NE REPORT No 292. Part II

Part 3: Results of growth studies at Woodchester

Introduction

Figures 3 to 6 show the changes of body mass, radius and condition for male and female juveniles separately from birth to 105 days of age. Data concentration falls with age for two reasons. First, juveniles become increasingly difficult to capture after they are able to fly. Second, mortality reduces their numbers, especially during growth phase 5, which follows weaning (Ransome 1990, and unpublished data), during which foraging range extension takes place (Duvergé, 1997).

These figures show that all parameters measured change in a similar manner in the two sexes. Body mass data during phases 1 to 3 are more widely scattered than are radius data. The radius data concentrate in a narrow band at birth (due to the method of age calculation used), but increasingly spread with age. The radius length peaks by 40 days, whereas body mass continues to rise until 50 days, then levels out before climbing steeply as hibernation starts. Condition data show a similar pattern, except that during phases 1 to 3 there are no discernible changes taking place because of the overlap of data points, so the details of changes during phases 2 and 3 are shown in Figure 6. The wide spread shown by the mass data, which may exceed 3g for two juveniles of the same age, suggests that a major factor in mass differences among the young at this age is the level of body reserves, rather than lean body mass.

How does growth differ between the sexes?

Table 2 compares various male and female growth parameters. It shows that around birth, at the start of growth phase 1, there are no significant differences between the sexes in their radius length, body mass or condition. The latter shows very low levels compared with those in growth phases 2 and 3.

Body reserve accumulation must therefore take place rapidly after birth, as shown by Kunz (1987) in his review of juvenile growth studies. However, females grow to a significantly larger radius and digit 5 size than males, and display faster mean early growth rates. Hence the nutritional demands upon the mothers of female young must be greater than those on the mothers of male young.

Mothers of female young have significantly larger radii than those having male young, and so are probably generally larger. Larger mothers may be better placed to cope with the additional demands of raising female young than smaller ones, and mothers of female young are expected to be more stressed during lactation than mothers of male young. They may be forced to forage for longer periods in order to consume more food, and produce more milk.

The sex growth differences between male and female young do not influence either their body condition or birth timing. These data for the two sexes are virtually identical.

Table 2. Comparison between male and female growth

Parameter	Male juveniles	Female juveniles	Significant difference?
New born babies' body mass (g)	6.36±0.37; 16	6.23±0.36; 16	t_{29}=0.99; P=0.33; No.
New born babies' condition (g)	13.88±0.84; 16	13.73±0.65; 16	t_{28}=0.56; P=0.58; No.
New born babies' radius length (mm)	25.69±0.84; 16	25.43±0.65; 16	t_{28} = 0.99; P=0.33; No.
Final radius length (mm)	**55.05±1.06; 85**	**56.06±1.16; 97**	**t_{179} = 6.14; P=0.0000; Yes**
Final digit 5 length (mm)	**71.41±1.54; 64**	**72.61±1.50; 76**	**t_{132} = 4.66; P=0.0000; Yes**
Early growth rate (mm/day)	**1.612±0.060; 92**	**1.639±0.055; 101**	**t_{184} = 3.16; P=0.0018; Yes**
Early mean condition (g)	15.49±0.77; 92	15.48 ±0.57; 102	t_{167} = 0.08; P=0.94; No
Birth date (days post June 1st)	40.3±8.1; 108	39.6±8.3; 112	t_{217} = 0.63; P=0.53; No
Mother's radius length (mm)	**55.96±0.942; 75**	**56.33±0.87; 82**	**t_{150} = 2.50; P=0.014; Yes**
Mother's digit 5 length (mm)	72.08±1.33mm; n=62	72.43 1.19; 65	t_{122} = 1.55; P=0.12; No

Data refer to the juveniles and their mothers from Woodchester which were measured in the summers from 1989 to 1996 inclusive, except for new born babies which only included 1990 to 1996.

New born babies were selected from 85 which had attached umbilical cords. Only data from those calculated to be within ±0.2 days of birth by log/log calculation (see text) were used. Radius lengths were adjusted by subtracting 0.8mm from forearm length measurements at birth, a similar proportion to the mean difference between the two (1.0mm) when the forearm reaches 31mm.

In columns 2 and 3 the data are mean, standard deviation and sample size respectively. Early mean condition derives from data obtained during growth phases 2 and 3 (see methods). Birth date is expressed as number of days from June 1st. Day 40 is July 10th.

In column 4 the statistics quoted derive from two-sample t tests (see Minitab reference manual) carried out at 95% significance levels; t is the test statistic and P is the significance level of the differences between male and female data.

Rows in bold type involve parameters showing significant differences.

Factors affecting the growth of male juveniles

Tables 3 & 4 summarise the significant statistical analyses carried out during the two periods of the study. First, 9 single linear regression analyses of final radius length and final digit 5 length on possible factors were performed on data obtained before heaters were installed. In addition to the 4 significant factors shown in table 3, regressions of mean early growth rate on birth date, radius length on birth date, digit 5 length on mother's digit 5, digit 5 and radius lengths on early mean condition were carried out. Mean early growth rate is the mean rate between 4 and 14 DAGE; early mean condition is the mean condition from data between 4 and 24 days (growth phases 2 and part of 3 - see above).

Next, the same analyses were repeated using data from the second period, after heater installation. This procedure should identify factors which consistently influence growth, and those that alter with higher, and more consistent ambient temperatures. Afterwards step-down multiple regression analyses were carried out to find the combination of factors which explained the most variation in the three growth parameters measured.

Single factor regressions before heater installation

Table 3 summarises the results of significant analyses. In order of importance, the significant factors which influenced radius length before heaters were used were: mean early growth rate of the radius; length of the mother's radius, and early mean condition. In regression equations 'length' is often omitted from 'radius length' and 'mother's radius length' to permit them to fit onto a single line for clarity. This also happened with digit 5 length in some equations.

Table 3. Statistics from significant single factor regressions on male parameters before heater installation

Regression	Sample size	P value (variable)	P value (constant)	F statistic	r^2 (%)
radius length on early growth rate	48	0.000	0.000	18.27	28.4
radius length on mother's radius length	35	0.013	0.010	6.97	17.4
radius length on early mean condition	48	0.020	0.000	5.83	11.3
early growth rate on early mean condition	54	0.003	0.000	9.42	15.3

F is the regression statistic. r^2 is the coefficient of determination.

Early growth rate is growth rate between 4 and 14 DAGE. Early mean condition is condition between 4 and 24 DAGE. See text for explanations.

Early mean condition had a significant influence upon the early growth rate. Digit 5 length was nearly significantly influenced by the mother's digit 5 length, but the sample size was rather small. Birth date had no significant impact upon any growth parameter measured. The closest it came to significance was in relation to early mean condition.

The equations for these significant regressions were as follows:

1. radius length = 40.9 + 8.86 mean early growth rate
2. radius length = 28.1 + 0.438 mother's radius length
3. radius length = 47.1 + 0.508 early mean condition
4. mean early growth rate = 1.05 + 0.0351 early mean condition

Multiple regressions before heater installation

Step-down multiple regression analysis of radius length on six possible factors (mother's radius length, mother's digit 5 length, mother's age, early growth rate, early mean condition and birth date), showed that male radius length was most influenced by the mother's radius length, its early growth rate and its early mean condition. The equation generated was:

5. radius length = 6.44 + 0.517mother's radius + 6.84growth rate + 0.55condition.

This equation explained 57.5% of the observed variation. (F=16.32; P=0.000)

The two most important factors in combination, and their equation was as follows:

6. radius length = 17.7 + 0.382mother's radius length + 9.87early growth rate

This equation explained 49.1% of the observed variation. (F = 17.37; P = 0.000)

Step-down multiple regression analysis of early growth rate on five factors (birth date, mother's radius length, mother's digit 5 length, mother's age and early mean condition) showed that variation in male early growth rate without heaters was best explained by early mean condition, birth date and the mother's radius length. The equation generated was:

7. growth rate = 0.338 - 0.00295birth date + 0.015mother's radius + 0.0345condition

These factors explained 31.6% of the variation. (F=6.69; P=0.001)

Birth date and mother's radius length explained the most variation in dual combination. The equation was:

8. mean early growth rate = 1.41 - 0.00404birth date + 0.00647mother's radius

This equation explained 20.6% of the variation. (F=5.81; P=0.007)

Single factor regressions after heater installation

Table 4 summarises the analyses carried out. As in the period without heaters, early growth rate remains the most important single factor. It explains a similar proportion of the variation. The mother's radius length remains the second most important factor affecting final radius length. However, mean body condition was no longer a significant factor influencing either radius length, or early growth rate. Although digit 5 was not quite significantly affected by the mother's digit 5 length, it was very nearly so as previously.

Table 4. Statistics from significant single factor regressions on male parameters after heater installation

Regression	Sample size	P (variable)	P (constant)	F statistic	r^2 (%)
radius length on early growth rate	32	0.002	0.000	12.04	28.6
radius length on mother's radius length	30	0.021	0.041	5.95	17.5

F is the regression statistic. r^2 is the coefficient of determination.

Early growth rate is growth rate between 4 and 14 DAGE. Early mean condition is condition between 4 and 24 DAGE. See text for explanations.

The equations for the other significant regressions are as follows:

9. radius length = 35.5 + 11.8mean early growth rate

10. radius length = 25.7 + 0.52 6mother's radius

Equations 9 and 10 should be compared with 1 and 2 from the first period. In both cases the impact of the variable has increased with the higher ambient temperatures produced by the incubator. These are the two partly heritable factors which influenced the radius length of males before heaters were installed. The other two (mainly environmental) factors, early mean condition and birth date, were no longer significant factors. This suggests that the heaters were important in removing their effects.

Multiple regressions after heater installation

Step-down multiple regression analysis using the same six factors as previously, showed that male radius length in the heated attic was highly influenced by mean early growth rate combined with the mother's digit 5 length. The addition of other factors did not increase the percentage of the variation in radius length which was explained. The equation generated was:

11. radius length = -8.7 + 0.547mother's digit 5 + 14.8mean early growth rate

These two factors together accounted for 54.1% of the observed variation. (F=16.32; P=0.000)

Step-down multiple regression analysis of early growth rate on the same five factors as previously, showed that none of them significantly influenced early growth rate in any combination. Heaters seem to remove the impact of many of the environmental growth constraints studied.

Summary for males

Before heaters were installed the three factors which separately and in combination explained the greatest variation in male radius length were mean early growth rate, mother's radius length and early mean condition. The first two of these are likely to be at least partly heritable, and the last one is probably partly environmentally controlled via food availability. Taken together the maximum level of variation in male radius length explained is 57.5%. Hence other factors, which were not assessed, also have important effects on the final growth achieved without heaters. They may well include dietary factors.

Heater installation reduced the impact of early mean condition upon male radius length and mean early growth rate. The energetic economies gained by higher roost ambient temperatures failed to alter body condition levels, which remained stable at similar levels in both sexes (t tests, both N.S.).

Of the factors investigated, only mean early growth rate and the mother's radius length exert significant influences. The percentage of variation in radius length explained by these two factors did not change with heating regime changes.

Factors affecting the growth of female juveniles

The same regression calculations were carried out separately on data from female juveniles in the two periods.

Single factor regressions before heater installation

Table 5 summarises the results of the significant analyses carried out. In order of importance, the factors which influenced female radius length before heaters were fitted were early growth rate, length of the mother's radius, and birth date. Large females that gave birth early in the season produced female young that grew rapidly and achieved large size, and vice versa. Although early mean condition had no significant effect upon radius length, it was just a significant influence upon early growth rate. Digit 5 length of females was significantly influenced by the mother's digit 5 length. In males it was nearly so, but regressions were not quite significant either with, or without, heaters.

