



ENGLISH  
NATURE

No. 292

**The impact of  
maternity roost  
conditions on  
populations of greater  
horseshoe bats**



**Lowlands  
Team**

**R D Ransome**

**English Nature Research Reports**

# PART I

English Nature Research Reports

Number 292

**Species Recovery Programme**

**The impact of maternity roost conditions on  
populations of greater horseshoe bats**

R D Ransome

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

ISSN 0967-876X

© Copyright English Nature 1998

# Contents

Summary .....	8
Introduction .....	12
Part 1: Literature review of the impact of roost conditions on the growth and survival of young bats .....	13
Introduction .....	13
Food supply variability in temperate regions .....	13
The high costs of reproduction in bats .....	14
Roost conditions and reproductive performance .....	14
Pregnancy length and birth timing .....	14
Birth timing and survival .....	15
Variation in food consumption by free-living female bats .....	16
Lactation requirements .....	17
Roost selection - underground or above ground? .....	18
Discussion .....	19
Part 2: Overview of the scientific plan used in the study .....	21
Introduction .....	21
Methods .....	22
Site descriptions relevant to growth studies .....	22
Thermal regimes within the Woodchester maternity attic .....	22
Growth studies of developing juveniles at Woodchester .....	23
Assessing the age of young bats .....	27
Treatment of body mass and radius growth data .....	28
Condition index calculation .....	29
Growth phases used .....	30
Early mean condition during growth phases 2 and 3 .....	33
Statistical calculations .....	33
Discussion .....	36
Part 3: Results of growth studies at Woodchester .....	37
Introduction .....	37
How does growth differ between the sexes? .....	37
Factors affecting the growth of male juveniles .....	38
Single factor regressions before heater installation .....	39
Multiple regressions before heater installation .....	39
Single factor regressions after heater installation .....	40
Multiple regressions after heater installation .....	41
Summary for males .....	41
Factors affecting the growth of female juveniles .....	41
Single factor regressions before heater installation .....	41
Multiple regressions before heater installation .....	42
Single factor regressions after heater installation .....	43
Multiple regressions after heater installation .....	44

Summary for females .....	44
Summary for both sexes .....	47
Part 4: How did heaters affect the final growth and survival of bats born at Woodchester? .	50
Introduction .....	50
Data relevant to male juvenile growth .....	50
Data relevant to female juvenile growth .....	51
What was the impact of heaters upon juvenile survival rates? .....	51
How did radius length affect the survival of bats over the first few years of life .....	52
Discussion .....	53
Part 5: How did the growth of Woodchester bats compare with growth in other regions? .	54
Introduction .....	54
How did the growth of Woodchester bats differ from those born in region 2? .....	55
Variation in growth among years at unheated roosts .....	55
Variation in growth among years at Woodchester, after heater installation .	56
How did the growth of bats at Mells differ from those in region 2? .....	56
Discussion .....	57
Part 6: Maternity roost field study in 1997 .....	58
Introduction .....	58
Methods .....	58
Part 7: Results of juvenile growth studies among roosts in 1997 .....	60
Introduction .....	60
Radius and digit 5 lengths by sex and maternity site .....	60
Radius and digit 5 lengths by sex and area .....	61
Radius and digit 5 lengths by sex and heating regime .....	62
Birth date impact on radius and digit 5 lengths by heating regime .....	62
Early condition and growth of radius and digit 5 lengths by heating regime .	63
Mells - is the growth of young born there abnormal? .....	63
Overall conclusions for the study .....	66
Part 8: Numbers and growth of young from unknown roosts in area 2 in 1997 .....	69
Introduction .....	69
Numbers of young and the size of populations .....	69
Growth comparisons between unknown and known unheated roosts .....	69
Discussion .....	69
Part 9: Recommendations for improving roost conditions at specific roosts .....	70
Introduction .....	70
Brockley Stables .....	70
Dean Hall .....	71
Iford Manor .....	71
Mells .....	72
Woodchester Mansion .....	72

Acknowledgements ..... 73

Appendices ..... 74

References ..... 76

## Summary

The objectives of this study were to:

1. Review the literature on the impact of roost temperature and conditions on the growth and survival of young greater horseshoe bats, and hence ultimately their populations.
2. Compile, analyse and review the historical data sets for the growth and survival of young born at the Woodchester Park maternity site under different temperature regimes, and compare these with growth data from other maternity sites.
3. Carry out a field study at selected maternity sites around Bristol to assess the potential impact of heaters upon juvenile growth

The literature review revealed that few studies have attempted to assess the growth of juvenile bats under varying roost temperature conditions, and other environmental factors, since the pioneering studies carried out by Tuttle in the 1970's. He linked successful forearm growth, and ultimately population size, with both high roost temperatures and close proximity to favourable foraging areas. He also argued that synchronised births were advantageous to growth of the young, because lactating females could share the costs of keeping warm, if cool caves were used as maternity sites. A recent study by Schofield (1996), however, failed to find differences between the growth of young bats at two sites which showed different temperature regimes.

The desk study of greater horseshoe bats, using a large historical data set from a long-term growth study at Woodchester Mansion, shows that the best field measure of growth achieved is the length of the radius. Its ultimate length is fixed within 40 days of birth. The most important single factor discovered which affects its length is the mean radius growth rate between 4 and 14 days of age (called the mean early growth rate). It explains 28% of the variation in males, and 45% in females. The second most important factor is the size of the mother's radius, especially for female offspring (17% for males; 23% for females). Together these two factors explain some 49% of the variation in radius growth. Part of the remaining variation (15 & 9% respectively) is caused by early condition in unheated roosts, but also mostly by other factors (43%) which remain to be identified. They may be diet related.

There are no sex differences between the estimated radius and body mass sizes of newly-born young, but as juvenile females grow to a larger size than males and show faster mean early growth rates, female young must be more stressful to rear. The mothers of female young are significantly larger than those of males, and so may be better able to cope with the additional stress than smaller ones.

Radius mean early growth rate may be reduced by various factors which can lead to stunted growth in specific individuals, especially in unheated roosts. These factors include low early mean body condition, and late birth timing. Late births are often associated with first-time breeders, whose young usually show poor mean early body condition, and grow slowly to produce stunted adults, especially if poor weather limits foraging success.

As female young are more expensive to rear, they pose greater lactation demands upon their mothers than do males. Hence poor environmental conditions may be more likely to seriously limit the growth of female young. In support of this view, heaters used to raise roost

temperatures at a previously unheated roost benefited the radius growth of females, rather than males.

The heaters installed inside the Woodchester Mansion maternity roost in 1994 raised mean temperatures during the main growth period (40 days) by about 5°C, to a mean level of about 27-29°C. Previously the mean level had been between 21 and 25°C, depending on the climatic temperatures and sunshine duration in a particular year. In the three summers since installation, mean early growth rates of all juveniles significantly increased when compared with the three previous years. Despite this, only females showed significantly larger radius lengths with heaters. This was because the mean size of the mothers of male young fell significantly after heaters were installed, opposing the effect of faster growth rates.

The heater effects were seen despite 1996 having the latest mean birth date since 1986. Although heaters do not seem to affect birth timing, they reduce the impact of birth date on the mean early growth rate and radius length of female young to non-significant levels. Hence the penalty of a late birth, possibly due to being out of synchronisation with other females, hardly applied.

Survival rates of male and female young (over a period of at least one year) was 41 and 39% respectively for the 5 years before heaters were installed. In the 3 years since, males have averaged 42% and females 57.8%. However, these differences are not yet statistically significant, primarily due to small sample sizes.

Comparisons made between the radius and digit 5 lengths of young born at other roosts, which hibernated in sites in the Mendip Hills and near Bath (called region 2) during the same two periods, showed that males from Woodchester were larger than those from region 2 until after heaters were installed, when they were the same size. Females were the same size at Woodchester and region 2 before heaters were installed, but significantly larger from Woodchester after heaters were used. Since bats in both regions were under the influence of similar climate, this supports the view that the mothers of females are most stressed during lactation, and are the main beneficiaries of heaters. They are able to rear larger offspring, which are potentially capable of long term survival and reproduction.

Young born at Mells, where the summer roost in an attic was destroyed by fire in 1988, had smaller radius and digit 5 lengths than those born elsewhere in region 2. The radius size differences were not quite significant, but the digit 5 differences were. Possibly the inferior growth recorded at Mells is due to growth in an underground, cooler, site. Alternatively it may be due to biased sampling, caused by young born earlier in the summer leaving the area first. Distinguishing between these two scenarios depends upon the results of the 1997 ringing studies.

Overall the study shows that heaters are beneficial to the growth of female young, and probably to their survival long term. Hence a colony in a cool roost, which has heaters installed, should increase in size until other factors, such as food supplies, limit growth. Although heaters promote the growth rates of males, they do not seem to increase their ultimate size. Heaters may be most beneficial to small populations, and especially to those in cool roosts, such as those underground. Such populations are currently most likely to become extinct.

A field study of first-year bats, ringed as juveniles and recaptured in winter, showed no radius growth differences in either sex, among the five maternity sites in 1997. However, the radii of males were very nearly different, and their digit 5s were different among sites. The digit 5s of

males born at Iford were larger than those born at Mells. However, the sample from Iford was biased towards early-born young, and that from Mells was biased towards late-born young. Furthermore, female growth at Mells was better than that at Iford, though not significantly so. Hence the smaller size of bats caught at Mells reported in the interim study is confirmed as being primarily due to biased sampling.

The failure to detect significant female growth differences among the five maternity roosts in 1997 is thought to be primarily due to the small sample sizes of recaptured bats. The means and standard deviations of data from heated and unheated roosts in 1997 are similar to those obtained from the interim study. By combining data into two groups, those from heated and those from unheated roosts, significant differences between the growth of female young are shown to have occurred in 1997. Females born in heated roosts have larger radii and digit 5s. These data therefore add further support to the findings of the interim report.

In contrast to the interim results, the growth of male bats from unheated roosts was highly significantly influenced by birth date in 1997, showing smaller radius and digit 5 lengths with later birth time. Female radius, but not digit 5 growth, was again influenced by birth timing at unheated roosts. The growth of both sexes from heated roosts was not significantly influenced by birth timing, confirming the results of the interim study.

A large number of unringed first-year bats captured in hibernacula, mainly at Cheddar, show that one, or more, unknown maternity sites exists in region 2. Growth data for these bats by sex was typical for unheated roosts. The similarity of growth data among colonies in unheated roosts suggests that females are able to largely compensate for any differences in the physical roost circumstances they experience, but not for the lack of heating. This may be particularly crucial when mothers leave their young for long periods during each night, especially when they are in growth phases 1 and 2. During these phases they are either incapable of thermoregulation, or it is rudimentary.

