over the next 2 or 3 years, increasing the ratio, and this colony build-up may begin to suppress the breeding frequency of mature females if they are resource-limited. Ransome (1995) showed that females were more likely to become earlier breeders after a population crash, and in the early years of the recovery phase, than later in the recovery period. Hence the proportion of immature females will fall after a population crash due to earlier promotion to breeding status. Later breeders show reduced breeding frequencies (85 % of their opportunities) as already discussed. If the proportion of non-breeding adult female bats reached 15%, it would raise the ratio significantly, as shown in table 9.

An even more important factor influencing the ratio would be the presence of sexually mature males in the breeding roost. Their numbers may equal, or even exceed the numbers of mature females. Hence they have the capacity to raise the ratio by about a further unit. It is feasible that with all breeding mature females, all non-breeding mature females, all immature males and females surviving at the levels shown to normally occur (Ransome 1991), and all adult males present together with the young of the year, the ratio NBFD: juvenile numbers could reach, or even exceed 4.0 in August. This figure was nearly reached at Dean Hall and Brixham in 1996.

Before the young start to fly in July, a ratio of 3.0 or above indicates that many, if not all, of these non-breeding bats are present in the roost. Again. Dean Hall, and Brixham, together with Stackpole, achieved these ratios or higher. Their roosts must therefore hold virtually the entire sex and reproductive range for their colony. This not the case for Woodchester, as adult males are currently rarely found in the maternity roost except briefly in May, despite being found in hibernacula nearby. Similarly large numbers of adult males are found at hibernacula near Iford, where ratios are also very low. They exist, but apparently do not utilise the maternity roost, judging by the ratios in tables 7 and 8.

Table 9 shows ratio calculations for a theoretical colony containing 100 mature female bats. In fact the size of the colony has no bearing upon the ratio produced, it merely makes the numbers easier to assimilate. They are intended to illustrate the potential impact of the presence of various non-breeding bats, and also reduced reproductive rate, upon the ratio.

Table 9. Calculations to show the effect upon NBFD: juvenile number ratios of the presence in the roost of different non-breeding age and sex groups

N breeding females (option)	N non-breeding mature 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.

What the calculations suggest, is that the presence or absence of adult males is the largest factor influencing the ratio at a site. Options (1) to (4) of the table, in which all males are present, generate a mean ratio of 3.12 in late July (range 2.50 - 3.76), which is a better time to use, as non-breeding bats leave roosts later in August. Options (5) to (9), in which all males are absent, generates a mean ratio of 1.90. (range 1.50 to 2.20) in July. These limited ranges, which do not overlap, apply despite the extreme ranges of female breeding rates, and juvenile survival used. Hence ratios at or above 2.5 in July, before young forage, may be taken to indicate adult male occupation of a roost, and those below 2.2 to indicate their absence, since immature females virtually always return to the maternity roost, and most of the immature males also do so (Ransome, unpublished. data). When attempting to estimate total colony size, it is important to include the males in calculations. I believe there is justification for adding 1 to the late July ratios for sites with low ratios, on the assumption that the number of adult males equals that of the breeding females. If these arguments are accepted, estimation of the total colony size in August for each site is possible, and are as shown below. The formula used was (number of young born x July peak ratio) + number of young born. The ratio was corrected by adding 1, if it was below 2.20, and it was used uncorrected if it was above 2.50.

They are:

Brixham: (23 x 3.0) + 23 = 92
Dean Hall (36 x 3.17) + 36 = 150
Slebech: (46 x 3.17) + 46 = 192
Iford (92 x 2.73) + 92 = 343
Woodchester: (32 x 2.72) + 32 = 119
Brockley: (49 x 3.02) + 49 = 197
Stackpole (63 x 3.16) + 63 = 262
Mells (min.) (68 x 2.29) +68 = 224

These estimates, which do not alter appreciably if the ratio is calculated from the mean NBFD during the second plateau period, produce the same rank order of size as that produced by using the number of young born at each site. This is because the adjusted ratios have a mean of 2.91, s.d. = 0.29, range 2.29 - 3.17, n = 8. If Mells is excluded, as it should be, due to counting difficulties at the roosts, the mean is 3.00, s.d = 0.18, range 2.72 - 3.17, n = 7. If these adjusted ratios truly reflect the state in each colony, it infers that colony structure is broadly similar over a wide range, in a given year.