Table 5. Statistics from significant single factor regressions on female parameters before heater installation

Regression	Sample size	P (variable)	P (constant)	F statistic	r^2 %
radius length on early growth rate	58	0.000	0.000	44.95	44.5
radius length on mother's radius length	47	0.001	0.031	13.43	23.0
radius length on birth date	58	0.004	0.000	8.18	13.5
early growth rate on birth date	60	0.001	0.000	11.49	16.5
early growth rate on early mean condition	60	0.017	0.000	6.03	9.4
digit 5 length on mother's digit 5 length	22	0.014	0.074	7.18	26.4

F is the regression statistic. r^2 is the coefficient of determination.

Early growth rate is growth rate between 4 and 14 DAGE. Early mean condition is condition between 4 and 24 DAGE. See text for explanations.

As well as digit 5 length, radius length was also influenced by the mother's radius length. Taken together, these regressions show that the early growth rate of female juveniles is more strongly influenced by female inheritance than that of the males. The early mean condition had no significant effect upon the digit 5 lengths of either sex. Birth date had a significant effect upon both radius length, and early growth rate, reducing both with later births.

The equations for these significant regressions are as follows:

12. radius length = 31.8 + 14.8early growth rate

13. radius length = 21.1 + 0.615mother's radius length

14. radius length = 57.4 - 0.0397birth date

15. early growth rate = 1.70 - 0.00199birth date

16. early growth rate = 1.26 + 0.0229early mean condition

17. digit 5 length = 29.9 + 0.586mother's digit 5 length

Multiple regressions before heater installation

Step-down multiple regression analysis, using the same six factors as in males, showed that female radius length was most influenced by early growth rate and the mother's radius length. Additional factors did not increase the level of variation explained. The equation generated was:

18. radius length = 14.5 + 0.348mother's radius length + 13.4early growth rate

This equation explained 49.3% of the variation in the female data. (F=23.32; P=0.000). A similar percentage was explained by the same factors in males (49.1%).

Step-down multiple regression analysis of early growth rate on the same five factors as for males, showed that early growth rate was most influenced by birth date, the mother's radius length and early mean condition. The equation generated was:

19. growth rate = 0.550-0.00236birth date + 0.0153mother's radius + 0.0200condition

This equation explained 36.3% of the variation in early growth rate. (F=10.11; P=0.000). For males the figure was 31.6%.

Birth date and mother's radius length explained the most variation in dual combination, as in males. However, these factors explained a higher proportion of the female early growth rate variation. The equation was:

20. early growth rate = 0.876 - 0.00236birth date + 0.0153mother's radius

This equation explained 30.2% of the variation. (F=11.38; P=0.000) For males it was 20.6% for the same two factors.

Single factor regressions after heater installation

Table 6 summarises the results of the analyses carried out. In order of importance, the significant factors which still influenced female radius length after heaters were used were early growth rate and the mother's radius length. The effect of birth date was reduced to a very low level. Early mean condition was also no longer a significant factor on radius length, although it remained a significant influence upon the early growth rate, and so is potentially important. Female digit 5 length was highly influenced by the mother's digit 5 length, even more so than in males, but not by the early mean condition. This was also true of males.

Table 6. Statistics from significant single factor regressions on female parameters after heater installation

Regression	Sample size	P (variable)	P (constant)	F statistic	r2 (%)
radius length on early growth rate	36	0.000	0.000	28.29	45.4
radius length on mother's radius length	29	0.020	0.090	6.16	18.6
early growth rate on early mean condition	41	0.036	0.000	4.72	10.8
digit 5 length on mother's digit 5 length	24	0.000	0.361	22.66	50.7

F is the regression statistic. r^2 is the coefficient of determination.

Early growth rate is growth rate between 4 and 14 DAGE. Early mean condition is condition between 4 and 24 DAGE. See text for explanations.

The equations for these significant regressions are as follows:

21. radius length = 25.8 + 15.0mean early growth rate

22. radius length = 23.4 + 0.586mother's radius length

23. early growth rate = 1.52 + 0.0350early mean condition

24. digit 5 length = 12.0 + 0.839mother's digit 5 length

Multiple regressions after heater installation

Step-down multiple regression analyses of female final radius length on the same six factors as previously, showed that female radius length was primarily influenced by early growth rate. The mother's radius length also has a small influence. The equation generated is:

25. radius length = 13.6 + 0.209mother's radius length + 15.2early growth rate

This equation explains 45.1% of the observed variation in radius length, only slightly above the level explained by early growth rate alone (43.8%). This indicates that the impact of the other factors which were significant in single-factor analyses, operate via growth rate. Certainly the installation of heaters increased the effect of early growth rate on her young's radius length. This situation applied to males as well.

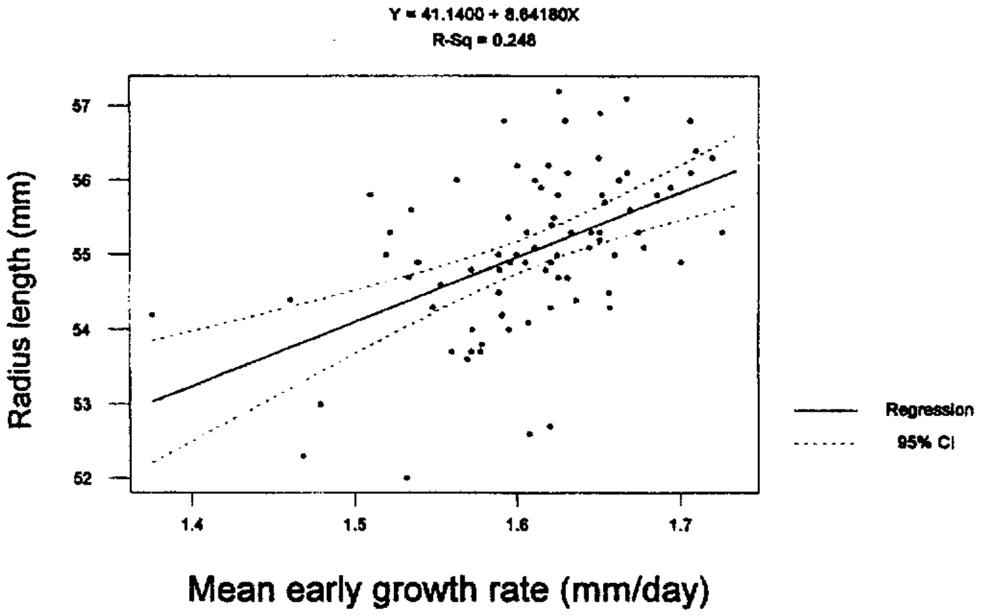
Summary for females

Before heaters were installed, two of the same factors that influenced male radius length also affected female radius length. They were mean early growth rate (see Figure 7) and mother's radius length (see Figure 8). However, these factors explained a much higher percentage of the variation in females, and only in females was digit 5 length affected by the mother's digit 5 length (Figure 9). An additional significant factor in females was birth date, with later births leading to smaller radius length. The cause of the smaller radius lengths was probably the reduced mean early growth rate, which also fell with birth date, as well as early mean condition. These effects are consistent with the view that female growth is more demanding than male growth, and therefore that stressful environmental conditions will have a greater impact upon female growth.

After heater installation the same factors influenced radius length and early growth rate of females as were discovered during the period before heater installation, with the exception of birth date. The impact of birth date upon radius length, early growth rate and digit 5 length was reduced to levels just below significance.

This is consistent with the prediction that the growth penalty paid by late births in an unheated roost will be considerably reduced by the provision of stable high temperatures. The energetic economies gained should free nutrients to promote mean early growth rates, once body condition levels are satisfied. Alternatively if foraging success gained by the mother is poor for a long enough period, and milk supplies are interrupted, torpor at high ambient temperatures is likely to permit faster growth than that at low ambient temperatures. Of the factors investigated, only early growth rate and the mother's radius length exert significant influences. The percentage of variation in radius length explained by these two factors did not change much with heating regime changes. However, the impact of the mother's digit 5 length upon that of her young increased considerably, nearly doubling.

Regression of male radius length on early growth rate



Regression of female radius length on early growth rate

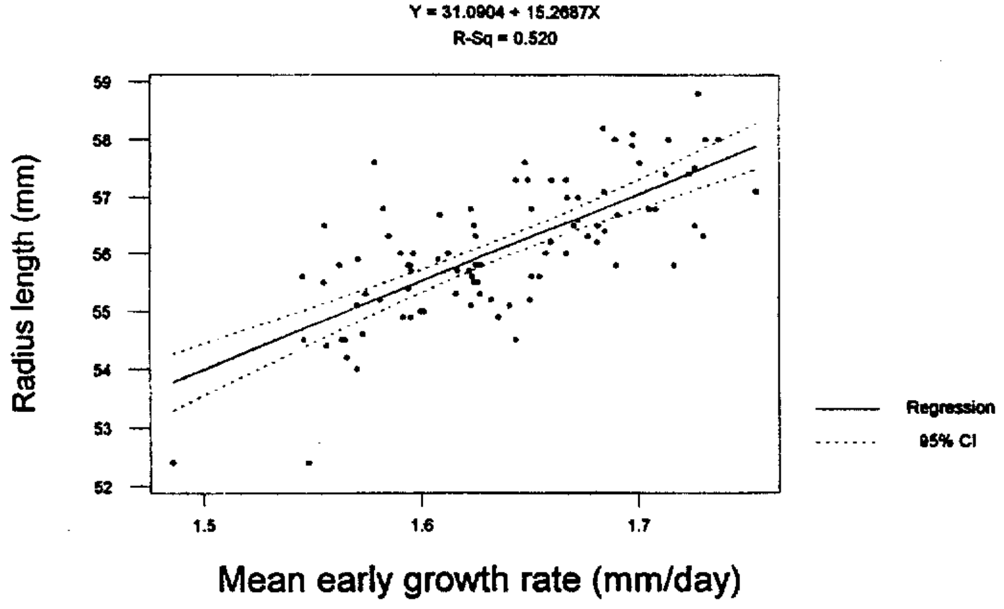
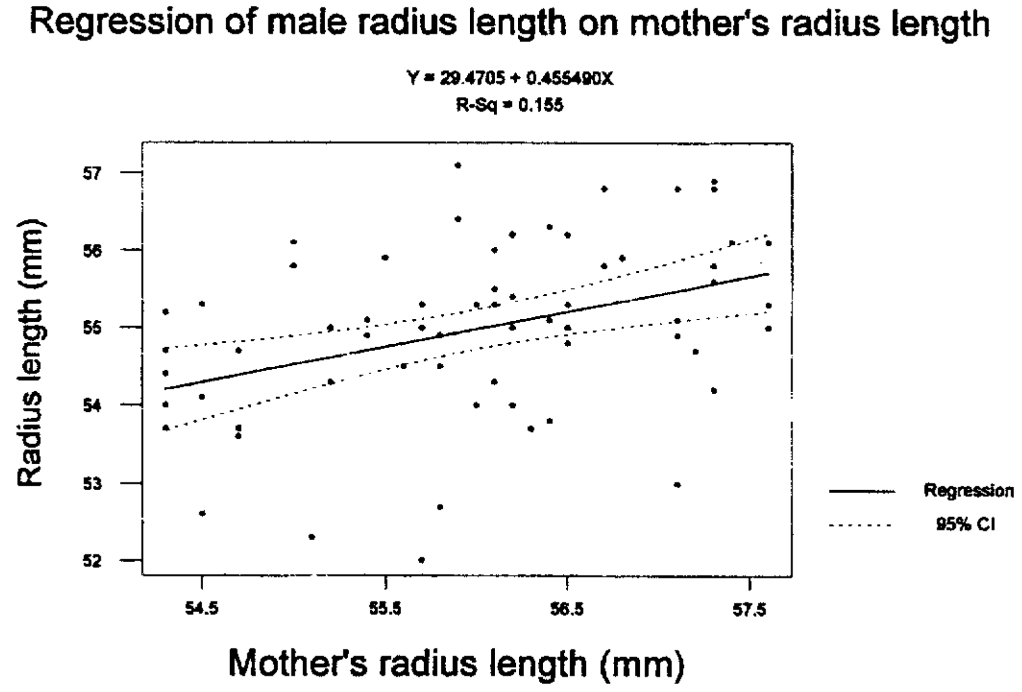