Significant differences occurred in the growth of males among years in unheated roosts, especially that of their digit 5s. These differences were greatest between 1995, when births were early and growth was superior, and 1996, when births were late and growth was inferior. No growth differences occurred in either sex, between 1995 and 1996 at Woodchester, which was heated.

### **Overall conclusions**

This study supports the view that maternity roost conditions affect populations of greater horseshoe bats via the growth and survival of the young. Young of both sexes born in heated roosts showed faster radius growth rates than those from unheated roosts. However, only female young achieved larger size ultimately. Larger females are more likely to have female young when they reach maturity, and are less likely to suffer mortality in their first year. Hence populations should rise after heater installation. Although the survival rates of females have risen, numbers are currently too low to achieve significant levels.

The growth of both the radius and digit 5 lengths of young bats born in different unheated roosts is remarkably similar in a given year, irrespective of the diverse physical and thermal conditions within roosts, and their colony size. It is argued that this is because the mother acts as a living incubator for her young whilst she occupies the roost, and is thermoregulating. This will only be possible for extended periods during daytime if the mother has foraged successfully. Adjustable



clustering behaviour by groups of mothers in response to changes in ambient roost temperatures shares the costs of thermoregulation.

Whilst lactating mothers forage, their young are unavoidably exposed to roost ambient temperatures, which may regularly fall rapidly at night in cool climates. Very young bats cannot thermoregulate, and so are likely to become torpid and reduce their growth rates during this period. As very young bats (about 4 days old) have the highest growth rates, torpor is likely to have important limiting effects upon the ultimate growth achieved. Synchronised births are probably advantageous to bats, since the young form creches as they age, and are also able to share the cost of thermoregulation.

At unheated roosts, significant growth differences occur between years with very early births (leading to good growth), and those with late births (leading to poor growth). The growth differences are especially evident in the digit 5s of males. Late birth timing, which has previously been shown to follow cold springs, can lead to serious population declines, via increased mortality of young and the lowered reproductive success of survivors. Heaters largely remove the growth penalty of mean late births by a cohort, and asynchronous late births by individuals, and hence their survival costs. Because of this, they are predicted to provide an important insurance against future climate-induced population crashes.

It is recommended that all greater horseshoe maternity roosts should be partly heated by the use of an incubator where it is feasible to do so. Besides the growth advantages listed above, incubators seem also to increase the length of occupation of a roost throughout the summer months. The failure to link incubators with earlier birth timing to date may reflect their low use by pregnant bats. There is evidence that this use is increasing at Woodchester, where formerly it was mainly occupied by the previous year's young and sub-adults in spring. Their survival rates may be enhanced by using it. The full response of a colony to incubator installation may take many years to realise.

## **Introduction**

The results of recent studies on the effects of climate (Ransome 1989, McOwat & Andrews 1994, Ransome & McOwat 1994), diet and foraging habitat (Ransome 1996 & 1997a) on the performance of greater horseshoe bat populations have shown that all have important impacts. However, there are cogent reasons why the physical conditions operating within maternity roosts should also include factors influencing populations. There is accumulating evidence, both from rhinolophids and other bat species, that roost quality, especially its temperature regime, has an impact on the growth and survival of the young. Heaters have been installed within an insulated inverted incubator in some maternity roosts for several years, and a study is now required to review their value. This review will assist in making recommendations for the future management of maternity roosts. The project will contribute towards the maintenance of favourable conservation status at a number of proposed SACs.

# Part 1: Literature review of the impact of roost conditions on the growth and survival of young bats

## Introduction

In an extensive review of the growth and survival of bats, Tuttle and Stevenson (1982) stated that 'Very little is known about bat growth and development. Even superficial studies are lacking for 14 of 19 chiropteran families, and less than 3% of the known species have been investigated. Of the few studies that are available, most were conducted in captivity, and 80% are restricted to a single family, the Vespertilionidae.' They went on to criticise those studies that were carried out, for a failure to mention important environmental factors known to have major impacts upon growth.

Their assessment of the literature at that time resulted in them being able to justify only these limited statements about bat growth and development. First that megachiropterans develop more slowly than microchiropterans. Second that the postnatal growth curves of bats more closely resemble birds than other mammals. Third, that *Myotis lucifugus*, the little brown bat of north America and Canada, may be typical of many bats. It completes most of its growth very rapidly prior to the start of flight (Burnett and Kunz, 1982; Kunz and Anthony, 1982). Body mass peaks prior to flying, and tends to decrease afterwards until weaning is complete. This pattern has recently been confirmed by Hughes *et al.* (1995) for a captive colony of *Pipistrellus pipistrellus*. fed *ad libitum*.

Since bats resemble birds, rather than other mammals, in their postnatal growth curves, the selective pressure of flight seems to be an important factor influencing the evolution of bat growth patterns. The short growing season in temperate regions forces microchiropterans living there to grow very rapidly. Flight requires mature skeletal systems which are extensively ossified to provide rigidity and enable precisely controlled movements to occur. These are especially important to most microchiropteran bats, since it is their exceptional manoeuvrability and agility which allows them to catch insects in flight. The precise flight capabilities of bats are species specific, and reflect the detailed design of the wing structure (e.g. Norberg and Rayner, 1987).

The relative lengths of the various hand bones, and the membranous areas stretched between them, although ultimately under genetic control, seem also to be considerably influenced by environmental factors. The latter exert their effects during genetic expression as growth takes place, generating a wing design which is irrevocably fixed within about two months of birth. The problem for temperate-zone bats, faced with a short period of reliable favourable foraging conditions each summer, is to grow fast and precisely enough to achieve their genetic potential, and hence their evolutionary-selected design. Roost conditions are potentially crucial to the growth process, since at high latitudes, adult bats may be forced to spend up to 20 hours of each day exposed to them, in the absence of fresh food supplies (Rydell 1989, 1993). Pre-flight juveniles spend all 24 hours of each day within the roost.

## Food supply variability in temperate regions

Bats are not only forced to go without nutrients whilst they are confined to their daytime roosts. Insectivorous bats living in temperate zones experience food supply variations during the summer which may be either due to seasonal emergences of abundant prey, or to the impact of low

temperatures (Taylor 1963). Unpredictable cold and wet or windy weather causes highly erratic insect availability to foraging bats (e.g. Stebbings 1966; Racey and Swift 1981), and has been shown to prevent or curtail foraging bouts by radio-tagged *Rhinolophus ferrumequinum* (Duvergé 1997). These variations in availability can cause serious reductions in the amounts of insects consumed by breeding females during specific dawn foraging bouts in poor weather at any time during the summer (Ransome 1997b). Temperate zone bats are therefore forced into narrow 'windows of variable opportunity' with regard to pregnancy, lactation and post-natal growth. In poor summers at high latitudes they rarely enjoy the luxury of regularly consistent, favourable food supplies during foraging bouts. The higher the latitude the greater the likelihood of frequent food restriction, and the lower the population densities (Rydell 1992).

## **The high costs of reproduction in bats**

Insectivorous bats are either small, or very small mammals, and because of their high surface to volume ratio, they suffer high energetic costs if they thermoregulate continuously, even when not involved in any aspect of reproduction, growth or storage of reserves. Such bats have the option of switching off temperature regulation and taking advantage of the enormous energetic economies produced by the use of torpor (Hock, 1951). The torpor option seems not to be readily used by female bats reproducing in a given summer season, unless forced to do so by high thermoregulatory costs and low food intake. Stones (1965) and Stones and Weibers (1965, 1967) estimated the food consumption consequences of continuous temperature regulation during reproduction by conducting experiments with a captive colony of *Myotis lugifugus*. Pregnant and lactating females required three times as much food to maintain constant body mass at 21-26°C as at 33°C. Hence the costs of continuous thermoregulation during reproduction can be considerable, even when ambient temperatures are quite high by temperate standards.

Bats can significantly reduce their energetic costs in cool roosts, without using torpor, by two major behavioural methods. First they can cluster with other thermoregulating bats, and effectively reduce their surface to volume ratio (Herreid, 1963, 1967; Tuttle, 1975). Second they can choose a warm roost, or region within a roost, which is much closer to their regulated body temperature (say 30°C), so that the energetic costs are minimised. These behavioural methods are predicted to permit more of the nutrients derived from foraging to be devoted to production. Production includes developing embryos, lactation, growth and the deposition of body reserves, such as fat.

If foraging is unproductive, however, such a warm roost will generate higher metabolic rates, and therefore higher body mass losses, than would occur in a torpid bat at 10 to 15°C ambient roost temperature. Hence a continuously warm roost does not necessarily satisfy the range of needs of a maternity cluster of insectivorous bats throughout the summer, since they are likely to have to cope with at least some periods of total food deprivation.

## **Roost conditions and reproductive performance**

### **Pregnancy length and birth timing**

Roost conditions may not only influence the growth and development of young bats directly, but also indirectly by affecting the length of pregnancy, and hence birth timing. The latter, if late in the summer season, impinges upon the length of the period during which favourable juvenile growing conditions are most likely to occur. Bats are unique among mammals in that there is no

fixed length of gestation (Racey, 1973). Pregnancy in bats has been the subject of numerous and extensive studies both in laboratories and the wild, starting with Eisentraut (1937). He showed that torpor could occur during the pregnancy of *Myotis myotis*, under the influence of low ambient temperatures, and that the lower the temperature the smaller the foetus after the same period of pregnancy.

Racey (1973) was first to experimentally clarify the effect of both variable temperature and food supplies upon pregnancy length. He studied groups of captive *Pipistrellus pipistrellus* females. In a series of controlled experiments he showed that the effect of a series of ambient temperatures between 10 and 25°C depended upon the food supply available. In the absence of food, the bats fell into torpor, and gestation was extended by the period of torpor. In the presence of freely-available food, gestation length did not differ from their respective controls. Only ambient temperatures of 5, 30 and 35°C caused significant differences to these results. The 5°C exposure delayed births and the warm conditions accelerated them.

These data illustrate the crucial impact of food supplies upon the reproductive performance of bats, which may be largely unaffected by a wide range of roost temperatures. In the presence of unlimited food supplies, groups of this very small species (about 5g ) could thermoregulate and maintain normal pregnancy lengths when exposed to roost temperatures between 10 and 25°C. In the absence of food they used torpor to survive, and pregnancy was suspended. Larger species are theoretically capable of coping with an even greater range of roost thermal conditions, provided they have access to unlimited food supplies. In natural conditions, however, this situation may never apply.

Ransome (1973), in a field study of *Rhinolophus ferrumequinum*, counted the births at the Woodchester Park maternity site over a 9-year period, and showed that the mean birth date varied from 8 July to 17 July among years. (Since then, up to 1997, personal observations have shown that the range has increased, and varied between 30 June and 27 July.) He attributed the variation in gestation length to two phases of heterothermy, an early and a late phase. He argued that the early phase was due to erratic insect supplies at times when sudden cold spells depressed insect flight, and the late one may have been due either to the physical bulk of the foetus within the abdomen restricting food intake, or to the limited opportunities for feeding due to long day length at high latitudes. Kunz (1974) also observed a similar food intake reduction at the end of pregnancy in *Myotis velifer*. He also attributed this as possibly due to abdominal crowding, but also suggested that reduced flight efficiency as a result of increased wing loading, may be the cause.

