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Phil. Trans. R. Soc. Lond. B 1995 **350**, 153-161
doi: 10.1098/rstb.1995.0149

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Earlier breeding shortens life in female greater horseshoe bats

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SUMMARY

Life history theory predicts that an individual may gain in fitness by postponing reproduction if, by doing so, future reproductive capacity or longevity is enhanced. To test this theory I studied the survival and fecundity of earlier (start age 2 years) and later (start age 3 years or later) breeding female bats. Mature females produce one young annually, may miss breeding in some years and can still breed at age 29 years. Earlier breeders (EB) have similar mean skeletal size and birth date to later breeders (LB), but they have higher fat reserves late in their first winter and in their second autumn, when follicular development starts, and are probably superior foragers.

EB averaged 5.6 and LB 8.1 years at death. Higher mortality in the former group was associated with parturition later in July during early breeding attempts. Lifetime reproductive success (LRS) of both groups was highly variable and strongly correlated with lifespan, which explained 99 and 96% of observed variation respectively. Differences in mean lifespan had no significant effect upon the mean LRS of EB and LB (4.4 and 5.1 births per female respectively). Although earlier breeding reduces lifespan, because it starts a year earlier and breeding rates are higher in EB than in LB (96% cf. 85% per year), overall there appear to be equal fitness benefits. During rapid population recovery after a climate-induced crash, earlier breeding was enhanced and may be advantageous until the population stabilizes.

Hence studies testing life history theory should take account of population trends and climate. These seem to be crucially interconnected via food availability, the growth of individuals, and fat storage.

1. INTRODUCTION

The fitness costs of reproduction to young animals may be higher than to old ones, leading to higher mortality, for at least three reasons. First the energetic costs of reproduction for a given level of output, and their subsequent influence on survival, may be higher in young animals (see, for example, Clutton-Brock 1984). Second, if growth continues after breeding starts, resources devoted to reproduction may delay the achievement of maximum size or cause permanent stunting (Gross & Sargent 1985; Berglund & Rosenqvist 1986). Third, if survival rates decline with age, the risk of dying as a result of breeding represents a larger cost to young animals than to old ones, especially in species that breed on a large number of occasions (Pianka 1976; Curio 1988).

For these reasons young animals may gain in fitness by delaying reproduction. Delay is especially likely to occur in long-lived and iteroparous species, since the loss of one breeding attempt may not seriously reduce lifetime reproductive success (LRS). Provided that survival rates are enhanced by delayed breeding, there will be an overall improvement in lifespan, and hence LRS, if all other factors remain constant. Lifespan was identified as the major determinant of LRS in a range of bird species, with year of birth and territory quality important additional factors in some species (Newton 1989).

Population density may also influence the age of first

breeding (AFB). Selection is predicted to favour early reproduction in an expanding population and late reproduction in a shrinking one, if the total number of an individual's offspring are to remain constant (Charlesworth 1980). When population size is static selection should be neutral to AFB. Population density may influence AFB via the availability of resources, especially food supplies, which can have significant effects upon growth and long term survival (Albon *et al.* 1987; Ransome 1989). Climate is a major unpredictable factor influencing populations at all densities, often via its impact on food availability during critical periods such as reproduction and growth (Albon *et al.* 1983; Ransome & McOwat 1994). Its effect may therefore complicate attempts to test life history theories, even when population densities are taken into consideration.

The greater horseshoe bat, *Rhinolophus ferrumequinum* (Chiroptera: Rhinolophidae), is ideal for population studies (Ransome 1989, 1990). Although small (13–34 g), it can live for up to 30 years (Caubère *et al.* 1984). Females may give birth up to 29 years of age (R. S. Cropper & R. D. Ransome, personal observation). They grow to full skeletal size in about 60 days (Jones *et al.* 1995), but delay sexual maturity, starting to breed at 2–5 years, and have single births, normally annually thereafter until death. This unusual combination of features make them valuable subjects for testing predictions from life history theories.

In this paper I investigate the causes and conse-

quences of earlier breeding in greater horseshoe bats, the occurrence of earlier breeding in cohorts born over a 15 year period, the impact of earlier and later breeding on female mortality rates in relation to their age and their first parturition, and parturition timing. I also develop the mechanism that leads to severe population crashes (Ransome 1989), and measure the LRS of both groups, using the number of offspring born, and the impact of lifespan upon it.