Figure 7. Regression of final radius length on early growth rate



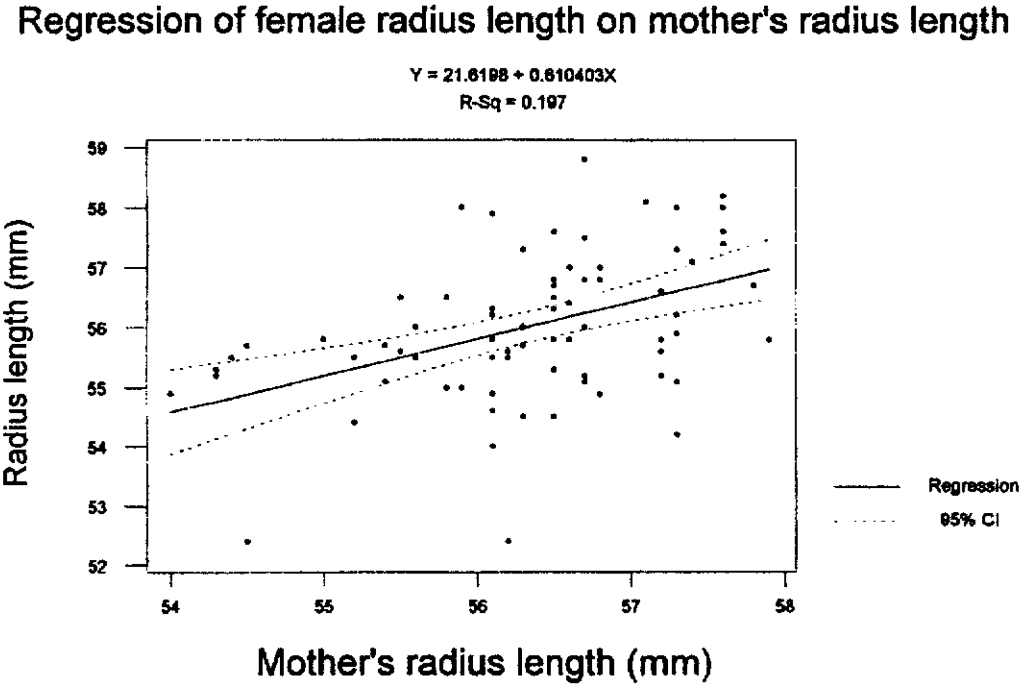


Figure 8. Regression of final radius length on mother's radius length

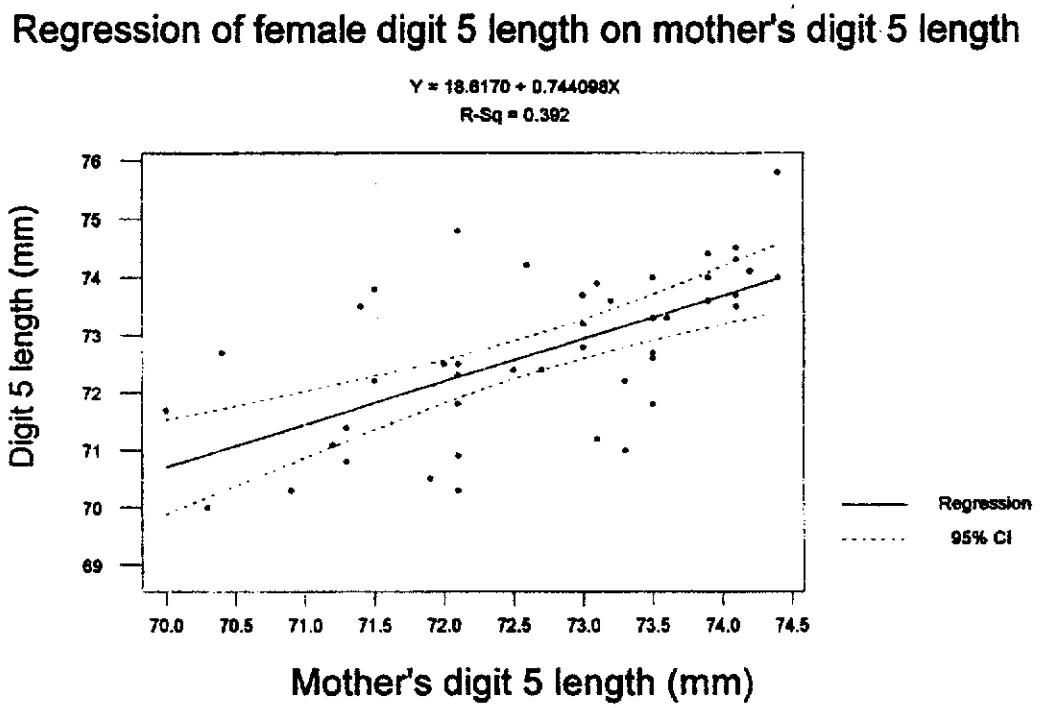


Figure 9. Regression of female digit 5 length on mother's digit 5 length

Summary for both sexes

The best judge of skeletal growth of the parameters measured is radius length. It can be accurately measured in the hand, using bats from a few days old up to adult status, permitting the calculation of its early growth rate. Digit 5 length can only be measured in the hand once the finger bones have stiffened sufficiently by the age of about 60 days. The photographic procedure described can be used to obtain data in younger bats. However, the curvature in the digit, produced by stretching the wing into its extended position, introduces measuring errors into the data obtained.

If known-age young are caught for radius growth measurement, they should also be weighed at the same time. Although body mass on its own is a poor guide to growth because of unknown body reserve levels, it permits the calculation of body condition. This can be compared with figures 5 and 6 to assess the nutritional state of samples, or individuals.

Radius length is primarily affected by mean early growth rate, and secondarily by the mother's own radius length. The former has been shown to be affected by juvenile early mean body condition which seems to be at least partly influenced by the weather conditions operating when its mother forages. Mean early growth rate peaks at about day 4, when the mothers tissues may contribute to her food consumption, to provide extra nutrients. These are needed to sustain both the rapid growth rate, and the deposition of fat in the baby after birth (see discussions in Part 1). Growth rate falls slowly with age, but the decline accelerates when condition falls below 14g. However, above about 14.5g a further rise seems not to be beneficial. It may merely reflect individual differences in the level of allocated reserves. Some juveniles have survived levels below 12g for very short periods, so 14.5g may represent a fairly safe reserve level during summer.

During phases 2 and part of 3, between the age of 4 and 24 days, there is usually no discernible pattern of change in condition (see Figure 6). As the radius and other bones are rapidly growing during this period, presumably juveniles possess an internal mechanism which normally allocates nutrients from its milk supply between the maintenance of stable body reserve levels, and sustaining appropriate rates of skeletal growth. The latter seems to be genetically controlled. If this is correct, any serious reduction of milk supply levels from the mother, whatever the cause, is expected to be reflected in reduced early growth rates, and condition. This is what happens periodically, and often erratically, during the life-histories of many individual juveniles, and is normally followed by a rapid recovery of condition and growth rate. Such episodes are usually associated with short-term poor weather conditions for foraging by mothers (Ransome 1997b). If prolonged, poor foraging during lactation has a permanent growth reduction effect in the young.

The installation of heaters greatly reduced the effect of mean early condition upon early growth rate and radius length of males, so that the relationships were no longer significant.

Heaters had a different impact upon female early growth rate and radius length. Prior to installation both were affected by birth date, being reduced by later births as found by Ransome (1989). Lower early mean body condition, lower ambient temperatures and reduced food consumption by mothers and/or young are all predicted to reduce early growth rates in young, particularly those born later in the summer which complete their growth late in September. Hence without separate assessment of these factors simultaneously, we cannot currently be sure which factor, or combination of factors is most important.

Mean early growth rate and mother's radius length were identified as the two major, and most consistent factors influencing the final radius length of both male and female juvenile bats. Of the two, early growth rate is the most important, and in the period with heaters, early growth rate improved in both sexes compared with the preheating period. Together early growth rate and mother's radius length explained between 45 and 49 percent of the observed variation in multiple factor regression analyses. This leaves over 50 percent of the variation still to be explained by other factors, including aspects of food consumption by both the mother and her young.

Ultimate radius and digit 5 lengths are highly correlated, but not directly related to each other (Pearson correlation coefficients: males=0.801, n=62; r^2= 64.2%; females=0.726, n=76, r^2=52.7%). Radius mean early growth rate was the most important single factor affecting ultimate radius length in regressions (Tables 3 to 6, males: r^2 = 28.4% & 28.6%; females: r^2=44.5% & 45.4% respectively before and after heaters were installed). Radius mean early growth rate is also correlated with the ultimate digit 5 length of both male and female young. (Pearson correlation coefficients: males=0.367, n=62, r^2=13.5%; females=0.565, n=76, r^2=31.9%). The lower r^2 values suggest that other factors modify the impact of early growth rate on the ultimate digit 5 lengths of both sexes. This may be due to the longer period of growth involved of digit 5 lengths (60 days) compared with the radius (40 days).

Overall, these considerations are consistent with the following hypotheses:

a. that higher ambient temperatures reduce the costs of thermoregulation by both a mother and her young, and so allow greater milk production by the former, and a faster early growth rate by the latter, since early growth rate is normally resource limited. This assumes that food quality and quantity consumed by the mother remain unchanged;

b. that in the presence of consistently high ambient roost temperatures, early growth rate is normally resource limited, probably via the quality and/or quantity of the mother's food consumption. These aspects are influenced by factors such as climatic conditions during foraging, habitat quality within the roost sustenance zone (Ransome 1996, 1997a, 1997b), photoperiodic effects upon the lengths of the mother's foraging opportunities, and her flight and ultrasonic capabilities. The latter is likely to be at least partly age-related (Jones & Ransome 1993);

c. that bats have a fuel gauge which is used to allocate nutrients to maintain a certain level of body condition appropriate to their current and future energetic needs, in competition with other demands, such as lactation and growth. At low levels of nutrient intake, as the body reserves of both the mother and her young begin to fall below the appropriate level, growth rate is also reduced.

Part 4: How did heaters affect the final growth and survival of bats born at Woodchester?

Introduction

The hypotheses made in Part 3 provide a mechanism which can be used to predict and explain changes in the ultimate growth parameters of bats. Tables 7 and 8 summarise data from the significant analyses carried out.

Table 7. Statistical data showing significant effects of heaters upon male juvenile growth

Parameter	Male juveniles without heaters	Male juveniles with heaters	t test results
Early growth rate (mm/day)	1.593±0.058; 54	1.639±0.053; 38	t_{83}=3.96; P=0.0002
Mother's radius length (mm)	56.19±0.91; 39	55.72±0.93; 36	t_{72}=2.24; P=0.028
Mother's digit 5 length (mm)	72.50±1.48; 28	71.74±1.09; 34	t_{48}=2.26; P=0.028

Data refer to the juveniles and their mothers measured in the summers from 1989 to 1993 without heaters, and 1994 to 1996 with heaters. Years in both periods are inclusive.

In columns 2 and 3 the data are mean, standard deviation and sample size in that order. In column 4 the statistics quoted derive from two-sample t tests (see Minitab reference manual) carried out at 95% significance levels; t is the test statistic; and P is the significance level of the differences between data sets.