### **Birth timing and survival**

Ransome (1989), in a study of population changes of *Rhinolophus ferrumequinum*, showed that the numbers of first-year bats reaching hibernacula was negatively related to mean birth time, rather than to the numbers of young born. This suggested that juvenile mortality rates are influenced by birth timing. Later births result in smaller forearms (actually radius length) of both male and female young. He suggested that this was the result of growth problems which were likely to develop in late August and September as climate deteriorated, and food availability became increasingly erratic. Stunted growth is related to poor female survival, not only initially, but also long-term. These findings provide an alternative mechanism to the view that the prime cause of high mortality in late-born bats is linked to their failure to deposit sufficient fat before their first hibernation period begins. I previously shared this view (Ransome 1990), but as my recent data indicate that fat deposition, at least in this species, usually occurs very rapidly in early

October, I am now less confident of its impact. Furthermore, even stunted bats may store very large reserves in autumn, but still suffer high mortality rates subsequently in their first spring and over the following few years (Ransome, unpublished data).

Ransome (1989) showed that several cohorts having a mean birth date after 20 July disappeared within 10 years, in contrast to other cohorts with a mean birth date before 10 July which still had many individuals still alive. Populations in hibernacula rose after early birth years, and fell after late birth years. Individual female bats which experience stunted growth seem to be stressed animals with a poor survival future, and reduced reproductive success levels, whatever their energetic state during hibernation. Ransome (1995), in a study of earlier and later breeding in this species, showed that a cohort's mean birth date is negatively related to the productivity of young from those individuals that survive long enough to become breeders themselves.

A flexible gestation length, gained through the use of torpor within the maternity roost, prevents female bats from aborting when faced with recurrent food shortages. As such it is a crucial adaptation to the normal mammalian reproductive pattern which prevents the inevitable breeding failures which would otherwise occur in temperate zones. However, if parturition occurs after the 20 July, which commonly happens, particularly in young female breeders, this ability generates high survival penalties. These penalties are paid in the lower survival rates of both young mothers and their offspring, which seriously limits their future reproductive potential (Ransome 1995). Such fitness costs are not unique to bats, but have previously been shown to occur in red deer, *Cervus elephas*, by Albon *et al.* (1987).

Ransome and McOwat (1994) refined the effect of climatic temperatures upon birth timing, showing that a rise of 2°C in mean April plus May temperature accelerated mean birth date by about 18 days via the increased number of foraging opportunities during early pregnancy. They argued that a mean temperature in April plus May of at least 9.4°C was necessary long term in a geographic region, to produce a mean birth date of 15 July. This date was likely to produce a stable viable population, since growth, which takes 60 days to complete (Jones *et al.* 1995), would end in mid September for most juveniles. They also showed that births in a given year were synchronised by climatic temperature at their three study sites, one of which was widely separated from the other two.

### **Variation in food consumption by free-living female bats**

Ransome (1997b) has shown that the amount of insect food consumed at dawn in good weather conditions by female bats depends upon their reproductive state. He measured consumption as estimated total dry faecal production. Consumption by pregnant bats was less than for any other female group apart from non-breeding adults.

The amount consumed by individual late-pregnant bats was found to be highly variable, sometimes reaching high levels but often it was very low despite very favourable weather and abundant insects. These data are not consistent with the hypotheses made above (viz.: abdominal crowding restriction; long daylength, and the wing loading effect). Instead they support the view that individual female bats consume highly variable amounts of food, at least partly through choice. Some individuals hardly eat at all, and these females may use torpor to delay their parturition timing, whilst others eat considerable amounts, and may thermoregulate and continue their pregnancy. Audet & Fenton (1988), in a radio-telemetry study of *Eptesicus fuscus*, showed some late-pregnant bats used torpor, whilst others thermoregulated in the daytime after the same foraging bout.

Such behaviour would either allow synchronization with a favoured period as was first suggested by Dwyer and Harris (1972) for *Miniopterus schreibersii*, or with most of the other females to share the thermoregulatory costs of lactation (Dwyer, 1971; Kunz, 1973; Humphrey, 1975, Tuttle, 1975). It is therefore not advisable to view pregnancy torpor as occurring in two distinct, separated phases, but rather as occurring at any time, due to at least two different underlying causes (either environmental restrictions on food consumption, or attempts at parturition timing/synchronisation).

The period when lactation by mothers and most juvenile growth occurs requires the highest levels of energy and nutrients annually (Anthony & Kunz, 1977; Barclay, 1989). It usually runs from late June to late August. This period includes the warmest months of the year in the northern hemisphere, when the highest and most reliable insect availability occurs, and night length becomes progressively longer, thus permitting longer and/or more frequent foraging bouts by lactating females (Rydell 1993, Duvergé 1997). All of these factors probably contribute to the high levels of foraging success normally shown by lactating females in favourable weather.

Food consumption by lactating bats doubles between pregnancy and lactation (Kunz 1974, Anthony & Kunz 1977, Kunz *et al.* 1995; Ransome, 1997b), necessitating longer foraging bouts (Audet & Fenton 1988). Kunz *et al.* (1995) also showed that food consumption rises during the lactation period in *Tadarida brasiliensis*. Foraging bout length nearly doubles from early to mid lactation in *Lasiurus cinereus* (Barclay 1989) and *Eptesicus nilssonii* with some females feeding up to four times a night (Rydell 1993). However, as lactation progresses, female *Rhinolophus ferrumequinum* show a decreasing total time of foraging activity (Duvergé 1997), which is matched by a reduction in faecal production from dawn foraging (Jones *et al.* 1995). These differences between vespertilionid and rhinolophid bat species may reflect growth pattern differences between the two families. Greater horseshoe bat young show a rapid growth rate increase in the first few days, then progressively slower rates afterwards (McOwat & Andrews 1994).

Duvergé (1997) showed by radiotelemetry that foraging is normally at dusk and dawn each night (bimodal), with the dusk bout the longer one. However, severe weather could reduce activity to dusk only, or even none. During lactation a trimodal foraging pattern developed, with an extra bout in the middle of the night which was the shortest. This pattern has been confirmed for the colony by automatic counting of bats present within the maternity roost (T. Chapman & R D Ransome, pers. obs.). Early in the summer, none, one or two foraging bouts occur nightly, when bats are pregnant, as also occurs in *Eptesicus nilssonii* (Rydell 1993).

Variation in food consumption is high (a factor of 3) among lactating female *R. ferrumequinum*, even during favourable weather (Ransome 1997b), suggesting that significant individual differences in foraging skills, or motivation occurs. This variation increases during poor weather, when some females do not feed at all, whilst others consume quite large amounts. Much of these variations reflect the age of the mother, with first-time breeders and old mothers (>15 years) frequently showing the lowest levels. This was possibly one of the underlying cause of the variation in early growth rates of young born to specific mothers in different years shown by Ransome (1990).

### Lactation requirements

In contrast to the considerable flexibility in the length of pregnancy shown by insectivorous bats, the growth of juveniles needs to occur within a fairly rigid time span. Any significant interruptions

in the milk supplies during this period are potentially very damaging to the growth rates achieved, and juveniles only seem capable of recovering from short-term deprivations. One possible insurance against poor foraging success by mothers during lactation is for them to store up reserves during pregnancy. There is evidence from body mass changes between early pregnancy and early lactation in *Myotis thysanodes* and *Myotis lucifugus*, that body reserves may be accumulated during pregnancy, and that they may be used to subsidise lactation during shortages (Studier & O'Farrell, 1976). These reserves may not merely be fat deposits, but also tissue reserves which are available to be converted into milk supplies (Burnett & Kunz, 1982; Stack, 1985).

Speakman and Racey (1987) in a study of *Plecotus auritus* found similar body mass changes between early pregnancy and early lactation, confirming observations made earlier by Stebbings (1976) for the same species. However, they argued that available reserves could only subsidise less than 5% of the estimated total metabolic costs of lactation (about 900 kJ). They suggested that the store could only sustain the energy needs of a lactating female for one or two days. They measured daily energy expenditure using the doubly-labelled water technique, and found it to be between 19 and 30 kJ/day.

A similar pattern of changes in the body masses of lactating female *R. ferrumequinum* occurs (Ransome unpublished data). The increased body mass levels which are present at the start of lactation usually show a steady decline in the first twenty days of lactation, then more or less stabilise until 45 days, after which time they rise after lactation ceases. The decline during lactation often occurs to the level of early pregnancy, or even beyond it in some individuals. Harrison-Matthews (1937) found that this species reached its lowest fat reserve levels in late lactation during August. The females therefore do seem to use their body reserves to subsidise lactation, at least in the initial two or three weeks. This is a characteristic of a wide range of other mammals (Reid, 1961; Easley, 1971; Randolph *et al.*, 1977).

In early lactation in July, when foraging bouts are unlikely to be interrupted continuously by poor weather for more than two or three feeding bouts consecutively, female body reserves seem likely to provide supplements to assist the rapid early growth of juveniles (McOwat & Andrews 1994). Later on in the summer, when female reserves are seriously depleted and inclement weather is more likely to occur, the risk of serious milk shortages restricting later juvenile growth, or even causing juvenile starvation, is likely to increase.

### **Roost selection - underground or above ground?**

Most insectivorous bats in temperate zones choose maternity sites which are traditionally occupied over many seasons. If the roost is of a substantial size, and offers a range of thermal conditions, within favourable foraging areas, it may be occupied by at least some individuals from April to October. Smaller roosts, with a restricted thermal regime, are more likely to show a much more limited occupation period. Caves may provide the conditions for successful maternity roosts if their structure favours the accumulation of metabolic heat loss by bats to generate suitable temperature regimes. Normally cave temperatures reflect the mean climatic temperature of the region, and so increase with decreasing latitude. It is only 10°C in southern Britain, and this level is well below the level needed for economical thermoregulation. However, if populations are large enough, a maternity colony may generate sufficient metabolic heat, especially post-foraging, to maintain a suitable temperature regime within part of a cave and allow successful postnatal growth. Tuttle (1975) carried out the first comparative study of the effect of temperature upon early growth rates of free-living bats. He found that the pre-flight early



growth rates of *Myotis grisescens* occupying similar roosts were proportional to cave temperature when colony size was constant, and proportional to colony size when cave temperature was constant. This study provides the most convincing evidence currently available which supports the need for heaters within the roosts of small maternity colonies, in order to boost reproductive performance. More recently Rydell (1989, 1992) linked the ability of *E. nilssonii* to exist at a latitude of 65°N with the use of heated parts of houses as maternity roosts.