2. METHODS

(a) *Study area and census methods used*

A small population of about 45 breeding females in a total population of some 180 individuals born at the Woodchester Mansion breeding site was studied (Ransome 1989). Most hibernated in the Stroud area nearby. The sites are described by Ransome (1968, 1989, 1990). The study started in 1956 and still continues. Cohorts born from 1975 to 1983 were selected for analysis since their census data were reliable and nearly complete by 1993, when only six bats (two early breeders (EB) and four late breeders (LB)) were still alive from the 69 that reached 2 years of age. For calculation purposes these bats were treated as if they had died at the end of 1993. This means that estimates of longevity and LRS are slightly lower than in reality, but they are much higher than occurs if the six bats are eliminated from calculations. Some analyses use data from bats born in other years, either to increase sample sizes or to provide data not available from cohorts born between 1975 and 1983.

The field data collected and census methods used to estimate populations are described by Ransome (1968, 1989). Census data from the breeding site for females are especially detailed and reliable. Over an 11 year period only one female bat born there, and shown to be alive by subsequent recapture in hibernacula, has missed a summer at Woodchester ($n = 119$; 297 bat year records). Females even returned in years when they failed to breed. Hence a failure to be recaptured at the breeding site was usually an indication of prior death in females. My study, involving a discrete female population whose members were reliably captured each summer, is therefore more similar to that of Coulson & Wooller (1976) of the kittiwake, *Rissa tridactyla*, than to those of Thompson (1987) of *Pipistrellus pipistrellus* and Boyd & Stebbings (1989) of the brown long-eared bat, *Plecotus auritus*. In these latter studies, as in most population studies, only samples of the total number of juveniles and females in the population were captured. The differences in the data collected affect the method of analysis that is appropriate. The sampling technique data set can be used to generate maximum likelihood estimates of annual survival rates. These estimates are less reliable than parameters calculated from complete population data sets, since four demanding conditions must be satisfied. One of them is that survival must be independent of age. I have already shown (Ransome 1991) that this is not true for the greater horseshoe bat, as did Davis (1966) for *Pipistrellus subflavus*. I have therefore analysed my data as annual percentage survival, to enable comparisons to be made between unequal sample sizes in figure 1. Sample sizes are provided in the legends.

One problem that results from using raw longitudinal population data is that sample sizes decrease rapidly with time so that obtaining statistically significant differences between samples is impossible. To overcome this difficulty I include data from individuals born between 1958 and 1962, just before the first major population crash (Ransome 1989). I captured the breeding cluster annually in August from 1961

to 1969; so mortality over the first 7 years of life was monitored for most individuals.

(b) *Assessment of reproductive state and parturition timing*

Female reproductive success was normally determined by captures in July or early August in the breeding attic at Woodchester. If parous, females had attached young, or showed bald mammary glands with enlarged nipples, and enlarged red or pink pelvic false teats. Females whose young died soon after parturition showed enlarged nipples and false teats that were white. In years when summer captures at the breeding site were not made (1978, 1979), the state of the false teats in winter showed whether a female had bred in the previous summer. Non-breeders, and those that aborted fetuses, show shrunken nipples compared with breeders that lactated, even for a short period. Non-parous females have no false teats. For analysis purposes females that aborted were treated as non-breeders, since it was usually difficult to determine miscarriage with certainty.

Birth dates of individual young were determined from growth parameters as part of an ongoing study started in 1984, which involved captures every 2–3 days during early growth (R. D. Ransome, unpublished data). From 1986 to the present, captures of mothers carrying their young allowed the parturition timing of specific females to be identified. The young's birth date is identical to its mother's parturition date for the year in question. In the text birth date is used with reference to the young, or to mother and young if it applies to both. Parturition date refers only to mothers.

(c) *Body condition index and feeding success calculations*

Body mass, accurate to 0.1 g, was measured on three very similar dates annually each October (about 24th), January (about 20th) and April (about 3rd) during the hibernation period from 1975 onwards. Data were converted to a condition index by dividing the mass by the individual's forearm length in millimetres (Speakman & Racey 1986), then multiplying by 56.0 mm (approximately the mean forearm length of breeding females). This procedure corrects for skeletal size differences between bats, without loss of mass units. For identical samples standard deviations for condition were almost always less than those for mass, whereas means were very similar.