Table 8. Statistical data showing significant effects of heaters upon female juvenile growth

Parameter	Female juveniles without heaters	Female juveniles with heaters	t test results
Final radius length (mm)	55.7±41.01; 58	56.54±1.21; 39	t_{71}=3.41; P=0.0011
Early growth rate (mm/day)	1.617±0.046; 60	1.670±0.054; 41	t_{76}=5.09; P=0.0000

Data refer to the juveniles and their mothers measured in the summers from 1989 to 1993 without heaters, and 1994 to 1996 with heaters. Years in both periods are inclusive.

In columns 2 and 3 the data are mean, standard deviation and sample size in that order. In column 4 the statistics quoted derive from two-sample t tests (see Minitab reference manual) carried out at 95% significance levels; t is the test statistic; and P is the significance level of the differences between data sets.

Data relevant to male juvenile growth

The two main ultimate growth parameters measured for males, radius and digit 5 lengths, showed no increase with the presence of heaters. Mean radius length remained virtually the same, and mean digit 5 length actually fell, though not significantly. The two factors which were shown to be important determinants of radius length above, were the early growth rate of juvenile males, which increased significantly, and the size of their mothers, which decreased significantly. As these effects oppose each other, they are assumed to explain the absence of a change in the size of male radius length in the presence of heaters. Similarly, the digit 5 lengths of the mothers after heaters were installed were shorter, and this may explain the slightly smaller digit 5 lengths of males born after heaters were installed.

Data relevant to female juvenile growth

The mean radius length of female young increased significantly after heaters were installed (Table 8). Only one significant difference in a relevant growth factor was discovered that relates to the ultimate size of the female radius. It was early growth rate. This factor was shown to be the most important single determinant of radius length in single-factor regression analyses above. The early growth rate of juvenile females increased significantly, as did that of the males. However, unlike the situation for males, the size of the radius of their mothers did not fall, so the size of the female radius' length increased significantly in the presence of heaters. The digit 5 lengths of the mothers after heaters were installed were slightly larger. Despite this, and surprisingly so, a significant increase in the digit 5 lengths of females born after heaters were installed was not recorded.

What was the impact of heaters upon juvenile survival rates?

Since the incubator system has only been installed since the summer of 1994, it is only possible to carry out a simple analysis of survival rates before and after their installation. I divided each sex into two groups, those that survived at least for one year, and those that died within a year of birth. Absence from the Woodchester breeding attic in its second summer is normally proof of a bat's death (Ransome 1995).

Tables 9 and 10 summarise the basic data obtained for the 5 years before heaters were installed, and the 3 years afterwards. Since mean birth date has a major impact upon the long term survival of juvenile cohorts from unheated roosts (Ransome 1989), I have included the mean of mean birth date for comparison. As the 3-year period after heater installation showed slightly later birth dates overall, we expect a slightly lower survival rate. Although the opposite effect is indicated by these two tables, chi-square tests on the effect of heaters on survival data for the two sexes separately showed no significant differences exist between the two periods (P=0.923 for male data; P=0.257 for female data). Sample sizes are currently too small to show up clear changes in survival rates, but the trend in female survival rates is encouraging.

Table 9. Survival of young born at Woodchester by sex for the 5 years before heaters were installed

Year of birth	MALES		FEMALES	
1989	11	5	12	6
1990	14	9	12	3
1991	12	5	14	5
1992	11	3	11	5
1993	13	3	10	4
TOTALS	61	25 = 41.0% survivors	59	23 = 39.0% survivors

In each of columns 2 and 3 the first figure is the number of births, and the second, the number of survivors for at least a year.

Mean of mean birth date for these years was 38.2, or 8th July.

Table 10. Survival of young born at Woodchester by sex for the 3 years after heaters were installed

Year of birth	MALES		FEMALES	
1994	11	4	14	8
1995	13	7	16	8
1996	16	6	15	10
TOTALS	40	17 = 42.5% survivors	45	26 = 57.8% of survivors

Data refer to the juveniles and their mothers measured in the summers from 1989 to 1993 without heaters, and 1994 to 1996 with heaters. Years in both periods are inclusive.

In columns 2 and 3 the data are mean, standard deviation and sample size in that order. In column 4 the statistics quoted derive from two-sample t tests (see Minitab reference manual) carried out at 95% significance levels; t is the test statistic; and P is the significance level of the differences between data sets.

Mean of mean birth date for these years was 40.4, or 10th July.

How did radius length affect the survival of bats over the first few years of life

Tables 11 and 12 compare the radius lengths of survivors and non-survivors for the two sexes separately. All data refer to years without heaters for bats which achieved full radius size. In both cases, between birth and age 1 year, survivors had significantly larger radii than non-survivors, showing a mean difference of about 0.6mm. Subsequently, radius size differences were not significant, with only a slight increase in mean size evident with extra years of survival.

Table 11. Radius lengths of female bats by survival over the first 4 years

Years of survival	Radius length of survivors	Radius length of non-survivors	t test results
0 to 1	**56.00±1.01; 108**	**55.38±1.33; 109**	**t_{201}=3.89; P=0.0001**
1 to 2	56.02±0.98; 85	55.95±1.16; 23	t_{30}=0.27; P=0.79; No
2 to 3	56.05±1.01; 66	55.92±0.88; 19	t_{32}=0.53; P=0.60; No
3 to 4	56.06±1.01; 59	55.97±1.04; 7	t_{7}=0.20; P=0.84; No

Data from birth years 1979 to 1993 from Woodchester and Stroud hibernacula only. Survival of females can reliably be determined from returns to the maternity site. All years without heaters.

Bold type indicates significant differences between data sets.

Table 12. Radius lengths of male bats by survival over the first 3 years

Years of survival	Radius length of survivors	Radius length of non-survivors	t test results
0 to 1	**55.09±1.17; 112**	**54.51±1.27; 113**	**t_{221}=3.55; P=0.0005**
1 to 2	55.17±1.14; 76	54.91±1.24; 36	t_{63}=1.10; P=0.28; No
2 to 3	55.19±1.20; 58	55.11±0.91; 18	t_{37}=0.34; P=0.74; No

Data from birth years 1979 to 1993 from Woodchester and Stroud hibernacula only. Survival of males can only reliably be determined for these years since they fail to return to the maternity site, and disperse widely once sexually mature, often to unknown hibernacula. All years without heaters.

Bold type indicates significant differences between data sets.

These data indicate that smaller, growth-stressed, bats of both sexes are less likely to survive than larger ones. The bulk of mortality related to size occurs within the first year following growth completion.

Similar analyses for the survival of bats in heated roosts are not yet possible because of insufficient data.

Discussion

As predicted on theoretical grounds, heater installation raised the mean early radius growth rates of both male and female young compared with previous rates. Despite the improvement in growth rates, only female radii ultimately reached a larger size (a 1mm increase). This was due a fall in the radius size of the mothers of males, and its impact on radius growth noted in part 3. Presumably more of the larger mothers had female babies.

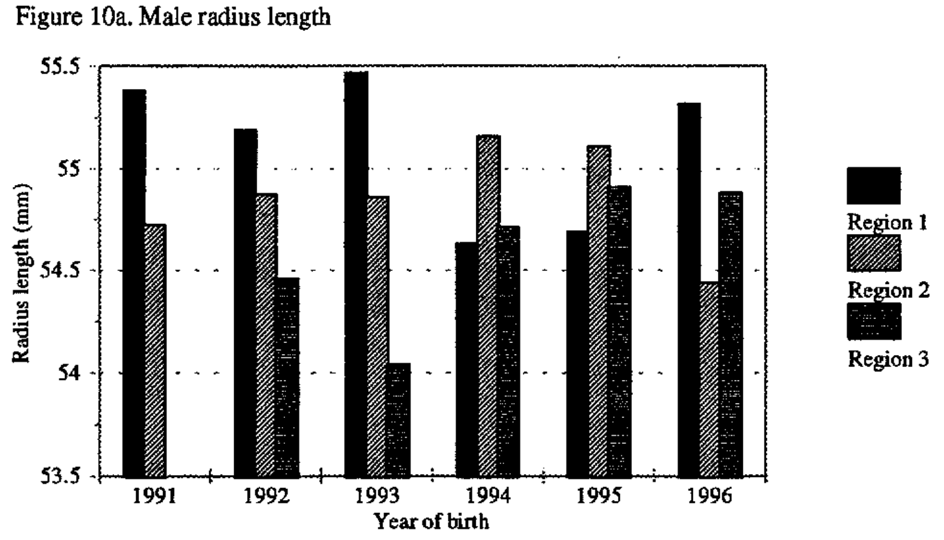
The survival rates for male young stayed the same at about 42%, whilst those for females rose from 39 to 58% following heater installation. However, these changes were not significant, probably due to small sample sizes.

Smaller bats of both sexes suffer higher mortality rates than larger ones in the first year of their lives. There was a 0.6mm mean radius difference between survivors and non-survivors. Hence the 1mm increase induced in female radius length by heaters is expected to improve female survival rates significantly over time. Male survival is expected to remain the same.

Part 5: How did the growth of Woodchester bats compare with growth in other regions?

Introduction

Figures 10 and 11 illustrate the means of the data collected, which are provided in tabular form in Appendices 1 to 6. Data from the Mendips and Bath/Wiltshire areas were combined as a single region (region 2) as no statistical differences existed between them. Juveniles from Woodchester (region 1) and Mells (region 3) were treated separately from the other areas since they showed clear differences relating to one or both sexes. As Mells was regarded as a special case, and no data from 1991 were obtained, analyses of its data were carried out separately.



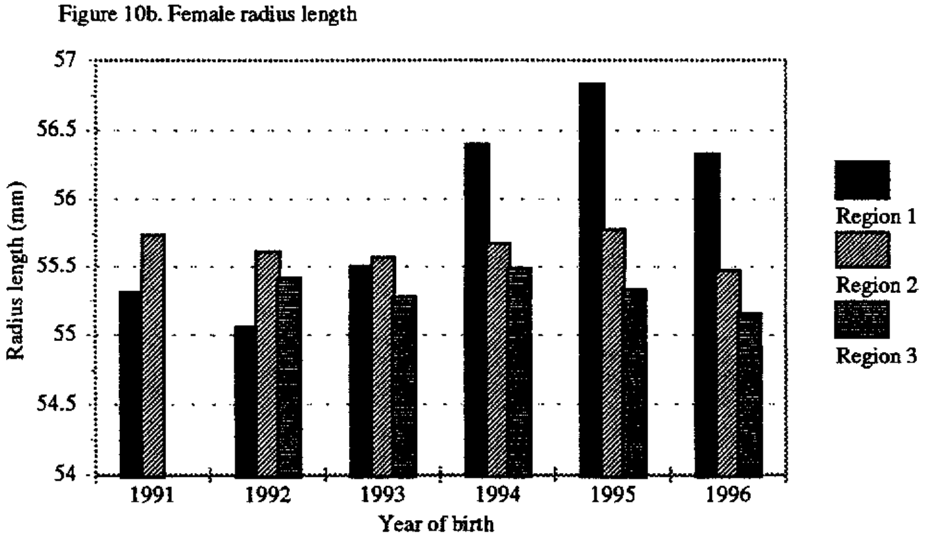


Figure 10. Mean radius length by year of birth and region. The 3 regions are (1) Woodchester/Stroud; (2) Mendips & Bath/Wilts; (3) Mells.

How did the growth of Woodchester bats differ from those born in region 2?

Appendices 1 to 4 show the statistics of the data obtained by region, sex and year. Data from the two regions were each divided into two periods, pre-heater years and post-heater years, and the radius and digit 5 lengths for each sex were compared by two-sample t-tests. A summary of the data obtained is shown in Table 13. As only bats in region 1 (Woodchester) were exposed to heaters from 1994 onwards, any significant differences between the regions which did not exist prior to heater installation, but which occurred afterwards, are likely to be linked to the use of heaters.