The estimates provided are maxima, as they apply immediately after the young start to fly. Since this is a period of high mortality, juvenile numbers fall quite rapidly to about half of these numbers by the following summer (Ransome 1991), and most of these deaths occur before hibernation starts (Ransome 1990). If half of the 32 young born at Woodchester in 1996 are deducted from 119, the estimate of 103 bats for the Woodchester colony agrees quite closely with the 94 bats known to be alive in 1996 by capture at the maternity roost and hibernacula in the winter of 1996/7. Ransome (1989) showed that some bats, especially adult males, which usually evade capture at hibernacula for several years, would subsequently be proved to be alive, mostly over the following 5 years. Hence the gap between the 94 bats definitely alive in 1996 and the estimate of 103 in 1996, is likely to close over the next five years.

As these ratio-derived total colony estimates do not significantly alter the previous orders obtained at the 8 sites using NBFD and juvenile totals, they provide useful base-line data for future monitoring programmes. In combination with the evidence provided in tables 7 and 8, the scientific argument for monitoring greater horseshoe bat roosts during the late July to mid August plateau period, should a national monitoring scheme be instituted, becomes compelling. This is especially true if the alternative is late June, at a time when exit counts are rapidly rising (see table 6).

We should keep an open mind on the possible underlying causes of ratio differences until more data are available. It may be that ratio differences in a single summer reflect different phases of demographic cycles among colonies, following the 1986 population crash, as well as the presence or absence of adult males in July. The availability of alternative suitable summer roosts to adult males, and the older immature males from a colony, may influence the latter situation. There is no evidence that dietary/foraging site factors exert important influences upon the occupation of maternity roosts by groups of non-breeding bats through the middle of the summer. They possibly influence the break-up of colonies in September, but evidence at present is too sparse. Roosts with high and low levels of key prey consumption, and large ranges of commuting distances to foraging areas, show quite different levels of non-breeding bats. For the 5 sites for which data were available, a chi-square test for high and low levels of these factors was not significant (= 1.67, d.f. = 2, N.S.).

Part 4: Characteristics of the eight sites possibly relevant to population levels

Introduction

Tuttle and Stevenson (1982) reviewed published literature concerning the many factors thought to influence the successful reproduction of female adults, the growth of their young, and the young's subsequent survival rates. Their review was both among species of bats, and among populations of the same species. In their view the factors that affected adult survival had a greater impact upon juveniles, which also had their own unique problems. Among the mortality factors they identified which can reduce population productivity, were:

1. prenatal mortality, by resorption or abortion of embryos, during pregnancy stress
2. post-natal falls from roost creche areas
3. predation
4. restricted availability of 'quality' maternity roost sites, 'quality' being mainly judged by roost thermal characteristics
5. roost location relative to suitable foraging habitat i.e. commuting distance
6. extent of maternal care shown by the species.

The major factors influencing growth and survival were thought to be temperature and food availability. In addition Tuttle and Stevenson (1982) identified the weaning period as one of considerable stress and apparent high mortality, and this was confirmed for greater horseshoe bats by Ransome (1990).

Ransome (1973, 1978, 1989, 1995) considered some of these factors in detail for greater horseshoe bats. Ransome (1989) linked population changes with birth-timing, showing that a series of summers with late mean births lead to colony and population declines and vice versa. Late births in a given year are due to the extended use of torpor by pregnant bats (Racey 1973, Ransome 1973) as a result of low spring climatic temperatures which reduce insect availability (Taylor 1963) and consumption by bats, as judged by faecal production (Ransome 1973). Birth timing affects the subsequent growth of juveniles born in a particular summer. Late-born young are smaller than those born early in the summer, and stunted females show reduced survival rates (Ransome 1989). Ransome and McOwat (1994), compared the birth-timing of juveniles born at 3 maternity roosts (the two Welsh sites, Stackpole and Slebech, and Woodchester) over a nine-year period, and showed that in most years births were synchronised at all three roosts under the influence of similar climate, but mean birth time varied widely from year to year. They showed that late births followed cold springs and vice versa, confirming the findings of Rydell (1989) for *Eptesicus nilssoni*. The mean climatic temperature in April and May combined was strongly negatively linked to birth time, especially at Woodchester. A difference of only 2 °C in mean April plus May temperature changed mean birth date by 18 days. However, there was one year (1984) in which significant differences in birth timing occurred between the three colonies. They showed that similar broad climatic temperature effects are not the only ones influencing birth-timing, especially between the Welsh and English sites. Clearly 1996 was another year of significant differences among colonies (see table 4).