Feeding success from dawn foraging was estimated from collections of faecal pellets from individuals bagged separately after early morning capture in the summers of 1990 to 1994. Methods are detailed in Jones *et al.* (1995).

All statistical calculations were done with use of MINITAB version 8.21.

3. RESULTS

(a) *Occurrence of earlier breeding*

The numbers of EB and LB recruited to the breeding population from different cohorts varied erratically among years throughout the main study period (table 1). However, no EB were recruited from cohorts born between 1984 and 1986, when the population crashed (Ransome 1989), and EB dominated recruitment from cohorts born from 1987 to 1990, as it recovered. As numbers were small, data from 4 year groups were used for statistical testing (table 1). The last period,

Table 1. Numbers of EB and LB from cohorts born between 1975 and 1990, and their productivity up to 1983

(EB, earlier breeders (aged 2 years); LB, later breeders (3 years or older). Four-year summaries are used in statistical analyses (see text). Figures in brackets are total numbers of young born per cohort for 1975–1983 only.). For example three EB from the 1975 cohort gave birth to a total of 19 young in their lifespan.)

year of cohort's birth	no. 2 year breeders (no. young)	no. 3+ year breeders (no. young)	total no. breeders	mean cohort birth date (July)
1975	3 (19)	6 (35)	9	11
1976	0 (0)	3 (31)	3	13
1977	3 (23)	5 (18)	8	15
1978	2 (8)	1 (1)	3	19
1975–78	8 (50)	15 (85)	23	14.5
1979	3 (7)	3 (8)	6	23
1980	4 (14)	8 (31)	12	10
1981	4 (20)	4 (19)	8	12
1982	3 (5)	1 (3)	4	12
1979–82	14 (46)	15 (51)	30	14.3
1983	3 (8)	2 (13)	5	23
1984	0	4	4	19
1985	0	5	5	17
1986	0	0	0	29
1983–86	3	11	14	22.0
1987	2	0	2	5
1988	2	2	4	9
1989	6	0	6	10
1990	1	1	2	5
1987–90	11	3	14	7.3
all years	36	44	83	14.5

Table 2. Condition of female bats in winters before and after breeding by age of first breeding

(Data are mean condition in grams (see text). Sampling dates for each month were kept constant to within 4 days from year to year. Data in italics were obtained immediately after first breeding. Standard deviations and sample sizes are given in brackets. * Indicates a significant difference ($p < 0.05$) between the condition of earlier breeders (2 years) and later breeders (3+ years).)

winter	month	age of first breeding		p (t test)
		2 years	3+ years	
first	October	24.3 (1.1; 10)	23.9 (2.5; 14)	0.61
first	January	21.0 (1.0; 14)	20.1 (1.4; 18)	0.032*
first	April	17.5 (1.0; 12)	16.7 (0.7; 18)	0.038*
second	October	26.9 (1.4; 14)	25.5 (1.9; 24)	0.011*
second	January	21.9 (1.1; 11)	21.5 (1.0; 23)	0.35
second	April	18.6 (0.8; 14)	18.2 (0.9; 26)	0.11
third	October	<i>28.8 (2.3; 12)</i>	27.5 (1.5; 14)	0.11
third	January	23.2 (1.4; 9)	23.0 (1.0; 16)	0.83
third	April	18.7 (0.6; 10)	19.1 (0.9; 16)	0.19
fourth	October	28.9 (0.9; 6)	<i>29.5 (1.2; 14)</i>	0.22
fourth	January	24.0 (0.8; 6)	23.7 (1.2; 10)	0.52
fourth	April	19.9 (0.6; 4)	19.5 (0.7; 9)	0.33

when the population was rising, was significantly different from the first and third periods ($\chi^2_1 = 8.34$, $p < 0.005$; $\chi^2_1 = 6.58$, $p < 0.025$ respectively).

(b) Factors influencing earlier breeding and its impact upon body condition

Comparisons of EB with LB showed no significant differences between forearm lengths which were respectively (mean/mm): 56.26 ± 0.86 (34); 56.21 ± 1.03 (40); $t_{51} = 0.88$, n.s. Also, the mean birth date of EB (10 July ± 7.5 days (15)) was not significantly different from that of LB (12 July ± 6.9 days (13)); $t_{25} = 0.81$, n.s.).