Table 13 Radius and digit 5 lengths of bats by region, sex and heating phase

Sex, heating regime and growth parameter	Region 1	Region 2	Statistically different?
Male pre-heating years; radius length (mm)	**55.33±0.86; 25**	**54.82±1.03; 102**	**t_{42}=2.58; P=0.013; Yes.**
Male post-heating years radius length (mm)	54.97±1.11; 38	54.82±1.13; 113	t_{64}=0.69; P=0.49; No.
Female pre-heating years radius length (mm)	55.64±0.93; 31	55.65±1.07; 119	t_{52}=0.08; P=0.94; No.
Female post-heating years radius length (mm)	**56.52±1.20; 35**	**55.64±0.92; 104**	**t_{73}=3.97; P=0.0002; Yes**
Male pre-heating years digit 5 length (mm)	**72.11±1.01; 25**	**70.73±1.36; 102**	**t_{47}=5.68; P=0.000; Yes**
Male post-heating years digit 5 length (mm)	70.93±1.61; 38	70.89±1.48; 113	t_{59}=0.15; P=0.88; No.
Female pre-heating years digit 5 length (mm)	72.26±1.45; 19	71.68±1.40; 75	t_{27}=1.57; P=0.13; No.
Female post-heating years digit5 length (mm)	**72.89±1.48; 35**	**71.84±1.36; 92**	**t_{54}=3.71; P=0.0005; Yes**

In columns 2 and 3 the data are mean, standard deviation and sample size in that order. In column 4 the statistics quoted derive from two-sample t tests (see Minitab reference manual) carried out at 95% significance levels.

Bold type indicates significant differences between data sets.

Table 13 shows that the impact of heaters affected the two sexes differently, as previously described above. Before heaters were installed, male bats in region 1 were larger, both with respect to radius and digit 5 lengths, than those in region 2. After heater installation and use by the bats in region 1 only, these differences disappeared. The radius and digit 5 lengths of the males in region 2 showed no changes between the two heating periods.

The opposite effect was seen in female bats. Before heaters were installed, females in regions 1 and 2 were virtually identical in radius length (P=0.94), and there were no significant differences in digit 5 lengths, even though they were slightly larger in region 1 (P=0.13; NS.). After heater installation both the radius and digit 5 lengths of females became significantly longer in region 1 only.

Variation in growth among years at unheated roosts

Growth differences occur among years in bats born at unheated maternity roosts, with smaller bats in years of late birth timing. One-way ANOVA of mean female radius length in winter samples from region 2 showed no significant differences occurred among years (1991-1996 inclusive), and only a weak difference (F_{299}=1.27; P=0.037) among their mean digit 5 lengths. Tukey post hoc tests showed no significant differences existed among years, but 1995 and 1996 were very nearly different.

Males born in unheated roosts in the same region, however, showed much greater variation over the same six year period, especially in their digit 5 means. One-way ANOVA, followed by Tukey tests showed that radius lengths were significantly larger (F_{307}=2.53; P=0.029) in 1995 (early births) than in 1996 (late births). These differences also showed up in similar analyses of digit 5 lengths (F_{307}=3.36; P=0.006), In addition to the 1995-6 differences, 1993 digit 5s showed poorer growth than 1995. Hence the mother's of male young, which tend to be smaller than those of female young, and possibly growth-stressed themselves, may be less capable of providing for the growth of their young in bad years. If populations within hibernacula need to be monitored for growth stress in a particular year, data from males, especially digit 5 lengths, should be collected. Radius lengths may be easier to measure accurately by inexperienced workers, however. Furthermore it is important to be sure that the sample is large enough, and not biased in its birth time.

Variation in growth among years at Woodchester, after heater installation

Only 3 years data (1994 to 1996) were available, but they included 1995 and 1996, the two years which showed significant growth differences in males at unheated roosts. One-way ANOVA of male and female radii and digit 5s separately showed that no significant differences occurred among these years for either parameter and sex (P ranged from 0.429 to 0.889, N.S). Heaters therefore removed the impact of birth timing among these extreme years.

How did the growth of bats at Mells differ from those in region 2?

Juveniles at Mells were raised in an underground roost, having lost their maternity attic in a fire. Since the underground roost existed previously, the breeding females selected the attic in preference to the underground roost. We therefore expect the underground roost to provide inferior, and probably cooler roost conditions to the attic. If this is correct, we predict that juveniles from Mells will show poorer growth than those from region 2, and achieve smaller radius and digit 5 lengths. Juvenile males and females born in region 2 provide better controls to compare growth with than those from region 1, since they share the same latitude, are exposed to a very similar climate, and have very similar diet qualities (Ransome 1997a). Also the sample sizes are much greater than those from region 1.

The analyses carried out involved combined data for all years from 1992 to 1996 only, since no data were collected from Mells in 1991. Two-sample t tests were carried out to discover whether the differences in radius and digit 5 lengths of male and female bats shown in Figures 10 and 11, were significantly different. Table 14 summarises the two-sample t test results.

Table 14. Growth comparison between juveniles captured at Mells with those from region 2.

Sex and growth parameter	Region 2	Mells	Statistically different?
Male; radius length (mm)	54.85±1.06; 192	54.62±1.13; 98	t_{164}=1.90; P=0.059; No.
Female radius length (mm)	55.61±0.98; 180	55.35±1.13; 93	t_{184}=1.70; P=0.092; No.
Male digit 5 length (mm)	**70.86±1.45; 192**	**70.24±1.61; 98**	**t_{178}=3.22; P=0.0015; Yes**
Female digit 5 length (mm)	**71.69±1.40; 180**	**70.98±1.57; 93**	**t_{178}=3.68; P=0.0003; Yes**

Data from birth years 1992 to 1996 combined. Remaining legend as for Table 11.

Although the radius lengths of first-year bats of both sexes born at Mells were smaller than those found in hibernacula in region 2, differences were not quite significant. However, the digit 5 lengths of first-year bats of both sexes born at Mells were significantly smaller than those found in hibernacula.

Discussion

Overall these results support the evidence and conclusions made in Parts 3 and 4 above, that heater installation was the crucial factor causing the increase in size of female juveniles in region 1. Only at Woodchester, where the incubator was used by breeding females from 1994, did an increase in female size occur. In region 2, where incubators were not used by bats, no changes in the size of either the males or the females took place between the two three-year periods.

Growth differences occur among years at unheated roosts, and are especially evident in the digit 5 lengths of males, which should be regarded as the most sensitive growth indicator. These differences are linked to birth timing, with poorer growth in years with late births. Incubators remove the impact of birth timing upon growth.

There are many hypotheses which could account for the smaller digit 5 size of juveniles born at Mells compared with those sampled in hibernacula in region 2 nearby. Among them are the following four possibilities. First, radius growth is less susceptible to lower temperature conditions than that of digit 5, and the inferior roost conditions there caused the poorer growth. Second, that available food supplies to young when they first forage at Mells are inferior to those maternity roosts which provide young to regions 1 and 2, limiting digit 5 growth which continues from 40 to 60 DAGE (unlike radius length which is complete by 40 DAGE). Third, that young at Mells are born significantly later than those at other roosts. Fourth that the Mells sample of juveniles, which has been captured in late October or early November of each year, is biased towards late-born young of the year, which tend to be more stunted in unheated roosts. First-year bats hibernating in the cellars and tunnels of Woodchester Mansion in early winter consist primarily of late-born individuals (Ransome *pers. obs.*).

Only the results of maternity studies carried out in the summer of 1997 will be able to shed further light on which of these hypotheses, if any, is correct.

Part 6: Maternity roost field study in 1997

Introduction

In Part 5 growth comparisons were made between young born at Woodchester and those from maternity sites in region 2, south of Bristol. The particular maternity roost in region 2 at which each bat was born was not known. It was therefore not possible to relate the growth of individuals to specific roost characteristics, except for those captured in the tunnel at Mells in each autumn. It was assumed, but not proven, that all young of the year caught there originated from the local maternity site.

In order to compare the growth of young from different maternity roosts, an attempt was made to ring all of the juveniles born at five known roosts in a single summer. Subsequent recapture in hibernacula, after linear skeletal growth was complete, would allow growth comparisons among roosts to be compared, and related to roost conditions and birth timing.

The study would also check for the presence of any substantial unknown maternity roost(s) within the study area.

Methods

Juvenile bats were studied at five maternity roosts. They were located in attics in Woodchester Mansion and Dean Hall, Forest of Dean (located in region 1); attics in Brockley Stables, near Nailsea, and at Iford Manor near Bath (all located in region 2), and an underground tunnel at Wadbury Camp near Mells (in region 3).

At all roosts except for Woodchester, older young were collected from creches after the exit of their mothers and ringed loosely with Mammal Society rings (see Methods in Part 2). Only young with a radius length of 42mm or longer were ringed, as experience at Woodchester showed that at this size the young were capable of being permanently ringed in a manner similar to methods used for adults in hibernacula. Young were also sexed, weighed, and had their radius measured before being replaced in the roost. As all young measured were in growth phases 2 and 3, condition indices could be calculated from data obtained to assess the nutritional state of young at each roost, for comparison with figure 5 and table 2. Individuals were aged to the nearest day from growth curves of known-age bats from Woodchester. This allowed the estimation of birth dates at each roost.

At least four visits to each roost were made, at roughly weekly intervals, in order to ring all of the young born. In order to cope with all five roosts, two experienced licensed assistants who had received special training to standardise measuring accuracy, visited Dean Hall and Brockley roosts. This left me with visits to the other two roosts and Woodchester, where studies of growth of the young continued as in previous years.

Births were exceptionally early at all roosts in 1997, as expected after a very warm spring (Ransome & McOwat 1994). However, food consumption deteriorated in August at Woodchester, with especially poor levels of moths. As moths are the preferred mid-summer prey of lactating females (Ransome 1996, 1997a), this may have adversely affected the growth of late-born young.

During the following hibernation season, between October and April, repeated searches were made of many hibernacula, including the tunnel at Mells, and the caves and mines in the Mendip Hills, Bath area, Stroud area and the Forest of Dean. This was aimed at recapturing first-year bats among samples of other age groups, so that their radii and digit 5's could be remeasured. In addition, if many unringed first-year bats were also caught, it would be proof that other maternity sites not visited in the summer of 1997 existed.

The data collected were the maximum feasible with the manpower and timespan available for working on quite large numbers of young in some roosts, before the return of their mothers.

Part 7: Results of juvenile growth studies among roosts in 1997

Introduction

The juvenile ringing study was successfully completed at all maternity sites except Brockley Hall. At least half of the mothers from this colony gave birth in an undergound roost several kilometres away, leaving their young in an inaccessible position. Consequently only a small number of young was able to be ringed at Brockley.

Table 15 summarises the number of young ringed, and the number recaptured fully grown, mostly in hibernacula. The percentages recaptured and measured fully grown varied considerably among roosts. Woodchester had a very high percentage, since recaptures within the roost occurred in late August and September, before the young dispersed to hibernacula. Mells had a high figure, possibly because many of the young remained in a tunnel close to the dome where they were born, as it was a suitable hibernaculum. Dean Hall and Iford bats completely desert their maternity roost in buildings, and seem to disperse widely to a potentially large number of suitable hibernacula. Hence the recapture rate differences probably do not reflect underlying survival rate differences.