High temperature maintenance underground should be aided by the insulation provided by the thick layers of rock and earth above them. Such roosts may be selected by bats, even at high latitudes, if warm summer air circulates between any two entrances of a dynamic cave system. Selection may be enhanced by the presence of a vertical blind chimney or dome along the air flow line, if it is of a suitable size to concentrate thermal losses from the bats.

Small maternity colonies may be unable to breed successfully underground, if they are unable to generate a sufficiently high temperature for a long enough period each day. They may require the higher temperatures which are often generated by solar radiation inside the roof spaces of buildings, particularly if parts are south-facing. The disadvantage of such spaces is the rapid loss of heat from the roof during the night. By dawn the ambient temperatures present may be well below those in nearby caves, so that even by clustering they are forced into expensive energetic costs for several hours until the roost warms up later in the day.

## Discussion

The growth of a specific young bat in a particular roost is likely to depend primarily upon the level of nutrients available for production after all of its other maintenance demands have been met. Production includes growth in lean body tissues, and deposition of reserves. Thermoregulation, especially in the absence of its mother whilst she forages, could be a major maintenance cost if roost temperatures are low, and the juvenile is old enough to carry it out. Hence there should be major energetic and growth benefits to be derived from the selection of either warmer roosts, and/or synchronised birth-timing. The mother should benefit from shared thermoregulation in clusters, as will the older young when they form creches whilst their mothers forage.

The level of foraging success achieved by specific lactating females during the same foraging bout in good weather varies considerably, and these differences accentuate in poor weather. Hence all young of free-living bats are likely to experience frequent interruptions in their nutrient availability, but the overall levels will vary with the mother's foraging performance. Later on, as a juvenile begins to forage, its own skills may assist the final phases of growth, assuming it can reach suitable foraging areas. We must therefore expect to see considerable variation in the growth of specific juveniles, even within a cohort born in the same season at the same roost. This is predicted to occur in spite of their exposure to many similar environmental factors such as climate and roost temperature regime.

By using heaters to raise the temperature regime within a roost up to a level of about 30°C, we expect the growth rates of the young to rise if their previous thermal conditions were limiting. Conclusions drawn from the review above suggest that the most likely colonies to benefit may be small ones in cool roosts, either above or below ground. These benefits in growth rate should also occur at other roosts, but may be modified by the foraging circumstances occurring around the roost. Large colonies, and those close to abundant food supplies, even if roosting in cool situations, may be able to afford the costs of maintaining sufficiently high temperatures

economically by sharing thermoregulation costs. Hence heaters may have less impact upon their early growth rates, and ultimately their population levels.

Heaters may also affect other aspects of reproduction which may impact upon populations. This includes birth timing via thermal influences upon the length of pregnancy. Hence this report considers the influence of heaters on a wide range of likely parameters.

## **Part 2: Overview of the scientific plan used in the study**

### **Introduction**

The ideal experimental arrangement to investigate the impact of heaters upon the growth of male and female young would involve simultaneous data collection from two matched maternity roosts, one of which was heated, and the other (the control) was not heated. The difficulty with this scenario is twofold. First it is impossible to match two maternity roosts in every aspect which is necessary to ensure that one roost is an effective control for the other. Maternity roosts of the same species vary in their colony size, occupation pattern, genetic constitution of the mothers, roost construction and microclimate, proximity to foraging areas, as well as the quality and quantity of insects available within foraging areas. Second, one experienced and skilled investigator can only visit one roost each night to obtain growth data. Hence two roosts would require two investigators, and their expertise and skills would have to be standardised. This has not been a practical option in the absence of a substantial budget.

The alternative strategy adopted here is to study the same maternity roost (Woodchester) in an identical manner by the same investigator for two time periods of several years each, to allow sample sizes to be sufficient for statistical analysis. One of the periods should involve an unheated roost, and the other a heated roost. This means that the roost variables are fixed, provided the colony size and the nature of the surrounding habitat remains constant. The major problem with adopting this strategy, apart from the extended length of the study, is that the climatic conditions operating during the two periods may not be similar. To overcome this valid criticism, I carried out parallel studies of the final growth parameters of young born over the same years in other regions.

Finally, an attempt was made to measure and ring juveniles within as many known maternity roosts as possible, in a single summer. By recapturing these juveniles in known hibernacula during the following winter, data concerning the final growth achieved in relation to specific nursery roosts will be obtained. Analysis of the data in relation to known nursery characteristics should discover whether certain roost types are significantly limiting growth.

An additional benefit of these ringing studies should also be an appreciation of the associations between specific maternity roosts and certain hibernacula. This information is likely to be important baseline data necessary to make informed conservation decisions to ensure the successful survival of each maternity colony.

The methods adopted were designed specifically to address the three objectives of the commissioned study. These were to:

- Analyse juvenile growth and survival data from years before and after heaters were installed in the Woodchester breeding attic. The analysis should include all available measures of growth and development.
- Compare growth parameters from young born at Woodchester with those found in hibernacula in the Mendips and Bath/Wiltshire areas. The latter should include data from Mells, a maternity colony whose favoured maternity roost was destroyed by fire and which now breeds underground in sub-optimal conditions.

- Compare the growth of young born at Woodchester, Dean Hall, Brockley Hall Stables, Mells and Iford Manor in 1997. This will require young bats to be ringed in maternity roosts for subsequent measurement in the hibernacula. This study will also shed light on the relationships between the various maternity roosts and specific hibernacula.

## **Methods**

### **Site descriptions relevant to growth studies**

Most data provided in the last part of this report came from bats captured in hibernacula of various kinds (see Ransome 1968 for distribution and site descriptions). Descriptions of the physical conditions at each maternity site are provided in Part 9.

I have previously divided the hibernacula regions into three areas (Ransome 1989) for population studies, since movements of individuals among the areas are very limited. They are the Mendips, the Bath area and Stroud. Limited data from ringing studies suggests that these populations draw juveniles from different maternity roosts. These include one at Brockley Stables near Nailsea, which seems to provide many of the juveniles reaching the Cheddar Gorge caves of the Mendips. The Stables were abandoned as a breeding site in favour of an underground site in nearby woods whilst the Stables were being rebuilt, and currently the bats use both sites.

Another maternity roost at Iford Manor, near Bath, is believed to provide juveniles to the many disused limestone mines around Bath. The remaining known maternity roost in the region is near Mells. Previously the bats occupied an extensive roofspace in an old ironworks building in a sheltered valley exposed to the sun. However, following a fire in May 1988 the bats moved. They did not abandon the area however, but bred underground in various sites, including a tunnel nearby, in subsequent years. Many of the juveniles born in a particular summer remain in the tunnel during the subsequent winter, but some are known to hibernate in the Bath stone mines, and occasionally individuals hibernate at Cheddar or Wookey Hole. Hence a population within certain hibernacula may derive from more than one maternity site.

The maternity roost in Woodchester Mansion, near Stroud, Gloucestershire, provides virtually all the juvenile bats found hibernating in the disused stone mines within a ten mile radius of the roost. However, some of the Woodchester juveniles regularly travel across the River Severn to hibernate in disused iron and limestone mines in the Forest of Dean, where they mix with others from the Dean Hall maternity roost.

### **Thermal regimes within the Woodchester maternity attic**

The breeding attic currently used is within a gabled structure in one corner of an enormous building. It is normally well ventilated, even draughty, but in summer the air-flow is reduced by blocking vents with curtains, and since 1994 an inverted incubator system has provided an ambient temperature of at least 27°C through most of the summer. The incubator consists of an insulated zone lined internally by 12mm plywood measuring 1.7m long by 1.3m wide at its base, tapering to 0m at the roof apex. The inside of the plywood surfaces is covered with a layer of carpet weave mesh, held in place with horizontal wooden battens, so that bats can hang easily from any part. It is heated by two electric tubular heaters controlled by a thermostat set at 27°C. Total heating power is 180 watts. Bats are prevented from burning themselves by screening the heaters with perforated zinc.

Ambient temperatures at four places in the roost, including the incubator after 1994, have been monitored every hour in each summer since 1989, using four Grant Instruments (Cambridge) thermistor probes and a squirrel data logger. Prior to incubator installation, bats normally had a choice of ambient temperatures whose range could exceed 20°C on a sunny afternoon, but was within 2°C just before dawn. The incubator is probably most beneficial to bats by providing a region of high ambient temperature on dull, cool days, and throughout every night and early morning. Occupation of this attic during cold spells in spring and autumn seems to have been boosted and extended by installing heaters.

Before the use of heaters, a mean ambient temperature of about 21°C occurred in the 30 days after births began in cool summers, and up to 25°C in warm summers. Earlier and later in the season the temperatures were much cooler, and whenever they fell below 8°C, bats abandoned the attic. Figures 1 and 2 show sample ambient temperature data from the same section of the attic roof before (1993) and after (1995) incubator installation. Both periods are 20 days long, the first in July, and the second in September. The incubator clearly does not eliminate daily fluctuations, but normally elevates temperatures significantly by between 5 and 9°C at low roost temperatures.

The distribution of droppings, and video recordings, confirm that bats spend virtually all of their night-time occupation of the roost within the incubator as expected. Once they complete the egestion of their faeces, they may leave the incubator to select warmer, or sometimes cooler, regions of the attic. During the afternoon on sunny days, one region may reach 45°C, whilst the incubator remains below 38°C, due to its extra insulation. These movements mean that it is impossible to compute the exact temperature exposure a juvenile bat receives over its growing period, even though the time period is known precisely. Furthermore, even if the incubator temperature remains stable at 27°C, a juvenile is normally tightly applied to its mother's ventral body surface up to the age of about 20 days, within a screen provided by her wings. Also the pair may spend time tightly wedged within a large cluster, where temperatures are likely to be above 34°C, at least whilst food is being digested by the majority of foraging bats. Consequently no reliable measure of ambient temperature regime for individual juvenile bats can be computed from data stored by the squirrel data logger.

### **Growth studies of developing juveniles at Woodchester**

Wing growth of juveniles born at Woodchester for the 24 days after birth was described by Hughes *et al.* (1989), following the initiation of detailed growth studies in 1986. They began after limited preliminary trials during previous years established that the rings and protocols used were not harmful to them, nor sufficiently distressing to their parents to cause them to remove their young. Currently most of the breeding females were themselves ringed as babies, and subjected to frequent recaptures in their first summer during studies of their own growth. Furthermore, they have been repeatedly captured within hibernacula and within the maternity roost over many years (Ransome 1995).