However, condition before breeding was significantly higher in EB during three periods (table 2); t tests were used, rather than analysis of variance (ANOVA), because data cells were not completely independent. The same bats, but not all of them, often appeared in successive samples. The periods were midwinter and spring of the first year and autumn of the second winter. EB appear to be better foragers than LB as they produced twice the dry mass of faecal pellets (mean 529 ± 129 mg (4)) after August dawn feeds during their second summer as non-parous females than did LB (mean 242 ± 63.3 mg (4); $t_4 = 4.00$, $p = 0.016$).

Mean body condition in October increased with each additional year of age by about 2 g for the first 3 years in both sets of breeders, but was highest in the former group (EB). Having the first baby did not prevent EB from continuing to improve autumn condition in their third year. However, they subsequently lost reserves in hibernation (October/April) faster than did LB (10.1 g cf. 8.4 g). They also failed to increase condition significantly in their fourth October, after having bred for their second time. Since the condition of LB also rose by 2 g after having had their first baby, they were heavier than EB for the first time in the October of their fourth winter.

Mean body condition in April, close to the end of the hibernation period when body reserves are quite low (Ransome 1968, 1990), increased in both groups by 1–1.5 g, but only between the first 2 years. No increase in mean spring condition occurred in the EB after their first parturition, but a further 1.2 g increase took place after their second parturition. In contrast, LB continued to increase at similar levels (0.9 g) in their third April, but only by 0.4 g after giving birth for the first time.

(c) The effect of earlier breeding upon mortality

The mean age at death was 5.6 ± 4.9 years (44) for EB and 8.1 ± 5.0 years (93) for LB (data for 1958–1962 and 1975–1983 births combined). These differences are significant ($t_{86} = 2.75$, $p = 0.0073$). Mortality through the female's early life for these periods was analysed by age and by parturition sequence (figure 1). As predicted, both analyses show that the highest mortality rates occur in EB, but the pattern is complex, with both groups of breeders showing higher mortality after their first and third births, and lower mortality after their second birth. Parturition sequence produces