To summarise, whilst many of the six mortality factors identified by Tuttle and Stevenson (1982) can influence populations of greater horseshoe bats, prenatal mortality and falls from the creche are known to be very low in the UK. Predation on bats by diurnal birds of prey, such as the sparrowhawk, *Accipiter nisus*, was thought to be a significant factor by Speakman (1990, 1991), and an influence upon emergence times from roosts by Jones and Rydell (1994). Certainly at Iford, sparrowhawks have been seen to catch greater horseshoe bats leaving the roost over several years, including 1996 (Tony Sladden pers. comm.)

The extent of maternal care is presumably essentially similar at each roost, since the same species is involved in each study site. Hence the remaining mortality factors they identified are roost 'quality' and roost location relative to quality foraging habitats. Since their review, Ransome (1989) identified birth timing as a further key factor affecting mortality and population levels in greater horseshoe bats. This study only attempts to investigate roost location relative to quality foraging habitats and birth timing. However, roost factors may exert considerable effects upon population levels, and this possibility should not be forgotten.

Quality foraging habitat for bats has, I believe, two fundamentally different aspects which need to be considered separately. First there is the structure of the habitat, which provides (a) soil and the plants which ultimately generate suitable insect prey, (with and without suitable grazers), and (b) the arrangement of vegetation to provide features acceptable to the bat's flight and echolocation capacities. Jones and Rayner (1989) studied these aspects for greater horseshoe bats, and showed that low-level hawking and perch-hunting were the major flight methods used. Bats stayed close to the shelter of large trees or bushes where their highly sophisticated echolocation capacities are very effective at detecting and discriminating moving prey within clutter (Schnitzler 1987). Second there is the potential of a habitat to generate flying insect prey in sufficient densities, and at sufficient frequencies, to allow regular successful feeding by hawking or perch-hunting bats. This is not to be confused with high populations of insect prey within the habitat. Insects have critical temperature thresholds, below which flight cannot occur (Taylor 1963). For many insects this figure is about 10 °C, but different species of insects may have quite different thresholds. Many moths require 12 °C or above to fly, most tipulids need about 10 °C, *Aphodius rufipes* requires 9 °C, ichneumonids of the *Ophion luteus* complex fly above 4 °C or possibly lower, and some small dipterans can fly at 2 °C or below. Hence the specific temperature regime experienced by a particular habitat at night will determine the flying prey available to foraging bats. If a specific area is to be regarded as a high-quality foraging habitat for bats, it must possess both features. First the vegetation structure needed for high populations of prey, and which is attractive for them to hunt in, and second a micro climate which ensures night-time temperatures from spring to autumn are warm enough for key prey to fly regularly.

Investigations into the precise nature, location and time-occupation of foraging areas by bats can only be carried out with the use of radio telemetry techniques. Radio telemetry studies of greater horseshoe bats were first carried out in the UK by Stebbings (1982), who published his preliminary findings from the colony at Stackpole in Wales. This was followed by Zahner (1984) who carried out a detailed study of a colony at Castrisch in Switzerland, including some dietary assessments. Later Jones and Morton (1992), Duvergé and Jones (1994), Jones *et al* (1995), and Duvergé (1997) reported on their findings in south-west England, at a similar time to Pir (1994) in Belgium, and Beck et al (1994), Bontadina *et al* (1995) and Bontadina *et al* (in the press) in further studies at Castrisch in Switzerland.

The concept of the roost sustenance zone (RSZ) as a circular area at 1 km and 3 km radius from the roost derived from studies by Duvergé at three inland roosts in south-west England. Although most of the studies listed above generally agree that most bats hunt within 3 km of the roost, some of them show that the range can be much greater around certain roosts, at least at certain times of the year, and the RSZ often involves complex polygons rather than circles. These findings greatly complicate attempts to quantify habitat availability to foraging bats at sites where radio tracking has not been carried out. Much time and effort could be spent accurately estimating the areas of various habitat types within fixed distances of roosts, only to find that the bats forage elsewhere.