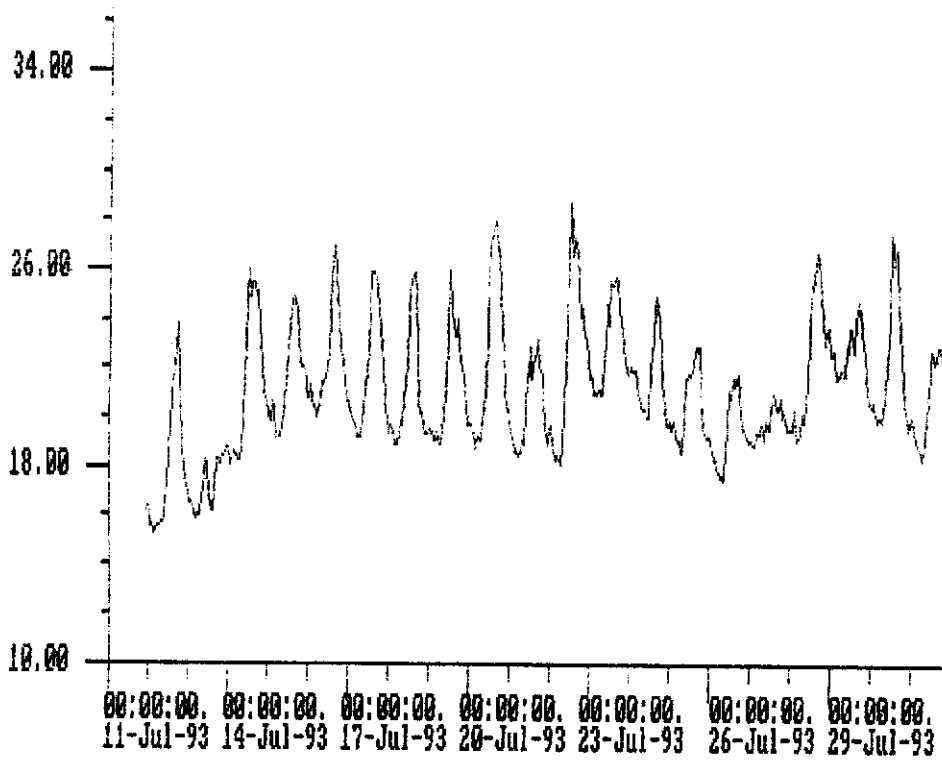


Figure 1.1 July temperatures before installation of the incubator

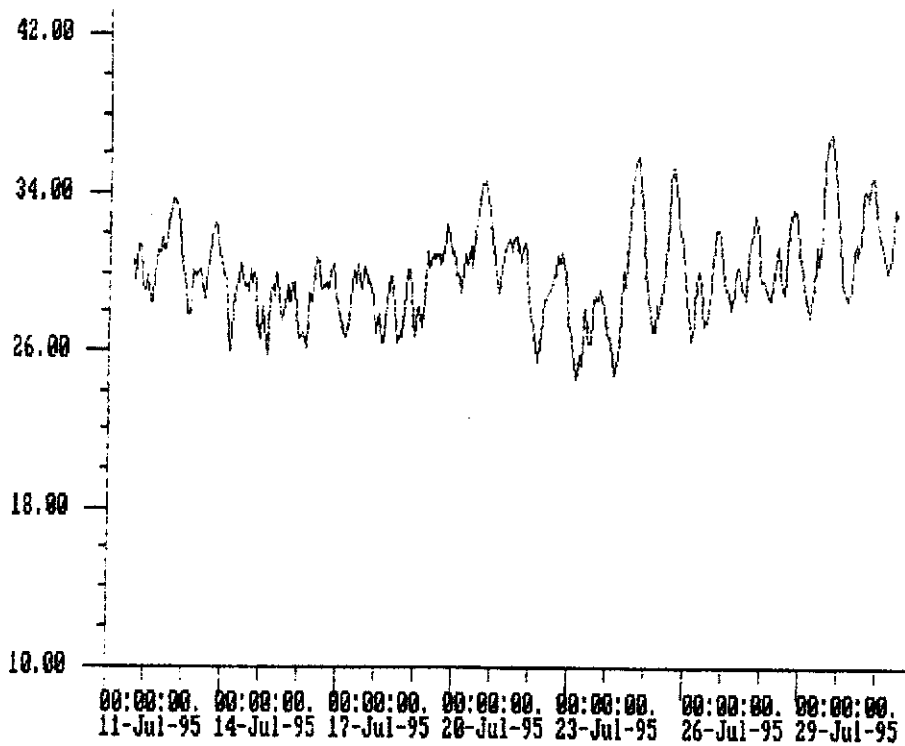


Figure 1.2 July temperatures after installation of the incubator

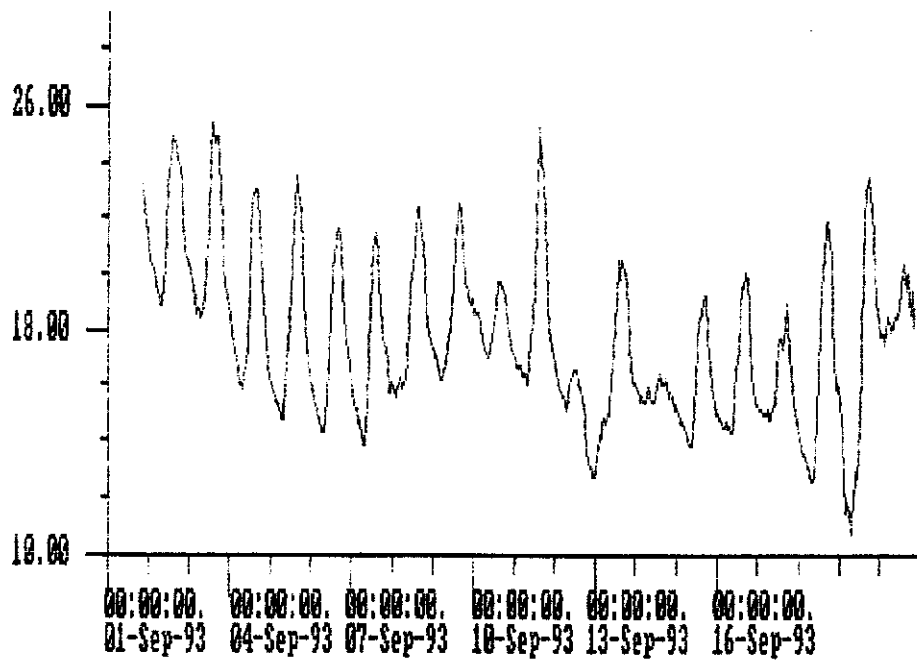


Figure 2.1 September temperatures before installation of the incubator

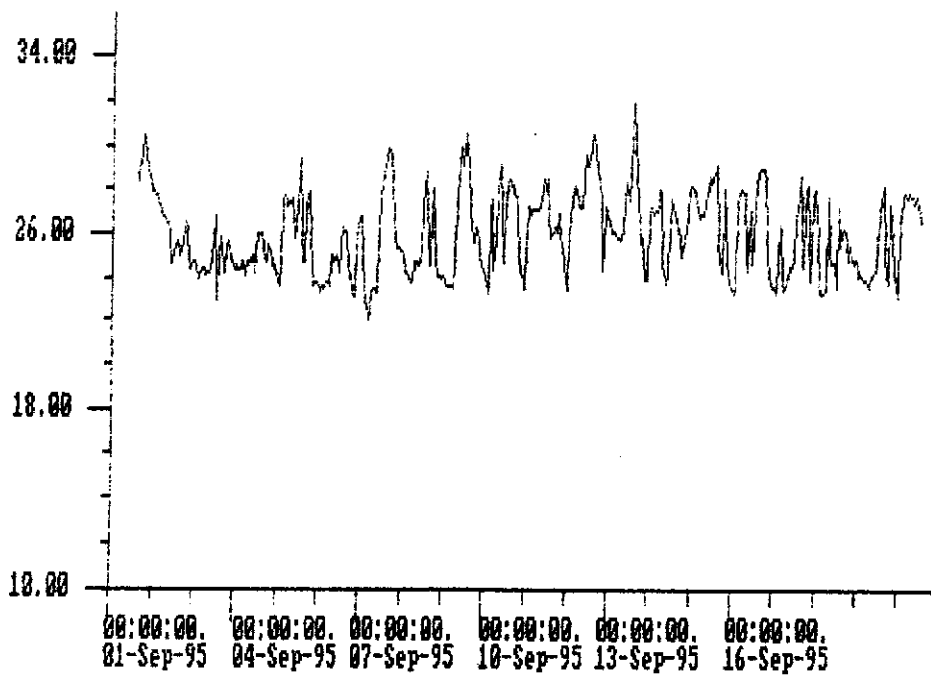


Figure 2.1 September temperatures after installation of the incubator

The procedures adopted were as follows. Adults were counted out from the maternity roost at dusk, until a five minute inactive period occurred. After this the roost was entered and all babies were counted, collected and placed into a pillow slip. They were taken to an adjacent roof space which was set up as a growth study workspace. It had tables, chairs, bench lamps and a permanently-ready photographic system. This consisted of a photographic enlarger base and stand to which a 35mm camera, with a ring-flash, was attached. The base had places for the juvenile's feet to hold onto, and a permanent scale adjacent to a large white reflective area. The white area was needed to improve the clarity of detail of the wing bones and blood vessels. This was found to be especially important as black pigmentation developed in the wings with age.

The camera shutter was controlled by a bellows unit, that was initiated by pressing with one foot. This allowed two free hands to handle the baby bat.

On each capture the young bat was treated as follows:

- it was ringed with a coded numbered ring if it was not already ringed;
- if very young, its precise appearance was recorded to assist in judging its initial age;
- it was sexed;
- it was weighed on an electronic balance to 0.1g accuracy
- the length of its radius was measured with dial callipers to an accuracy of  $\pm 0.1\text{mm}$ . This was only possible after the baby was about 3 days old.
- the right wing was photographed spread to full size alongside a scale, with the ring number and date recorded on sticky labels (recently both wings have been photographed) to allow the growth of all hand bones to be measured.

All data were written down by an assistant whilst processing continued as rapidly as possible. As only between 20 and 32 young have been born each summer since studies began, it has been possible to process all of them in less than 1.25 hours. This is much less than the time their mothers spend foraging after dusk during lactation of some 2.5 hours, as shown by radiotelemetry (Duvergé 1997; plus video data). Hence the mothers did not endure forced separation from their young, which might delay suckling. Baby bats were replaced into a second pillow slip until all had been processed. They were then returned to the breeding attic and recounted as they were replaced into the incubator, to ensure all had been returned.

The radius length, rather than the total length of the forearm was used, since the ulna projection beyond the end of the radius at the elbow varied in shape and length among adult individuals. By using the end of the radius, a constant and precise reference point was used, and in growth studies, measurement of a single bone is preferable to a combination of two overlapping bones.