Table 15. Summary of numbers of juveniles ringed by sex and maternity site in 1997

Maternity site	Number of male juveniles	Number of female juveniles	Total juveniles ringed
Woodchester	15 (11)	15 (14)	30 (25) 83.3%
Brockley Stables	11 (3)	19 (9)	30 (12) 40.0%
Dean Hall	22 (6)	17 (9)	39 (15) 38.5%
Iford	40 (13)	31 (12)	71 (25) 35.2%
Mells	41 (19)	41 (17)	82 (36) 43.9%

In columns 2 - 4 the first number is the number ringed in the maternity site, and the number in brackets is the number recaptured and measured when fully grown, at least 60 days after birth. In column 4 the % of those born which were measured is given. For all sites, excluding Woodchester, this % represents the recapture level in hibernacula. Young born at Woodchester were captured in September within the maternity roost. Only 15 of these young (50%) were recaptured in hibernacula. Mells recaptures were mainly made within the tunnel close to the maternity roost.

Radius and digit 5 lengths by sex and maternity site

Table 16 summarises radius growth data for each maternity site by sex. Table 17 provides the same analyses for digit 5. Sample variances were tested for significant differences, and since none were found, a one-way ANOVA was carried out on the means for each sex separately. Neither sex showed significant radius growth differences among the maternity sites in 1997, although male lengths were very nearly so. The digit 5 lengths of males were just significantly different among sites, and Tukey post hoc tests subsequently showed that the differences only occurred between Mells and Iford. The failure to demonstrate other significant growth differences was almost certainly due to very small sample sizes at two sites, and the generally small sample sizes obtained overall. The winter of 1997/8 was remarkably mild, and the large congregations of bats which would normally have been expected in some important hibernacula, did not occur.

Table 16. Final radius length by sex and maternity site in 1997

Maternity Site	Final male radius length (mm)	Final female radius length (mm)
Woodchester	55.55±1.36; 11	56.56±0.99; 14
Brockley Stables	55.10±0.72; 3	56.21±0.94; 8
Dean Hall	54.43±1.55; 6	55.79±1.12; 9
Iford	55.39±1.08; 13	55.67±0.94; 12
Mells	54.52±0.86; 19	55.94±1.18; 17
Analysis of variance of means	P = 0.073 NS	P = 0.231 NS

Figures in columns 2 and 3 are mean, standard deviation and sample size in order.

One-way ANOVA of means show that neither male nor female radius lengths were significantly different among maternity sites in 1997.

Table 17. Final digit 5 length by sex and maternity site in 1997

Maternity Site	Final male digit 5 length (mm)	Final female digit 5 length (mm)
Woodchester	71.19±1.86; 11	72.76±1.25; 14
Brockley Stables	72.23±0.75; 3;	72.68±0.62; 8
Dean Hall	71.03±1.77; 6	72.02±1.30; 9
Iford	71.95±1.39; 13	71.87±1.42; 12
Mells	70.25±1.19; 19	72.02±1.13; 17
Analysis of variance of means	**P = 0.021 Significant**	P = 0.233 NS

Figures in columns 2 and 3 are mean, sample size and standard deviation in order.

One-way ANOVA of means show that female digit 5 lengths were not significantly different among maternity sites in 1997, but that there were significant differences among the male data. Tukey tests showed that only differences between Mells and Iford were significant.

Radius and digit 5 lengths by sex and area

To raise sample sizes, data were combined into two areas, area 1 north of Bristol, and area 2 south of Bristol (as previously) as shown in Table 18. Two-sample t tests showed no significant differences existed in the growth of either sex between the two areas.

Table 18. Growth comparison by sex and maternity site region in 1997

Growth Aspect	Area 1	Area 2	Statistically different ?
Male: Radius length (mm)	55.15±1.48; 17	54.89±1.01; 35	t_{23}=0.66; P=0.52; No.
Female: Radius length (mm)	56.26±1.09; 23	55.91±1.05; 37	t_{45}=1.22; P=0.23; No.
Male: Digit 5 length (mm)	71.14±1.77; 17	71.05±1.50; 35	t_{27}=0.17; P=0.87; No.
Female: Digit 5 length (mm)	72.47±1.29; 23	72.11±1.16; 37	t_{43}=1.10; P=0.28; No.

Area 1 is Woodchester plus Dean Hall - maternity sites north of Bristol. Area 2 is Brockley, Iford and Mells - maternity sites south of Bristol.

Data from birth years 1979 to 1993 from Woodchester and Stroud hibernacula only. Survival of females can reliably be determined from returns to the maternity site. All years without heaters.

Radius and digit 5 lengths by sex and heating regime

Data were combined by sex and heating regime as shown in Table 19. Two-sample t tests showed that only female growth was significantly different. Female radius and digit 5 lengths were both greater in bats from heated roosts than from unheated ones. Furthermore the means and standard deviations for both sexes and groups of bats showed very similar levels to those obtained in previous years (see the comparable sections of Table 13).

Table 19. Growth comparison by sex and heating regime in 1997

Growth Aspect	Heaters in roosts	No heaters in roosts	Statistically different ?
Male: Radius length (mm)	55.45±1.24; 14	54.80±1.12; 38	t_{21}=1.72; P=0.10; No.
Female: Radius length (mm)	**56.43±0.96; 22**	**55.82±1.07; 38**	**t_{47}=2.28; P=0.027; Yes.**
Male: Digit 5 length (mm)	71.41±1.72; 14	70.96±1.53; 38	t_{21}=0.88; P=0.39; No.
Female: Digit 5 length (mm)	**72.73±1.05; 22**	**71.97±1.23; 38**	**t_{49}=2.53; P=0.015 Yes.**

Maternity roosts with heaters used by bats in 1997 were Woodchester and Brockley. Maternity roosts without heaters were Dean Hall, Iford and Mells.

Data from birth years 1979 to 1993 from Woodchester and Stroud hibernacula only. Survival of females can reliably be determined from returns to the maternity site. All years without heaters.

Bold type indicates significant differences between data sets.

Birth date impact on radius and digit 5 lengths by heating regime

Male and female birth dates have previously been shown to be similar (Ransome & McOwat 1994) and combined data for all sites were not significantly different in 1997 (t test T_{249}=0.59; P=0.55). One-way ANOVA showed that significant differences in birth timing occurred among sites, both using all young born, and recaptured samples mostly in hibernacula (0). Tukey post hoc tests showed that births at Woodchester (heated) were significantly earlier than births at all other sites, and Iford births were significantly earlier than at Mells. Both of these sites were unheated.

The statistics of regressions of birth date on growth by sex and heating regime are summarised in Table 21. In contrast to the Part 3 (see table 3), 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, as in Table 5. However the regression was less significant than that of males, and less variation in radius length was explained by birth timing.

The growth of bats from heated roosts was not significantly influenced by birth timing, confirming the results of the interim study (see tables 4 and 6).

Early condition and growth of radius and digit 5 lengths by heating regime

Two-sample t tests showed there were no significant differences between the sexes in the early condition of young caught in 1997 (data from all roosts combined; t_{313}=0.32; P=0.75; males: mean=15.35±0.79g; n=170; females mean=15.37±0.63g; n=147). All further analyses therefore combined the sexes, unless there were sex differences in the factor concerned. These data are remarkably similar to those in table 2, and support the consistency of data measurement among the three collectors.

One-way ANOVA, followed by Tukey tests, showed that there were significant differences between the condition of young at Woodchester (heated) and those at the unheated roosts at Iford, Mells and Dean Hall (table 22). When data from unheated and heated roosts were combined, a two-sample t test showed that heated roost young had significantly lower early condition than those in unheated roosts (t_{138}=3.65; P=0.0004; mean heated roosts: 15.15±0.74g; n=69; mean unheated roosts: 15.49±0.69g; n = 183).

Regressions of the final radius and digit5 lengths on early mean condition were carried out separately for the sexes. None were significant, and all r^2 values were either 0 or very low, showing that early condition had very little impact on the ultimate growth achieved in 1997. As female juveniles from heated roosts grew larger than those at unheated ones, despite their significantly lower early mean condition, this supports the arguments given in the summary of Part 3, that levels above about 14.5g are not beneficial to growth.

Mells - is the growth of young born there abnormal?

Four hypotheses were offered earlier which could account for the significantly smaller size of the digit 5 lengths of juveniles born at Mells compared with those in the hibernacula of region 2 nearby (table 14). First, radius growth is less susceptible to lower temperature conditions than that of digit 5, and the inferior roost conditions there caused the poorer digit 5 growth . Second, that available food supplies to the young when they first forage at Mells are inferior to other maternity roosts. Third, that the births at Mells were significantly later than births at other roosts. Fourth that the Mells sample of juveniles, which has been captured in late October or early November of each year, is biased towards late-born young of the year, which tend to be more stunted in unheated roosts.

Table 16 shows that in 1997, radius growth at Mells was not significantly different to that of other maternity sites in both sexes. The male data was close to being significant, however. The digit 5 lengths of males from Mells, but not females, were significantly smaller than those born at Iford (table 17). These data confirm previous findings for radius growth of both sexes, and the digit 5s of males. The female digit 5 data in 1997, however, did not confirm previous findings.

At Mells the late-pregnant and lactating females pack tightly together with their young in a vertical chimney some 1.5m diameter, and 1.5m high. With over 150 to 250 bats present during and after lactation, temperature conditions when adults were not foraging are likely to have been very favourable throughout the growth period. Furthermore dietary quality at Mells was shown to be among the best in 1996 (Ransome 1997a). Hence the first two hypotheses seem unlikely.

Table 20. Mean birth dates of recaptured bats by maternity roost in 1997

Maternity roost	All young ringed at maternity roosts	Young recaptured in September or in winter hibernacula
Woodchester	30.1±7.6; 30	29.6±7.9; 25
Brockley	36.8±4.8; 30	35.1±5.1; 11
Dean Hall	38.8±12.4; 39	39.0±13.3; 15
Iford	35.6±6.7; 71	34.6±6.8; 25
Mells	39.9±6.1; 82	41.9±7.1; 36
One-way ANOVA	**F=10.27; P=0.000**	**F=9.23; P=0.000**

Data are number of days after June 1st. Statistics are means, standard deviation and sample size in order.

Data were from young ringed at maternity sites and also from those recaptured when fully grown either in the maternity roost in September (Woodchester), or in hibernacula (other roosts). One-way ANOVA and Tukey post hoc tests showed that Woodchester births were significantly earlier than those at Dean Hall and Mells. Iford births were significantly earlier than those at Mells in both analyses.

Table 20 shows analyses of mean birth dates by roost and capture period in 1997. The data allows us to test hypotheses three and four. There were significant birth date differences between Woodchester bats (earliest) and all other sites, and between Iford and Mells. This is true both for all young born and ringed, and for those recaptured when fully grown. Births at Iford were significantly earlier than at Mells, which showed the latest births of any roost.

The Mells sample captured in hibernation is clearly biased towards late-born young, but this may not have had any growth significance. Data for recaptured bats of each sex were therefore divided into two groups (table 23). First, those born before the mean birth date of 10th July, and second those born afterwards. Two-sample t tests were separately carried out on the radius and digit 5 lengths to discover any significant differences. Table 23 shows that late-born bats of both sexes tend to be smaller, but only in males were differences significant.

Table 21. Regressions of Birth Date on Radius and Digit 5 lengths by sex and heating regime in 1997

Growth Aspect	Heated roosts	Non-heated roosts
Male: Radius length (mm)	$F_{1,13}=1.61$; $P=0.228$; $r^2=11.8\%$	**$F_{1,37}=26.94$; $P = 0.000$; $r^2=42.8\%$**
Female: Radius length (mm)	$F_{1,21}=0.58$; $P=0.456$; $r^2=2.8\%$	**$F_{1,37}=7.28$; $P=0.011$; $r^2=16.8\%$**
Male: Digit 5 length (mm)	$F_{1,13}=0.54$; $P=0.476$; $r^2=4.3\%$	**$F_{1,37}=23.39$; $P = 0.000$; $r^2=39.4\%$**
Female: Digit 5 length(mm)	$F_{1,21}=0.47$; $P=0.502$; $r^2=2.3\%$	$F_{1,37}=1.70$; $P=0.201$; $r^2=4.5\%$

Maternity roosts with heaters used by bats in 1997 were Woodchester and Brockley. Maternity roosts without heaters were Dean Hall, Iford and Mells. Regression statistics are provided in columns 2 and 3. Significant regressions are highlighted in bold print.