The preferred habitat situation found by Duvergé at 3 sites in England (in Jones et al 1995) was ancient semi-natural woodland or substantial hedgerows, adjacent to cattle-grazed pasture. Throughout the UK, the abundant small scarabaeid dung beetle, *Aphodius* has been identified as a key prey for juvenile bats when they first feed (Ransome 1996, this study). This explains the importance of cattle-grazed pastures to the survival of the species. However, pastures may be cattle-grazed during one period of the year, and not another, or farmers may discontinue keeping cattle in an area altogether and convert the pasture to arable use, and vice versa. The ephemeral nature of some habitats adds further complications to habitat assessments around roosts. I have therefore used only approximate levels of habitat availability within the 1 km and 3 km ranges from the roost, rather than absolute quantities, to compare sites before attempting to relate significant differences in the consumption of various prey items shown in Part 1. However, in addition to this, I have included climatic and topographical differences among sites. These aspects are added in an attempt to explain the observed differences in the timing of appearance of various prey items through the study period, since the differences affect local microclimates, and hence insect availability to foraging bats.

Methods

The eight sites were not chosen randomly, but were selected for the reasons already explained. Broad habitat differences were assessed from maps (1:10,000), discussions with local field workers, and site visits. Major topographical features were assessed from maps alone (1:25,000). Climatic data for a 50 year period were obtained for each region from White & Smith (1982).

Results

Geographic position, elevation, topography and availability of major habitat types to foraging bats

Tables 10 and 11 briefly summarise these features for the eight sites.

Table 10 Some important characteristics of the sites

Site (region)	Latitude	Height above SL (metres)	Major habitats in 3 km RSZ	Topography within RSZ
Dean Hall (Glos) wd/p	51° 86'	168	wd/pcg urban/orch.	steep slopes; few but well sheltered
Slebech (SW Wales)	51° 77'	15	pcg/pog/wd arable/estuary	flat or gently undulating; few sheltered wd/p valleys
Woodchester (Glos)	51° 74'	135	pcg/wd arable/aquatic	many steep sided valleys; lots E/W with wd/p
Stackpole (SW Wales)	51° 59'	18	pog/lakes copses/dunes estuary	mostly flat; few sheltered valleys with wd/p low wd at distance
Brockley (Men/Avon)	51° 42'	20	wd/pcg/pog arable/urban	flat to NW; steep slopes to SW; several E/W with wd/p
Iford (Men/Avon)	51° 38'	45	pog/pcg/wd urban arable rivers/canal	many deep, steep E/W valleys with wd/p edges
Mells (men/Avon)	51° 31'	90	pcg/pog/wd arable rivers/lakes	undulating with several shallow E/W valleys + wd/p edges
Brixham (S Devon)	50° 43'	18	sea/urban pog/coastal cliffs/wd	in steep basin-like quarry; little cover; some E/W valleys with wd/p at RSZ fringes

Key: SL = sea level; RSZ = roost sustenance zone @ 3 km radius from the roost;
wd = all types of woodland combined; pcg = pasture which is cattle grazed; pog = pasture which is grazed by other grazers.

Glos. = Gloucestershire bordering the Severn Estuary; Men/Avon = the Mendip region of south Avon or adjacent to it; S. Devon. = south Devon.

Table 11. Approximate availability, within 1km and 3km of the roost, of the two key foraging habitats at different sites

Site	Deciduous woodland (1 km)	deciduous woodland (3 km)	grazed pasture (1 km)	grazed pasture (3 km)
Dean Hall	10	45	40	35
Slebech	30	25	45	50
Woodchester	40	25	45	55
Stackpole	30	15	15	35
Brockley	30	35	50	40
Iford	10	15	45	55
Mells	30	10	50	60
Brixham	5	5	10	15

Brixham figures are for land areas, excluding the sea, which forms the major habaitat around the roost.

According to the recommendations made by Ransome (1996) of 50% woodland and 50% grazed pasture areas within the 3 km RSZ, the best foraging sites on structural habitat features should be Dean Hall and Brockley, followed by Woodchester, with other sites deficient in woodland, and Brixham in very inferior habitat.