Babies were initially ringed with coloured C-type aluminium rings, that were filed to remove any sharp edges and corners. They were ringed tightly enough to prevent the ring from slipping up the arm and restricting blood-flow through the forearm muscles. This was necessary as baby bats initially spend most of their time closely attached to their mothers in the 'head up' position when not suckling. This is because they suck on the posterior (false) nipples, which act as dummies, and these are located in the groin.



Once young grew to about 42mm radius length and began to spend increasingly longer periods detached from their mothers, the rings were replaced by flanged alloy rings issued by the Mammal Society. At this stage they were ringed loosely, with a 1.25 to 1.5mm gap in a manner used on older bats captured within hibernacula. Experience shows that ringing baby bats using these methods, even within an hour of birth, causes virtually no ring injuries either during growth or subsequently.

Early in the morning, on one occasion in July each summer when most young were less than 20 days old, the whole colony was captured in the breeding attic. Many attached mother/offspring pairs were caught on each occasion. Lactating females normally will only suckle their own young (e.g. Davis *et al.* 1968, Brown 1976, Brown *et al.* 1983), and have been experimentally shown to recognise them by scent and isolation calls (e.g. De Fanis & Jones, 1995). Furthermore, DNA studies support discriminate suckling (Bishop *et al.* 1992). Hence the capture of a mother/offspring pair, combined with ringing studies over years, permit the identification of matriline. The growth performance of a baby in relation to its mother's growth, could therefore be determined in many instances.

Early morning captures were repeated on at least two further occasions during the summer, once in August, and again in early September. This was essential to obtain data on body mass levels, final radius and digit 5 lengths, as well as survival data for juveniles after they began foraging, and it was no longer possible to catch the young within the attic after their mothers had left to forage. It is the ability to determine the ultimate growth state of all surviving marked young which makes this part of the study unique.

### *Assessing the age of young bats*

On several occasions young were observed being born during the hour before dusk exits. This was possible using a telephoto lens attached to an image intensifier with an infra-red light. Capture and examination of such a baby within an hour, showed it has a reddish-brown attached umbilical cord remnant, which may be up to 1.5cm long. The cord is flexible, and the ventral body surface is virtually bald and translucent, unlike the dorsal surface which is lightly furred. Because of the translucent state of the ventral surface, the internal organs show through as reddish-pink structures. Sometimes the remains of amniotic membranes can be seen stuck to the forearms, and a pinna may still be stuck onto the forehead.

Normally the forearm length (the radius is not yet visible, but can be estimated) is about 26.3mm long, and the body mass is about 6.3g (see Table 2). Slightly older babies, a few hours after birth, have a cord which becomes progressively drier, harder and a darker brown. Repeat capture a day later shows that the cord falls off a baby within 24 hours, initially leaving a moist red umbilical scar. This dries and darkens quickly, and the development of ventral fur soon obscures the internal organs.

Forearm length and body mass increase rapidly over the first few days to reach about 30mm and 8g at 3 days. By this time the radius can usually be clearly seen and measured. It is about 1mm shorter than forearm length at this stage. After this age the estimation of birth date by visual characters becomes increasingly difficult and less accurate. It is possible to estimate birth date for an older juvenile with a radius below 49mm (up to about 16 days old) to the nearest day by comparison with the regression line from known-age individuals, provided it has not been malnourished.

Once a juvenile bat is 30 days old, it usually cannot be captured after dusk, since it leaves the roost and starts to forage for itself. However, its skeletal growth is not yet complete. The radius may continue to increase in length up to 40 days of age, and some of the hand bones, such as digit 5, grow until 60 days. This means that a juvenile's foraging success may slightly influence its own radius growth, and significantly influence its finger growth.

After 60 days of age, increase in length of the bones ceases, and there is some evidence for a slight shrinkage as ossified tissue replaces cartilage. The bat remains the same skeletal length for the rest of its life.

### *Treatment of body mass and radius growth data*

Changes in body mass and radius length both show rapid changes with age. Mass changes are more erratic than radius changes, with occasional negative changes during periods of poor weather when foraging by mothers is likely to be severely reduced in both quantity (Ransome 1997b) and quality (Ransome 1996, 1977a). Radius length always increases, but its rate of increase varies considerably with the juvenile's age, and probably with its nutritional state. Early growth rate rises to a peak of about 2.0mm/day between 3 and 6 days after birth, then gradually declines to about 1mm/day between days 12 to 14, confirming observations by McOwat & Andrews (1994).

Three growth curve models are available to describe growth data. They are the logistic, Gompertz and von Bertalanffy models. Each provides 5 statistics, including asymptotic mass or radius length, a growth constant (k), and sums of squares of data points from the model line. The complete radius growth curve for a well-nourished juvenile greater horseshoe bat is best described by the logistic curve, in which the upper half is a mirror image of the lower half. The logistic curve was found to best describe the forearm growth of *Plecotus auritus* by De Fanis & Jones (1995), *Pipistrellus pipistrellus* by Hughes *et al.* (1995), and *Rhinolophus hipposideros* by Schofield (1996). The first two of these studies involved captive colonies, watered and fed *ad libitum*, and allowed free flight, and the last one free-living colonies.

Tuttle and Stevenson (1982) report published early growth rates as mean forearm growth in mm/day for a range of species over the first 14 days of life, since growth tends to be more or less linear during this period, and the young can easily be captured. Many estimates were based on small numbers of data which were extrapolated to day 14. Ransome (1990) followed this procedure in his comparison of the growth of young born to the same mothers in different years. Early growth rates calculated by this method, are very sensitive to estimates of birth time, and also the precise age of the juvenile when the last measurements are taken. These problems also affect the use of growth models. In field studies, because visits are usually made every 3 to 4 days, it is impossible to guarantee that every juvenile is measured immediately after birth and just before day 14. If the last capture is on day 11 or 12, and the line is extrapolated to day 14, the early growth rate estimate for that individual will be higher than for an identical juvenile which is captured on day 14.0. This happens because early growth rate in this species follows a rapidly declining curve.

To overcome this problem I adopted a different procedure. Between the age of 4 and 14 days, radius growth follows a curve which can be converted to a straight line by regressing the log of radius length on the log of the juvenile's age in days (DAGE). For individual juveniles with at least 3 data points, and usually 4, a correlation coefficient (r) of 0.999 is always achieved if body

mass changes are favourable. This corresponds to a P value <0.001, showing a very strong linear relationship exists.

The regression coefficient B (slope of the regression line) is considerably influenced by the radius estimate at the time of birth, which was outside the period which the log/log plot produced a straight line. To standardise the data so that it was comparable among individuals, I first calculated the regression line using my visual estimate of DAGE, using only data between 4 and 14 days. Then I made the radius length at birth 20.5mm ( $\log = 1.312 = A$  of the regression line) for all juveniles by adjusting the estimated time of birth to the nearest 0.1 of a day. I then took the antilog of B as the early growth rate of the juvenile between 4 and 14 days of age and adjusted it for the discrepancy between the size of the radius at birth and 20.5mm (5.0mm), to obtain the mean early growth rate according to this formula:

$$\text{Mean early growth rate} = ((\text{antilog } B \times 14) - 5.0\text{mm})/14$$

Mean early growth rate data generated from this formula are in mm/day for juveniles up to 14 days old. This method usually gives very close agreement between the estimated time of birth of newly-born babies from visual characteristics and those from these calculations. Using different estimates of radius size at birth decreases the r correlation coefficients generated by the log/log regressions in bats showing good growth. Furthermore the mean early growth rate data generated are very close to those produced by juveniles which were measured just after birth and almost exactly on day 14. Whenever there has been a serious disagreement between the two methods, it has been due to either an obvious premature birth (forearm <25.5mm; body mass usually below 5.5g), or a delayed birth. Of the two kinds of miss-match, the former is much more common, and is especially likely to happen in protracted periods of poor foraging weather, especially when births are late, as in 1996.

In this report all DAGE data obtained from Woodchester bats refers to estimated birth time based upon log regression calculations, since for most babies born during the study, accurate visual estimation was impossible. This was because of the gap of several days between visits.

When regressions involving mean early growth rate were carried out, F values, the probability values, and  $r^2$  percentages are all exactly the same whether B or the antilog of B was used, with or without the transformation described above. I used the transformed correction primarily to obtain data which can be more easily related to previously published data, such as that in the review by Tuttle and Stevenson (1982).

### ***Condition index calculation***

As soon as the radius becomes visible, and so is measurable, it is possible to calculate a condition index (Speakman & Racey 1986, Ransome 1995) throughout the growth period. This index has not been validated by direct measurements of body reserve levels, since to do so would require the deaths of the bats used to obtain data. However, it provides the only feasible measure of the body reserve state changes of a juvenile as it ages. The condition index is calculated by dividing the body mass by the radius length, and multiplying the result by 56mm. In effect it gives the body mass in grams, of a fully-grown, 56mm-radius bat. This is about the mean size of an adult female bat. Although the condition index of bats at the end of winter varies with female age, increasing by about 1g up to at least 3 years (Ransome 1995), within the same age group it probably provides a reasonable estimate of the body reserve state of a bat. It should only be calculated if

recent feeding has not taken place, and complicating factors such as pregnancy are not involved. It assumes that the radius skeletal growth is a reliable measure of body growth generally.

Since all juveniles up to 30 days of age were captured soon after dusk, they should all have been in a similar state with regard to suckling. Whether they are suckled just before their mothers depart is not clear. However, infra-red video surveillance shows frequent frenzied suckling immediately after mothers return from dusk foraging, but none prior to leaving.

### *Growth phases used*

For descriptive purposes and to facilitate certain statistical analyses I divided the growth of the young into 6 phases. They are described in Table 1.