Table 22 Condition during growth phases 2 and 3 by maternity roost in 1997

Maternity Roost	Condition statistics (g)
Woodchester	**15.00±0.63; 30 ***
Brockley	15.41±0.81; 30
Dean Hall	15.38±0.76; 40
Iford	15.47±0.74; 77
Mells	15.55±0.61; 91
One-way ANOVA of mean:	**F=7.46; P=0.000**

Only data for juveniles with radius length >42mm and younger than 22 days were used in the analyses.

Statistics are means, standard deviation and sample size. Data marked with * are significantly different from all others.

Table 23. Growth comparison of recaptured early and late born young from Mells by sex in 1997

Sex and growth aspect	Early-born bats	Late-born bats	Statistically different?
Male:Radius length (mm)	**55.27±0.67; 7**	**53.91±0.55; 10**	**t_{10}=4.46; P=0.001; Yes**
Male: Digit 5 length (mm)	**71.20±0.64; 7**	**69.47±1.04; 10**	**t_{14}=4.24; P=0.0008. Yes.**
Female: Radius length (mm)	56.30±1.17; 6	55.65±1.35; 8	t_{11}=0.96; P=0.36; No.
Female: Digit 5 length (mm)	71.98±1.11; 6	71.70±1.01; 8	t_{10}=0.49; P=0.63; No.

Early born bats were those born before 10th July, and late born bats were born on or after 10th July, which was the mean birth date for Mells in 1997. The remaining legend is as for Table 7.

Table 24 Growth of young from unknown maternity roosts in region 2 by sex in summer 1997

Growth parameter	Male statistics	Female statistics
Radius length (mm)	54.82±0.90; 39	55.85±1.10; 39
Digit 5 length (mm)	70.64±1.50; 38	71.71±1.50; 37

Statistics are means, standard deviation and sample size in order.

Data in Tables 20 and 23 therefore support the two hypotheses that the births at Mells are later than elsewhere, and also that the tunnel sample in October is biased towards late-born young, which show poorer male growth than early-born young. Although the same trend also exists for females, differences were not significant.

In summary, the most likely scenario explaining the observed differences between male growth at Mells and Iford is that they were due to a combination of two factors. First later birth timing at Mells, and second biased sampling in both fully-grown samples. The later a male is born the greater its chances of being stunted in the absence of heaters. Frequent stunting of males may have resulted from colder roost conditions later in the summer, the deterioration of moth availability in late August (as happened at Woodchester), or because of a high level of old or inexperienced mothers of males in the colony.

If this interpretation is correct, it seems unlikely that roost structural differences between Mells and Iford played an important direct role in controlling the growth of the young. The mean growth of bats in all unheated roosts seems to be remarkably similar, provided samples are large enough and randomly obtained by birth date. However, poor roost conditions may well contribute to the later births occurring at Mells compared with Iford and Woodchester. If they do, they will indirectly hamper growth there.

Overall conclusions for the study

In Part 3 it was argued that female young are more stressful for a mother to rear than male young. Hence the benefits of higher ambient temperatures provided by heaters within a large roost were likely to be reflected in the improved growth of female young. Comparisons of juvenile growth between years without heaters, and years with heaters, supported this prediction at Woodchester in Part 4. In region 2 over the same years no change in the growth of females was noted (Part 5). Bats born at Mells, using the presumed coolest (underground) roost, showed the poorest growth (Part 5). However, it was not previously possible to relate the growth of first-year bats to specific roosts, and hence to roost conditions, in most of region 2, until the synchronised maternity study carried out in 1997. It was based on the prediction that female growth at heated roosts should be better than that at unheated roosts, if all other circumstances were similar.

Part 3 also showed that the most significant factors influencing radius length of female young were the mean early growth rate and the mother's radius length. The proportion of variation in radius length explained by these two factors in single regressions were about 45 and 20% respectively before and after heater installation (tables 5 and 6). In multiple regressions they explained about 45-49% of the variation together, only slightly higher than growth rate alone. No other factors considered explained a higher level of variation in multiple regressions, so over 50% remained to be explained. Dietary factors were thought likely to be important contributors to this unexplained variation.

Studies carried out by Ransome at these roosts in 1996 (Ransome 1997a) showed that the diets at all of the currently studied roosts were very similar in the proportions of key prey consumed. No comparative studies on the quantity of food captured at these roosts has yet been carried out. Hence we cannot be sure that the quantity of food consumed was not a factor influencing growth among roosts.

Overall the growth data from the two sexes from unheated sites are remarkably similar despite the structural and probable thermal differences among roosts. The data from Mells suggests that large groups of female bats are capable of compensating for poor roost circumstances to a remarkable degree, at least during a favourable summer like the one in 1997. Between birth and about 20 days of age a juvenile spends most of its time attached to its mother within the roost. If she is continuously thermoregulating, her heat production will incubate her young to a temperature which probably exceeds 30°C. Especially if the mother is one of a large colony, she can minimise her own thermoregulatory stress by clustering. Since lactating females seem to synchronise their foraging bouts, especially the dusk one, unheated attic roosts show a rapid temperature fall immediately after dusk, no matter how many adults are in the colony.

Underground roosts may cool more slowly, but are unlikely to reach high temperatures during the daytime unless a large colony clusters together into a small dome (as happens at Mells).

Growth was shown to vary significantly among years in winter samples from region 2, under the influence of climate. These samples combined bats from several unheated roosts. However, no data exists to compare performance at specific unheated roosts among years.

The major factor identified by this study, which influences the ultimate size of the radius achieved by a young bat, is its mean radius early growth rate (between age 4 to 14 days). Growth rates rise to a peak near day 4, and slow to about half the peak rate by day 14. Mean early growth rate was raised by about 3% in both sexes at Woodchester in the years following the provision of an incubator kept at 27°C. This improvement led to an increase in mean radius length of about 1.5%, or 1mm, in females only.

Early growth rate is affected by the young's mean early body condition, which rises rapidly in the four days after birth from about 13.8g, then tends to remain stable at about 15.4g up to age 24 days. Significant growth rate reduction does not occur until condition falls below 14g, so 15.4g probably provides a good safety margin. The mother's body condition reflects that of her young (*pers. obs.*). Her condition is presumed to reflect her foraging success levels, via the allocation of assimilated nutrients between condition, lactation and body maintenance.

Foraging time and food consumption by mothers in favourable weather increases markedly during lactation, compared with pregnancy, in order to provide the extra nutrients necessary for milk production to fuel rapid juvenile growth. The more time a mother spends foraging, the longer her young is left alone in the roost, where temperatures may fall to 12°C or lower on cool nights in unheated roosts. Up to 4.25 hours a day (18%) of low-temperature exposure may take place during a mother's three nightly foraging bouts (Duvergé 1997, figure 12). The first (dusk) bout may be the most crucial one, since it is the longest, and the young do not appear to suckle before the dusk exit. In these circumstances they may become torpid, and reduce their growth rates. A 2.5 hour foraging bout represents 10% of the day. It may be during this time that an incubator is most valuable, since it would theoretically allow rapid growth rates to continue. (A 10°C rise in ambient roost temperature should double the growth rate.)

Whatever the detailed mechanism is, a thermostatically controlled heated incubator clearly benefits the growth rate of both male and female young, once the bats adopt it. This may take several months, or longer to happen. The higher ambient roost temperatures available are predicted to reduce the energetic demands, and hence stress levels, upon all mothers. The reduced stress levels may have induced subtle changes in the population over and above those stated in Part 3. Besides largely removing the growth penalty of late birth-timing effects (which varies among years), it may raise the frequency of medium or smaller females having female young.

To date there is no evidence that birth timing has been significantly altered by adding the incubator to the attic at Woodchester. However, this may be because the majority of older pregnant females do not return early enough in the summer for any effect to occur. Several first-time breeders on the other hand have returned by early June, and given birth much earlier than is normal (Ransome 1995).

Incubators clearly result in larger female offspring, which are much more likely to fulfil their genetic potential. Larger females have a higher proportion of female offspring, as well as a higher survival rate. Over time a population which is below the carrying capacity of its habitat (as

Woodchester almost certainly is at present) is predicted to increase faster with an incubator than one without. Ultimately poor quality or limited food supplies and/or increased distances to foraging sites are likely population regulators, presumably via reduced growth rates and the opposite mechanism to the one above.

Perhaps a more crucial benefit of an incubator may be in helping to prevent or mitigate population crashes such as those in the early 1960's and mid 1980's. These resulted from several cold winters and springs concurrently, when populations were high. The signs of problems developing were evident during the early 1980's (with hindsight) in the frequent dominance of male births, and the poor skeletal growth of both sexes. Monitoring of these two aspects is clearly highly advisable, but need not necessarily include checking birth sex ratios, or detailed growth studies at maternity sites. Overall birth sex ratios at Woodchester (years 1982 to 1997) of 1 male:0.88 female are very similar to those captured in hibernacula of 1 male: 0.84 females. (Chi-square test on 16 years combined data between sex ratios at birth and in hibernacula; χ^2=0.067; P-value=0.796.) Provided samples are large enough, winter monitoring of first-year bats at a range of sites should be acceptable to determine birth sex ratios and summer growth performance. Monitoring of colonies at known maternity sites should also be carried out, with exit counts during the two 'plateau periods' and dietary checks (Ransome 1997a). This is necessary, since any problems discovered at hibernation sites need to be linked to specific maternity roosts, and the circumstances which may have contributed to them. It is therefore important to have a good understanding of the relationships between specific maternity roosts and the hibernacula used in winter.

Part 8: Numbers and growth of young from unknown roosts in area 2 in 1997

Introduction

If virtually all of the young born at all of the five maternity sites were caught and ringed in the summer, the growth study should also provide a check on the existence of any unknown roosts. If these roosts fed young into the hibernacula populations surveyed in winter, these young would not be ringed.

Numbers of young and the size of populations

A total of 103 young were refound in hibernacula in the winter of 1997/8 from the 252 ringed at the five known maternity roosts in 1997. Assuming no young were missed, these young originate from colonies totalling about 830 adult bats (using a ratio of 3.3 adults: 1 young; Ransome 1997a). During the same winter 78 unringed first-year bats were also captured in the hibernacula of area 2. None were found in hibernation sites close to the two maternity roosts studied in area 1, but a small number of first-year bats were seen in caves at Symonds Yat in the northern part of the Forest of Dean. These were presumed to originate from a known maternity roost near Monmouth, which is nearby.

Applying the same ratio of young born to those captured in hibernacula above, 78 first-year bats represent about 190 young born at unknown roosts in the same area, or which missed capture at the other roosts. This number of young originates from one or more colonies of about 625 adult bats.

The majority of the unringed young (58) were captured in the caves of Cheddar Gorge, which suggests that a breeding roost is not far away. The greatest number of ringed young from a known roost (9) at Cheddar in the winter of 1997/8 came from Brockley Stables. However, only about half of the young born to this colony were able to be captured in 1997, as many mothers bred undergound out of reach in a nearby wood. Hence possibly another 9 young originated from the Brockley colony, leaving about 50 young originating from the unknown roost(s). These are likely to have come from about 120 young born at roosts containing about 400 adult bats.