Since all radio tracking studies confirm that urban areas are usually avoided by bats, and dietary studies above show that trichopterans can be important secondary prey items at some sites in spring, a comparison of sites by rank order at 1 km and 3 km range is given in table 12, which also includes an urban habitat area rank order. The total area of water may be less important than its nature and proximity to the roost. Fast-flowing rivers or streams generate different trichopterans to those in stagnant water in canals or lakes, which tend to be larger (Chinery 1973), and so may be less useful to foraging bats. The area of the former cannot easily be determined, and greater horseshoe bats have never been observed foraging over large open tracts of water, despite numerous radio-tracking studies, although in Switzerland they frequently hunt alongside the wooded edges of rivers. Hence the length of edges of aquatic habitats , especially tree-lined ones, are likely to be more important than the area of water available. This could not easily be measured, so a subjective decision was made from maps and site visits. Large areas of stagnant water were judged to be more important than streams or rivers, and estuaries the least important, since Butcher et all (1937) found that caddis flies did not penetrate the saline regions of the Tees estuary.

Table 12. Rank order within 1km and 3km of the roost, of aquatic fresh-water and urban habitats at different sites

Site	fresh water (3 km)	fresh water (3 km)	urban (1 km)	urban (3 km)	mean rank score
Dean Hall	6	6	3	6	5.3
Slebech	5	5	1	1	3.0
Woodchester	1	1	2	3	1.8
Stackpole	1	1	4	2	2.0
Brockley	6	7	6	6	6.3
Iford	3	1	7	5	4.0
Mells	3	1	4	4	3.0
Brixham	8	8	8	8	8.0

Key: 1 = highest rank of fresh-water or low level of urban areas; 8 = lowest level of fresh water, or highest level of urbanisation The ranks are reversed since fresh water areas are advantageous, and urban areas are harmful within the RSZ.

Mean rank scores for these two structural habitat aspects in table 12, equally weighted, at the two ranges from the roosts indicate that again Woodchester has the most favourable conditions, followed closely by Stackpole, then Slebech and Mells, Iford, Dean Hall, Brockley and Brixham. The latter also scored lowest in the woodland/pasture analysis.

Since freshwater is only important as a source of caddis flies in spring at some, but not all of the sites close to it, and urban levels in all regions are generally low, it is probably more important to consider the woodland/grazed pasture habitat scores as the best overall measure of structural quality habitat, and adjust the order slightly to incorporate the advantage of freshwater, if a site was high in freshwater availability. I therefore promoted each of these sites by one position in the woodland/pasture order to achieve a final rank order of habitat structure 'quality'. Woodchester showed the best habitat structure features, followed by Brockley, then Slebech, Dean Hall, Mells and Stackpole, then Iford and lastly Brixham. The latter site is greatly inferior to all of the others in its habitat structure quality.

Climatic differences due to geographic position and their impact upon colony sizes.

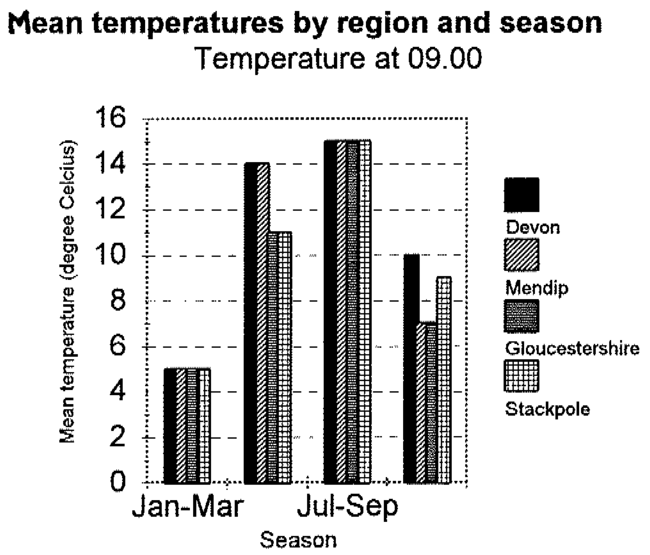
Figures 4 (a) to (d) show data from White and Smith (1982) summarising the broad climatic differences between the four main regions occupied by the 8 roosts. These differences primarily relate to latitude and proximity to the sea. Coastal regions enjoy milder autumns and winters, but cooler summers than inland regions. Table 13 summarises those aspects of their climatic data which are particularly relevant to bat populations.