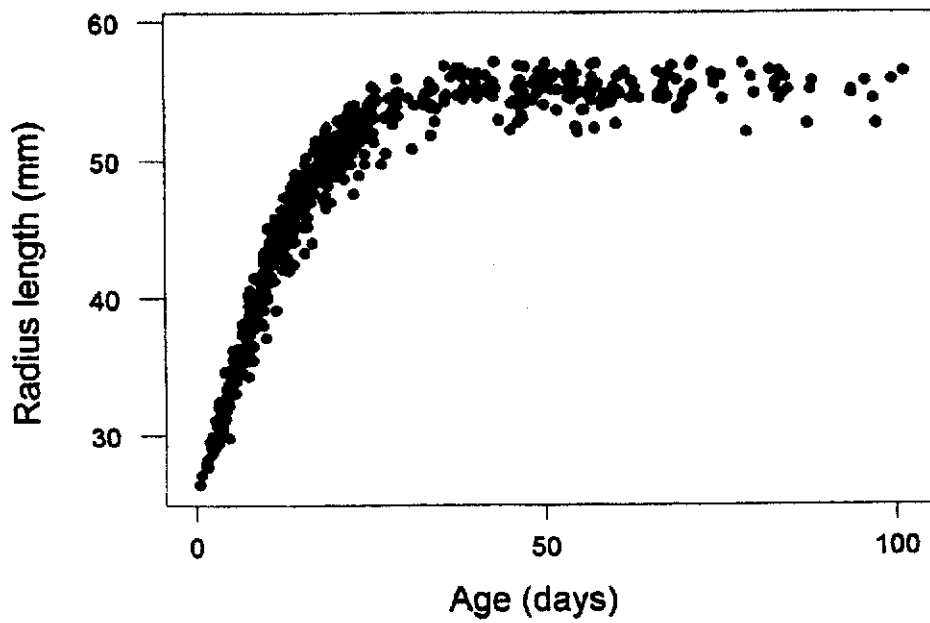
**Table 1. Description of growth phases used**

Growth phase	Age (days)	State	Flight ability	Food source
1	0 to 4.0	baby; rapid growth in mass and skeleton; no temperature control	none; stays still often hanging alone	mother's milk only
2	4.1 to 14.0	continued rapid growth in mass and skeleton; begin to temperature regulate; form creches	none; more active with flapping	mother's milk only
3	14.1 to 30.0	radius and mass growth slows; temperature regulate; explore attic and corridors	from limited to quite skilful inside building	mother's milk only
4	30.1 to 45.0	radius growth ending; cannot Doppler shift compensate	forage outside within 1 km of roost. Often perch to feed	milk plus slow flying insects such as <i>Ahodius</i> .
5	45.1 to 60.0	final growth of finger bones is completed; can Doppler shift compensate	extend foraging range to adult levels up to 4 km; learn hibernacula sites?	Insects only; can catch all insects eaten by adults
6	60.1 to 105	bones complete ossification; fat deposited for hibernation	learn and later occupy hibernacula	as above

Foraging distances are from Duvergé(1997).

Figure 3 shows the radius growth by sex over the 110 day period after birth that growth was studied. Growth is essentially similar in the two sexes, and shows an increasing spread of data with age, but females ultimately grow larger. In both sexes growth is always positive, slowing rapidly to reach a peak between 35 and 40 days of age. Figure 4 shows body mass changes with age by sex over the same period. It rises more slowly from an initial level of about 6.3g, and often shows brief periods of decline, followed usually by recovery. Mean levels peak around 50 DAGE, at about 20g. After this age it slightly decreases until about 70 days. Finally it rises rapidly as the hibernation period starts, rather than prior to it starting. In both sexes, as with radius length, mass change data spreads more widely with age. Females not only have larger skeletons, but are usually heavier as well.

### Radius length changes with age of male juveniles



### Radius length changes with age of female juveniles

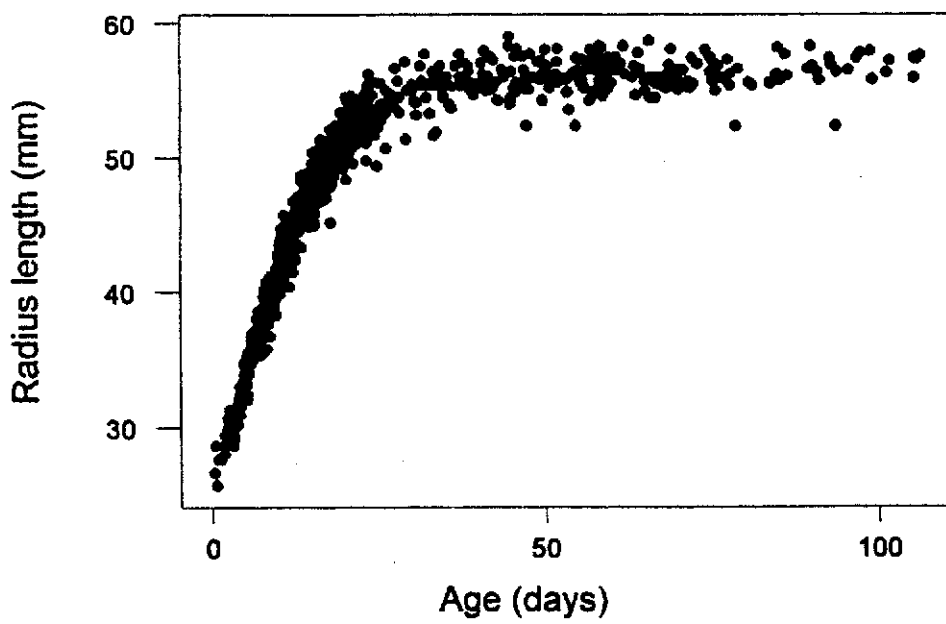
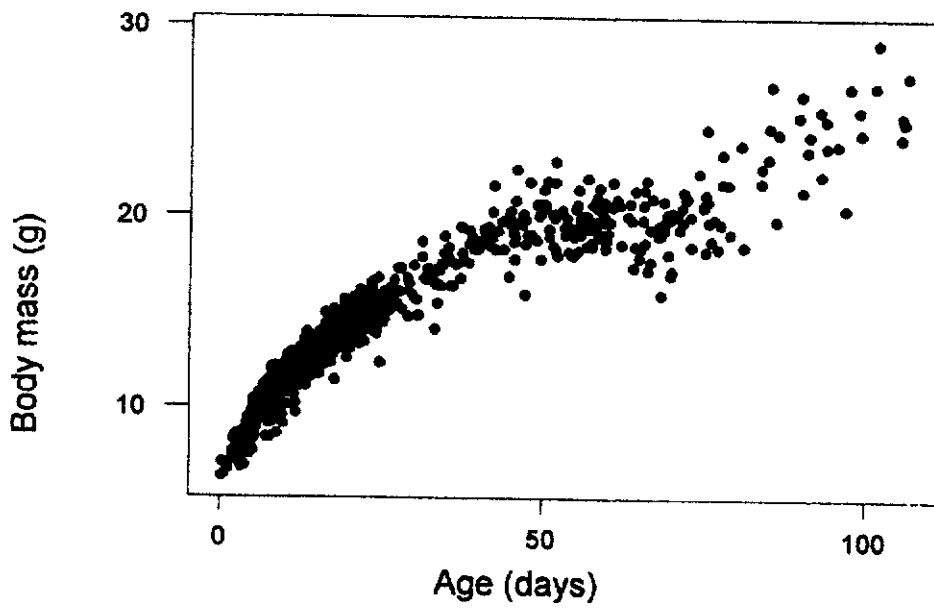


Figure 3. Radius length changes with age

### Body mass changes with age of female juveniles



### Body mass changes with age of male juveniles

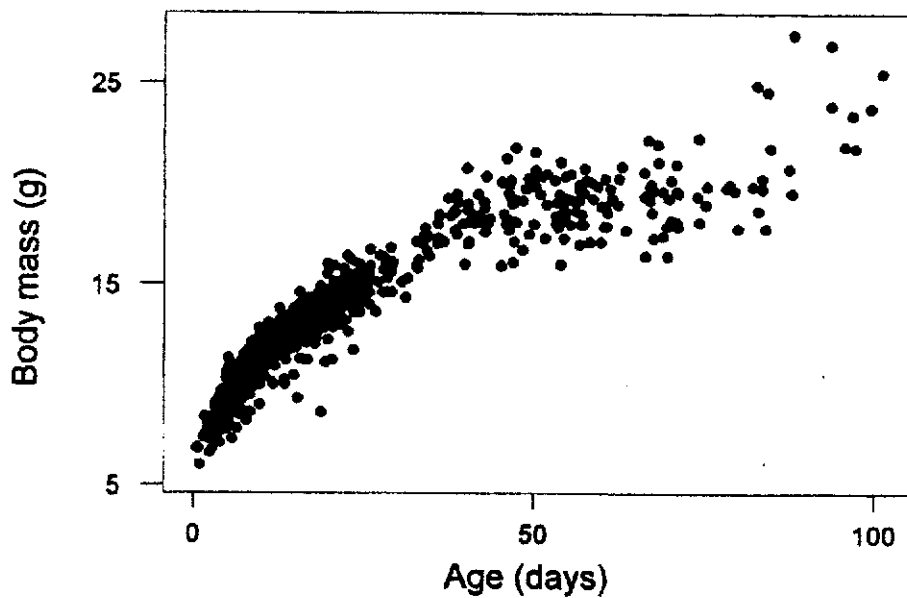


Figure 4. Body mass changes with age

### *Early mean condition during growth phases 2 and 3*

Plots of condition indices against DAGE for both male and female juveniles (Figure 5) show that condition normally rises rapidly from a mean of about 13.8g, but in a highly variable manner among individuals, during phase 1. A further rise takes place again late in phase 3, as radius growth slows, and through phase 4. Much later, well into phase 6, condition finally rises rapidly as fat is stored at the start of hibernation. There is a slight fall between 50 and 70 days, which is well after initial flight and foraging commences, and in fact takes place post weaning, just about the time when mother's abandon their young. They are then totally independent until the following spring.

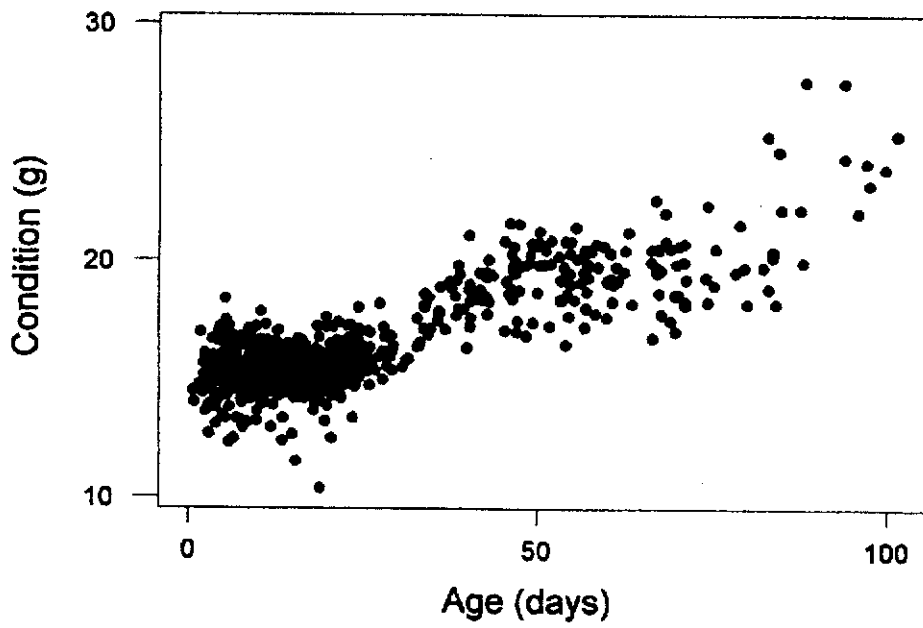
During phase 2 and most of phase 3, between the age of 4 and 24 days, there is usually no discernible pattern of condition change (Figure 6). Condition data points are widely spread between 14 and 17g, with a concentration between 15 and 16g. However, brief reductions in condition may occur in some juveniles during cold, wet or windy weather periods when their mothers do not feed successfully. These are usually very short-lived spells, and levels normally rapidly recover by the next capture. Early growth rates of juveniles were only measured between 4 and 14 DAGE, i.e. only in growth phase 2. If condition is only measured during this ten-day period, a maximum of only 3 estimates of condition can possibly be used to calculate a mean figure. A single low figure can therefore have a major distorting impact on the mean. By using data from both phases 2 and the early part of 3, up to 7, and usually at least 4 data points contribute to the mean figure. This makes the early mean condition index more reliable for use in statistical analyses of the impact of body condition upon final radius and digit 5 lengths.