Growth comparisons between unknown and known unheated roosts

The statistics of radius and digit 5 lengths of young from the unknown roost(s) were very similar to those of unheated roosts in the same region for the same sex (see tables 24 and 19), except for slightly smaller digit 5 lengths. Hence the growth conditions operating at the roosts of these young appear to be typical of other roosts within area 2.

Discussion

This study has shown that one or more significant breeding roosts remain to be discovered in area 2. One substantial roost is probably close to Cheddar Gorge. The unknown roost(s) seem(s) to provide similar conditions for growth to the unheated roosts in the same region. The slightly smaller digit 5 lengths may reflect biased birth-time sampling as at Mells.

Part 9: Recommendations for improving roost conditions at specific roosts

Introduction

An ideal roost needs a dark void offering a range of temperatures. The range should provide high ambient temperatures (about 27°C or above) for economic thermoregulation after successful foraging, and a region of low ambient temperatures (about 12°C) for torpor if foraging is unsuccessful. It is therefore a mistake to heat the whole roost to high temperatures.

At temperatures of about 27°C bats select incubators for most of each 24 hour period and carry out normal behaviour, including the formation of tight clusters after foraging. Higher temperatures may not be helpful, and may even induce dehydration.

The dark void should be large enough, and of an internal structure which permits juveniles to practise wing flapping and later exploratory flights within it. Time-lapse, infra-red video shows that juveniles carry these out from a very early age, and such flight behaviour may be important in the growth and ossification of the wing bones.

Brockley Stables

This roost is in a very large attic void of a derelict stable building which was re-roofed some years ago. The stable has been converted into several occupied units. During the building works the main colony moved permanently underground within an old ochre mine in a wood nearby, called Kings Wood. This mine is one of a series used as winter hibernacula.

A satellite roost in a church porch, occupied by up to 35 adult female bats from April to June (Jones 1990), probably joins the other two roosts at the time of birth. The full size of the colony, and the number of births involved annually is currently poorly understood. Limited ringing studies in the past and in 1997 indicate that some bats from Brockley hibernate in Kings Wood, Cheddar and Banwell Ochre Mines.

In the winter of 1996/7 the Brockley Stable attic had substantial roost improvements carried out inside it. An internal, black-painted cowl was used to reduce draughts and light penetration through the access window. Boarding was fitted across the roof apex to further reduce both problems. Finally an incubator, similar to the one at Woodchester, was fitted beneath the inner roof apex. Initially the bats were slow to use the roost, presumably preferring the Kings Wood roost. However, in July about half of the mothers, thought to be about 60 altogether, moved into the roost and used the incubator. Many of them gave birth to female babies.

No further internal roost improvements are currently needed at this site. Hopefully the recent changes implemented will lead to a greater proportion of the colony using the incubator from 1998 onwards, with similar beneficial effects as seen at Woodchester since 1994. It is important to monitor the population performance of bats at this roost, partly as a check on the value of incubators reported at Woodchester.

Dean Hall

This colony numbers about one hundred and forty plus adult bats, with currently about 40 births annually. From the limited ringing studies carried out, most seem to hibernate locally in the abundant disused mines and scowles of the Forest of Dean. In summer the bats occupy a substantial roofspace in the attic of a long barn used at Dean Hall. It was re-roofed some years ago, and the colony has steadily built up again after the population crash in the mid 1980's. It enjoys extensive favourable foraging habitats nearby.

This is a roost which should show great benefits from installing an incubator in one section of the roofspace, and sectioning parts of it to reduce draughts. In cold weather the bats return late in the spring, or abandon this roost, presumably for a warmer underground roost elsewhere. Temperatures within the roost were from 7-10°C colder than at Woodchester in September 1997. The incubator there seems to improve the occupation of the Woodchester maternity roost over a longer period of the summer, and by a larger numbers of bats. It may also accelerate birth timing, especially in cold springs, as well as benefiting growth.

Iford Manor

This is the maternity roost for a colony of nearly three hundred adult bats, with about 90 births annually. It is a very important maternity roost, some of whose bats hibernate at Winsley, Combe Down, Brown's Folly and occasionally Cheddar. In recent years bats at Iford Manor have occupied two barns which exist on the estate. The larger one is very high, and its roost is only in semi-darkness. When its large double doors are closed, flight access is via a rather narrow vertical slit which is difficult for bats to negotiate. This building is regularly visited by people and used for various activities related to running the estate, some of which are noisy. Electric lights are switched on for these activities. This barn could be modified without restricting its use by the owners. A high-level false floor needs to be built, supported by strong beams. This would darken the roost section. The entrance slit should be widened, and a safe metal ladder attached to the wall for human access for dropping removal annually. Within the roost, a section at the far end from the entrance should have a large incubator (3m long) installed.

The smaller barn by the mill stream, which currently houses the maternity colony, is in need of major structural repairs. It is a much lower building, with two levels in the part used by the bats, which means that they are only just out of reach from the first floor. It also suffers from disturbance, but to a lesser extent, as it is mainly used to store equipment, some of which has been placed immediately underneath the bats. The internal attic section used by the bats as their main roost has smooth boarding. This is difficult for the bats to hang on, and probably restricts their ability to form dense circular clusters in cold weather.

Apart from securing the long-term future of the building, the boards in the bat section should be covered in coarse mesh, such as carpet mesh held securely by cross battens, and a large incubator installed. Human use of this section of the building from April to October should be strictly controlled.

Whether only one, or both barns should be treated as suggested will be a matter for considered debate, and discussion with the owners. It may be that the more isolated position of the mill-stream barn makes it the better option for the bats long-term.

Mells

This is the maternity roost for the largest colony in the current study, with over three hundred and ten bats, and about 95 births annually. A high proportion of the young remain hibernating in the tunnels through their first winter, whilst others use the disused limestone mines near Bath and Winsley, where they mix with bats from Iford. Most use unknown hibernacula.

In summer the colony currently occupies a number of scattered underground roosts, not all of which are known, after the loss of attic roost in the Fussell's Ironworks building in a fire some 10 years ago. A large incubator (3m long) was provided by English Nature funding and placed in an underground tunnel close to the cellars of a large old house nearby. Although this happened several winters ago, apart from occasional occupation in spring, the bats have not made serious use of it during lactation. Hence juvenile growth at this site has been regarded as 'unheated'.

The pregnant females seem to wait until just prior to giving birth before congregating in a vertical chimney some 1.5m diameter, and 1.5m high where they pack tightly together. There must be great difficulty in mother/offspring pairs reforming after foraging, in practice flight behaviour by juveniles, and the disposal of urine and faeces without soiling other bats.

The best solution would be the restoration of the ironworks building, so that a purpose-built attic roost could be provided again, with a large incubator, as suggested for the Iford barns. However, complete restoration would be very expensive. Some human habitation of the site may be essential to fund it.

Woodchester Mansion

This enormous building has an attic which is a maternity roost for a colony of some one hundred and ten bats, with currently about 34 births per year. Most of the bats hibernate locally in the disused limestone mines in the Stroud area, but some regularly travel across the River Severn to hibernate in the Forest of Dean mines. It has been intensively studied for over forty years continuously, providing important information of both scientific and conservation value on a wide range of bat ecological aspects.

The roost conditions within the building are very good at present. The maternity attic has draught-reducing measures in place, and a small incubator was installed in 1994. This was the prototype for those built in other roosts.

No further improvements are currently needed at this roost. If the population rises significantly over the years, a larger replacement incubator may eventually be required.

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Appendices

Appendix 1: Summary data for radius lengths of male bats by birth year and site

	MENDIPS/BATH AREA	WOODCHESTER
BIRTH YEAR	mean radius length (mm)	mean radius length (mm)
1991	54.72±1.14 34	55.38±1.04 10
1992	54.87±0.89 32	55.19±0.89 9
1993	54.86±1.06 36	55.47±0.52 6
1994	55.16±1.01 34	54.63±1.51 6
1995	55.11±0.92 39	54.69±1.09 9
1996	54.44±1.17 52	55.32±1.20 11
TOTAL	54.83±1.07 227	55.13±1.08 51

The first number in each cell is the mean, the second the standard deviation, and the third the sample size. The incubator was effectively installed at Woodchester from 1994.

Appendix 2: Summary data for radius lengths of female bats by birth year and site

	MENDIPS/BATH AREA	WOODCHESTER
BIRTH YEAR	mean radius length (mm)	mean radius length (mm)
1991	55.74 ± 1.11 44	55.31 ± 0.89 13
1992	55.62 ± 1.11 44	56.06 ± 0.96 12
1993	55.57 ± 0.98 31	55.50 ± 0.75 6
1994	55.68 ± 0.96 24	56.40 ± 1.62 11
1995	55.78 ± 0.81 39	56.83 ± 0.93 12
1996	55.47 ± 0.98 41	56.33 ± 1.06 12
TOTAL	55.64 ± 1.00 223	56.11 ± 1.08 51

The first number in each cell is the mean, the second the standard deviation, and the third the sample size. The incubator was effectively installed at Woodchester from 1994.

Appendix 3: Summary data for digit 5 lengths of male bats by birth year and site

	MENDIPS/BATH AREA	WOODCHESTER
BIRTH YEAR	mean digit 5 length (mm)	mean digit 5 length (mm)
1991	70.57±1.22 34	72.56±1.14 10
1992	70.92±1.36 32	71.63±0.75 9
1993	70.71±1.49 36	72.07±0.92 6
1994	70.19±1.33 34	70.73±2.20 6
1995	71.27±1.25 39	70.96±1.60 9
1996	70.39±1.58 52	71.16±1.66 11
TOTAL	70.82±1.42 227	71.54±1.50 51

The first number in each cell is the mean, the second the standard deviation, and the third the sample size. The incubator was effectively installed at Woodchester from 1994.

Appendix 4: Summary data for digit 5 lengths of female bats by birth year and site

	MENDIPS/BATH AREA	WOODCHESTER
BIRTH YEAR	mean digit 5 length (mm)	mean digit 5 length (mm)
1991	71.77±1.41 44	72.31±1.36 13
1992	71.52±1.40 44	72.42±1.53 12
1993	71.55±1.39 31	72.15±1.76 6
1994	71.77±1.67 24	72.72±1.87 11
1995	72.16±1.2.8 39	73.24±1.37 12
1996	71.57±1.19 41	72.69±1.22 12
TOTAL	71.72±1.38 223	72.62±1.49 51

The first number in each cell is the mean, the second the standard deviation, and the third the sample size. The incubator was effectively installed at Woodchester from 1994.

Appendix 5: Summary data for radius and digit 5 lengths of male bats by birth year at Mells

	MELLS	MELLS
BIRTH YEAR	mean radius length (mm)	mean digit 5 length (mm)
1991	no data collected	no data collected
1992	54.46±1.08 16	70.74±1.38 16
1993	54.04±1.14 20	69.29±1.38 20
1994	54.71±1.32 13	69.79±1.45 13
1995	54.91±0.93 24	70.86±1.58 24
1996	54.88±1.11 25	70.32±1.71 25
TOTAL	54.62±1.13 98	70.24±1.61 98

The first number in each cell is the mean, the second the standard deviation, and the third the sample size.

Appendix 6: Summary data for radius and digit 5 lengths of female bats by birth year at Mells

	MELLS	MELLS
BIRTH YEAR	mean radius length (mm)	mean digit 5 length (mm)
1991	no data collected	no data collected
1992	55.42 ± 1.23 11	71.37 ± 1.97 11
1993	55.28 ± 1.08 24	70.85 ± 1.24 24
1994	55.49 ± 1.45 22	70.61 ± 1.86 22
1995	55.33 ± 0.93 18	71.52 ± 1.58 18
1996	55.16 ± 1.00 19	70.67 ± 1.37 19
TOTAL	55.33 ± 1.14 94	70.95 ± 1.59 94

The first number in each cell is the mean, the second the standard deviation, and the third the sample size.

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