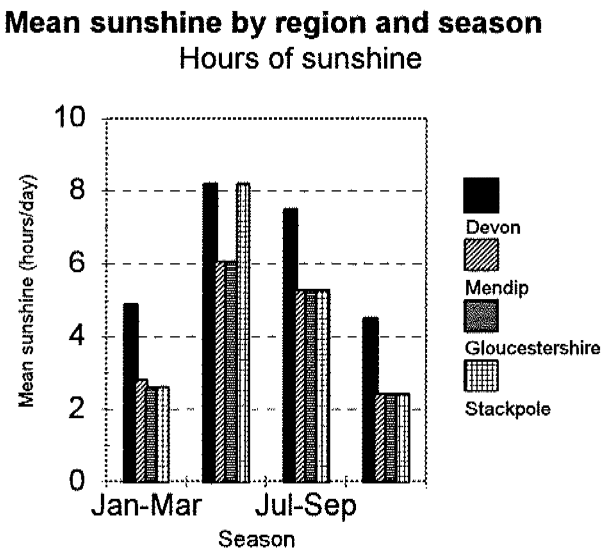
Table 13. Summary of broad climatic differences by region and season

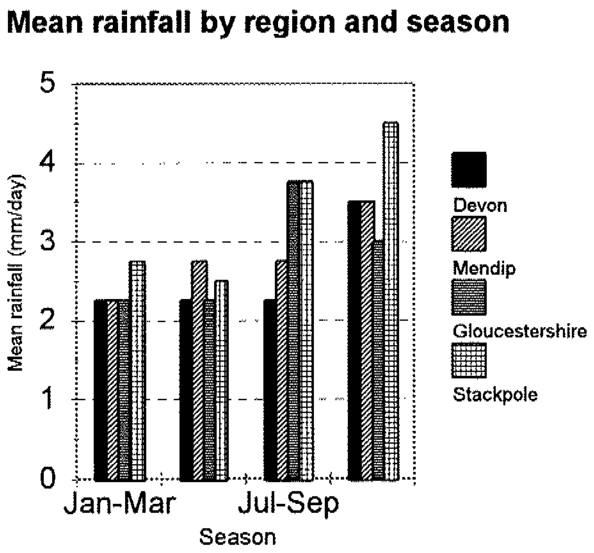
Region	**spring**	**summer**	**autumn**	**winter**
Devon	**= warmest**	same temperature	**warmest**	same
	= highest sun	**highest sun**	highest sun	highest sun
	moderate wind	**= lowest wind**	= lowest wind	low wind
	similar rainfall	lowest rainfall	= medium rain	similar rainfall
Mendips/Avon	**= warmest**	same temperature	**= coldest**	same temperature
	= lowest sun	**= lowest sun**	= lowest sun	= lowest sun
	= lowest wind	**= lowest wind**	= lowest wind	= lowest wind
	similar rainfall	medium rainfall	= medium rain	similar rainfall
Glos	**= coldest**	same temperature	**= coldest**	same temperature
	= lowest sun	**= lowest sun**	= lowest sun	= lowest sun
	= lowest wind	**= lowest wind**	= lowest wind	= lowest wind
	similar rainfall	**= highest rainfall**	lower rain	similar rainfall
SW Wales	**= coldest**	same temperatrue	**warmer**	same temperature
	= highest sun	**= lowest sun**	**= lowest sun**	**= lowest sun**
	= highest wind	**highest wind**	**highest wind**	highest wind
	similar rain	**= highest rainfall**	highest rain	

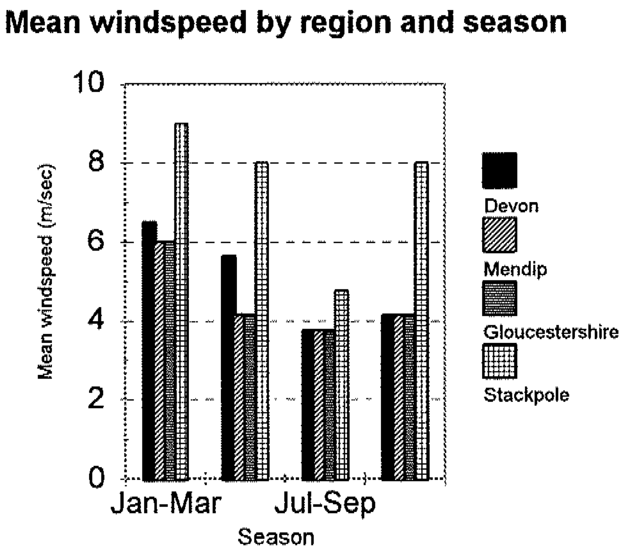
Bold differences are those most significant to mortality levels affecting colony size, or those influencing either the populations of prey items, or bat foraging activity.