### *Statistical calculations*

All calculations were made using Minitab v. 11.21, from data entered into a large spreadsheet. Each variable was checked for normality before carrying out parametric statistical tests. Before simple regression analysis, each data set was plotted as a scattergram to check linearity and even scatter of points around the line (Zar 1984, Fowler & Cohen 1992). Only one set of ultimate growth data, and other variables such as birth date, were used from each juvenile bat. However, size data from some of the mothers breeding at Woodchester were used more than once in certain regression analyses, as they produced several young over the study period. This meant that their data were not independent. Data from 41 of the 54 individual females were totally independent, as they were only used once in regressions for each sex. However, the use of single data sets from the other 13 mothers required the selection of randomly matched mother/offspring pairs. I carried out selections using random numbers and compared regressions with and without selection. As regressions using such selected data gave similar  $r^2$  values to those obtained without selection, the complete data sets were used in this report.

Analyses of data from bats found in most hibernacula were restricted to the birth years 1991 to 1996 inclusive, since complete data sets were only collected from 1991. This period was subdivided into 1991-1993, the four years during which Woodchester was not heated, and 1994-1996, the three years when heaters were present. However, in order to increase the number of different mothers in the sample, and also the number of years, data from 1989 to 1996 were used in regression analyses of growth at Woodchester.

### Condition changes with age of male juveniles



### Condition changes with age of female juveniles

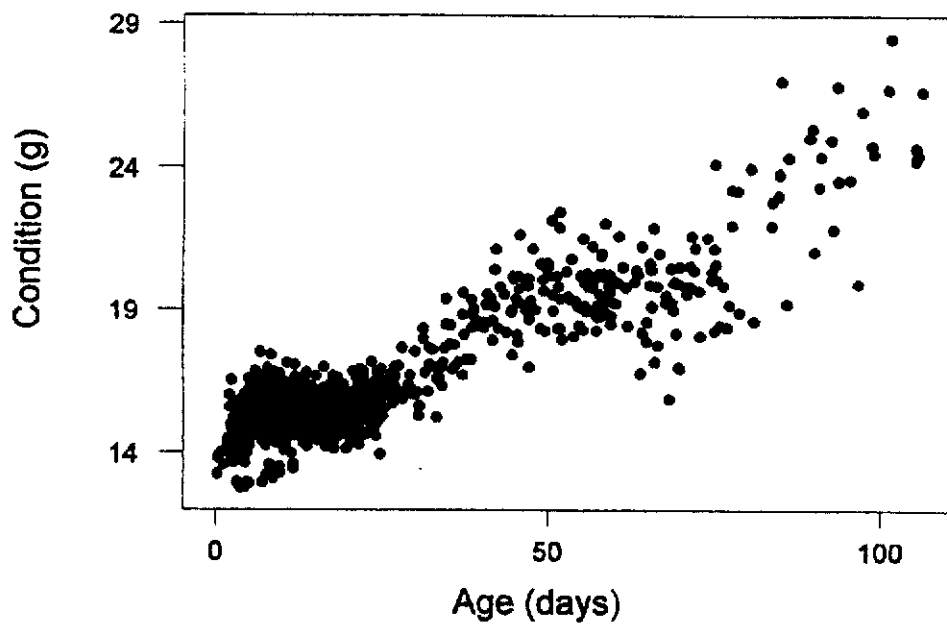
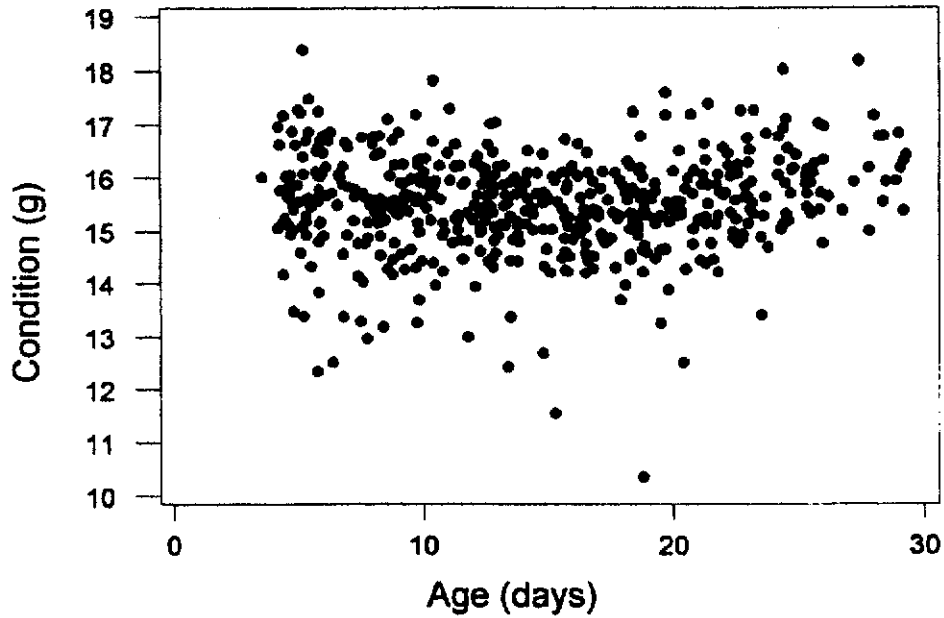


Figure 5. Condition changes with age.



Condition changes with age by males during growth phases 2 and 3



Condition changes with age by females during growth phases 2 and 3

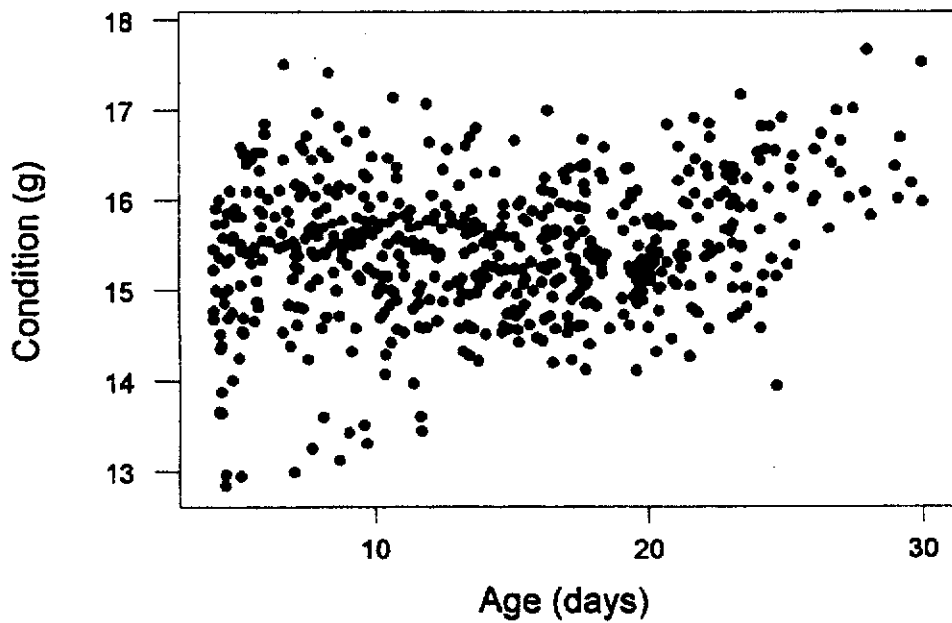


Figure 6. Condition changes with age during growth phases 2 and 3.

## Discussion

The best growth parameters available to assess juvenile growth will depend upon the circumstances of the investigation. If small numbers of juvenile bats can be repeatedly captured at 3 or 4 day intervals without causing too much disturbance, body mass, radius length and hand-bone length changes (from photographs) provide the most comprehensive growth data set. However, as only the bones show continuous increase with age, unlike the erratic mass and condition changes which often occur, radius length is the best, and most widely accepted reliable growth parameter (Kunz 1987). Radius length is preferable to digit 5 length because it is a single bone which is fairly easy to measure in the field, even before ossification occurs. Digit 5 requires greater skill in field conditions, and the extreme flexibility it shows before about 30 DAGE makes it almost impossible to measure. However, since digit 5s grow over a longer timespan, they may be more sensitive indicators of growth problems, reflecting the early foraging success of a juvenile, and any climate deterioration in late summer.

Burnett and Kunz (1982) used the length of the cartilaginous epiphyses of the metacarpal-phalangeal joint of the fourth digit, and found this measure (abbreviated to the 'total gap length') to be the most accurate measure for use in estimating the age of juvenile bats up to 50 days old. However, whilst this method is superior in predicting the age of older juveniles, it requires the use of a dissecting microscope with substage illumination and an ocular micrometer. It would also add considerably to the handling time of the juveniles. As my visits were very frequent, ageing the juveniles accurately was not a serious problem, and so this method was not used.

The collection of data in isolation is of little value, unless growth studies are linked to the factors which are likely to influence growth. These should include both the quantity and quality of food consumed by the mothers, and roost climatic conditions. Few studies at maternity sites have investigated these factors. This study only addresses the impact of roost conditions, although some data on diets are also held for future analysis.

Bats captured at hibernation sites include first-year individuals born in the previous summer. They can be recognised by their greyish fur and smoothly tapered finger joints from older animals, which have brownish fur, and knobbly joints. Regular capture and measurement of these first-year bats over years permits comparisons of the final growth achieved in different summers in different populations. The only feasible growth parameters which can reliably be measured in hibernacula are radius and digit 5 lengths. The photographic method has been tried but is too cumbersome for most underground sites. Furthermore, as it is quite time-consuming, it results in extended handling times if large numbers of bats are caught. Body mass and condition data are greatly influenced by fat deposition levels, and so cannot be used to assess growth.

We cannot, at present, be confident of the maternity site of origin for most juveniles captured in hibernacula, however. Therefore it is currently not possible to relate the growth measured to specific maternity roosts, and hence roost conditions.