Fig 4 Weather by region and season









For the reasons already explained in the introduction to Part 4, considering the broad climatic data alone, Devon is predicted to support the largest colonies. It enjoys the warmest springs and autumns, which allow the longest period of favourable conditions for the completion of pregnancy, birth and growth of the young, and permit frequent moth flight activity. Late birth timing should have the least impact in this region. It enjoys high levels of sunshine in spring and summer, which with higher ambient temperatures should combine to elevate roost temperatures still further, and enough rainfall to sustain high levels of *Aphodius* beetles (see review in Ransome 1996). Finally it enjoys generally low wind speed levels, which favour foraging by these bats, especially during heavy rainfall (Ransome, in the press). This prediction is supported by the colony at Buckfastleigh (latitude 50° 31'), which is not only the largest in the UK, but also probably one of the largest in western Europe, with over 900 foraging bats present in July, and over 300 juveniles born annually in recent years. Although adjacent to an urban area, it has rapid access to considerable wooded areas and extensive grazed permanent pastures on sheltered slopes and valleys. Brixham is clearly an exception to this prediction, probably partly due to its inferior habitat structure, but also since the colony occupies an underground roost. Some of these reasons will be fully discussed in Part 5.

In contrast, for the opposite reasons, considering the broad climatic data alone, Gloucestershire is predicted to support the smallest colonies. Colonies there will be most sensitive to late births, since autumns often experience cold spells in early September. This prediction is true according to the estimated colony numbers for Woodchester and Dean Hall. Similarly the Mendip/Avon and south west Wales regions are predicted to support medium-sized colonies. This is also essentially the case, but wide variations occur among sites. As Woodchester enjoys the most favourable structural habitat circumstances, climatic factors seem to be the more important ones regulating population levels there.

Topographical features, latitude, altitude and distance from the sea, as factors influencing local climates and insect phenology

Table 10 shows that the various roosts are located in terrain which varies markedly in its topography. On the basis of the extent, depth and steepness of valley or slope the roost is located in or on, and those of the region around up to the 3 km RSZ, a topographical rank order was devised. The rank order, from flat to highly vertically structured, the order is:
1 Stackpole, 2 Slebech, 3 Brixham, 4 Mells, 5 Dean Hall, 6 Brockley 7 Woodchester 8 Iford.

Local climatic temperatures around roosts are affected by the topography of the habitat within the RSZ, as well as roost latitude, distance from the sea and its height above sea level. Normally temperatures fall with increasing altitude by about 1 °C per 180 metre rise. We therefore expect the low-lying coastal roosts at Stackpole and Brixham, and those not far inland at Slebech and Brockley to experience warmer conditions than those at Dean Hall, Woodchester, Iford and Mells.

According to the population regulation mechanism proposed above, Dean Hall and Woodchester, since they are located in the coldest sites should have the smallest colony sizes, with the Slebech colony the next smallest. This prediction follows if the coldest sites have the latest births, and produce the most stunted juveniles, which have the lowest survival rates and future reproductive success (Ransome 1995). In fact in 1996 Woodchester, Dean Hall, Brockley and Iford, which are within, or close to, steep-sided valleys, with extensive areas of south or west-facing slopes, showed earlier births than those with flat or gently undulating roost sustenance zones. However, south or southwest-facing slopes produce local climates similar to regions hundreds of miles south of those typical of flat regions at a particular latitude. On sunny days solar radiation is absorbed and warms up the surface vegetation, and if it is covered by short grazed grassland, the soil beneath it as well. Prolonged sunshine during a day often results in the development of anabatic winds in such valleys during the afternoon. They are local warm winds which rise up from heated slopes, raising the temperature by several degrees at higher altitudes. These temperature effects may be responsible for varying the phenology of prey items on south facing slopes, and may be especially important within sheltered valleys, such as at Iford and Woodchester. As solar radiation absorption raises soil surface temperatures on south-facing slopes well above those on north-facing ones, the lengths of larval or pupal stages occupying the two slopes should be markedly different from each other, and from surrounding flat land. They are predicted to do so because of the Q_{10} effect upon the metabolism of ectothermic organisms, which ultimately affects growth and life-cycles, but also because high temperatures after cold exposure usually terminates diapause (see review in Leather et al 1993). All of the key prey items of the greater horseshoe bat are soil dwellers as both larvae and pupae, as are most of the secondary prey. Only the larvae of trichopterans are not found in soils.