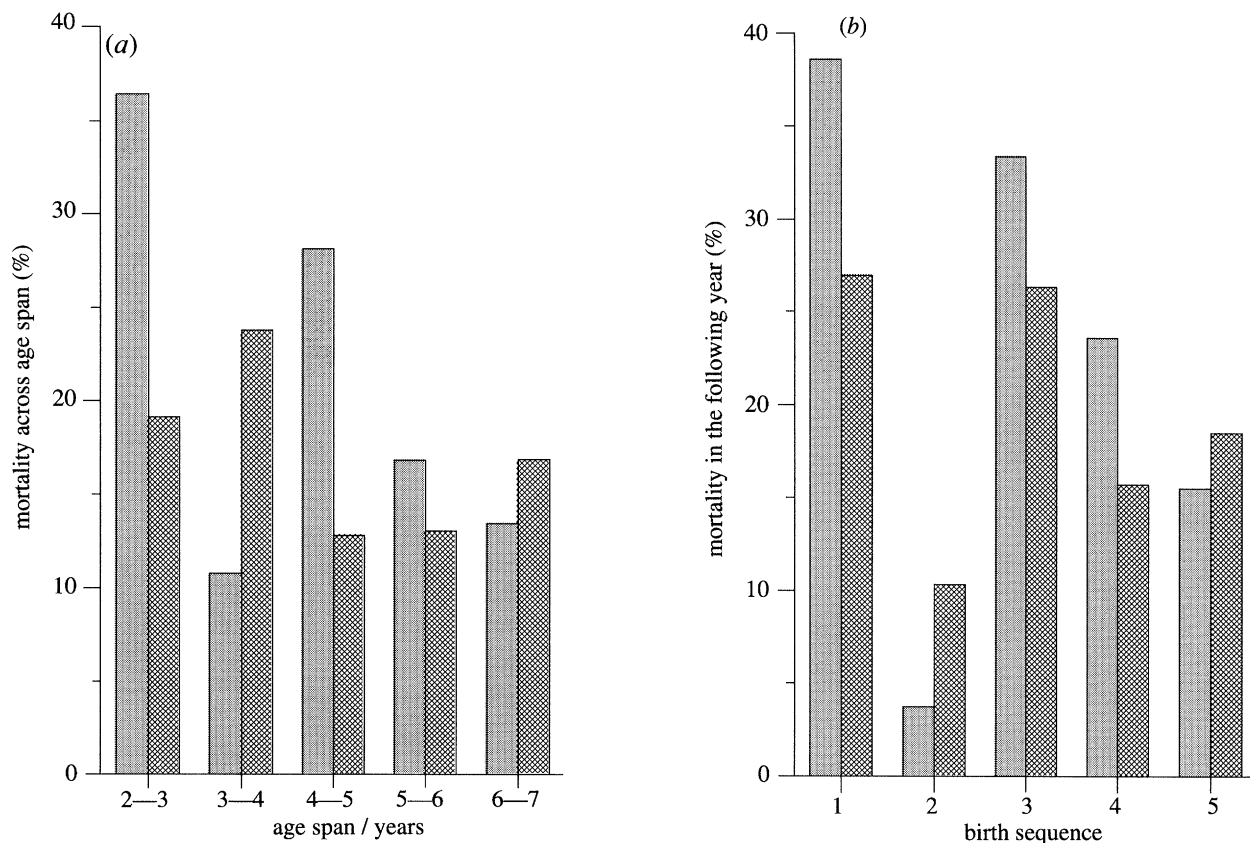


Figure 1. Mortality of earlier and later breeders by age span and by birth sequence. In each graph data for earlier breeders are given in the first (paler) column of each pair. (a) Mortality between specified ages. (b) Mortality in the year following the specified number of births. Mortality levels are higher in graph (b) owing to the exclusion of immature and non-breeding years (see text). Sample sizes: (a) EB, 44 aged 2, 13 aged 7; LB, 115 aged 2, 45 aged 7; (b) EB, 44 first birth, 13 fifth birth; LB, 93 first birth, 38 fifth birth. Data for 1958–1962 and 1975–1983 combined.

the most similar pattern between the two groups (figure 1b).

Mortality of 28% occurred between ages 1 and 2 years (Ransome 1991), and it fell to 19% ($n = 115$) between the ages of 2 and 3 years in non-parous LB, compared with 36% ($n = 44$) after EB's first birth at the same age (figure 1). Mortality was also high after first births by LB at 27% ($n = 93$) when these females were a year older. Females usually show mortality in the range 9–14% from 6 to 12 years of age, rising afterwards (Ransome 1991).

Birth timing is known to be important in determining the long term survival of cohorts of young mammals, with later breeding leading to higher mortality rates (Albon *et al.* 1983; Ransome 1989). Regression of the parturition date of breeding females aged from 2 to 8 years against their age showed a significant negative relation ($F_{1,98} = 20.07$, $p < 0.001$; $y = 25.9 \text{ July} - 2.15 \text{ years of age}$). Hence younger females give birth later than older ones. The mean parturition date at first breeding was 24 July for EB and 17 July for LB ($t_{22} = 2.20$, $p = 0.04$; 1986–1993 data). This significant difference seems to be linked to the higher mortality rates shown by EB (figure 1b). The mean parturition date of all females dying in the year after giving birth to their first to fourth young was 24 July, whereas for survivors it was 15 July ($t_{23} = 3.76$, $p = 0.001$). These data are important, since they show that late parturition carries an increased risk of

mortality to the mother, as well as her offspring, over the following year. After cold springs, such as in 1986, when mean birth dates are very late (Ransome 1989; Ransome & McOwat 1994), some females may survive giving birth very late in July, or even in early August, owing to the death of their young from starvation in early or mid lactation. Alternatively they may survive a severe summer by aborting during pregnancy. These events are all more likely to occur in LB. EB usually complete lactation, but produce stunted young in severe summer climates (R. D. Ransome, unpublished data).

(d) *Earlier breeding and breeding frequency*

Females may give birth annually until death, or miss parturition in one or more summers. EB show significantly higher breeding frequencies at 96.1% of opportunities compared with 84.7% for LB ($t_{129} = 4.96$, $p < 0.0001$). The frequency of breeding is especially low in LB in the year following their first parturition, when only 73% bred compared with 96% of EB. Breeding frequency in both groups falls during periods of severe climate and vice versa (R. D. Ransome, unpublished data).

(e) *The effect of earlier breeding upon LRS*

The mean number of young born to EB over the

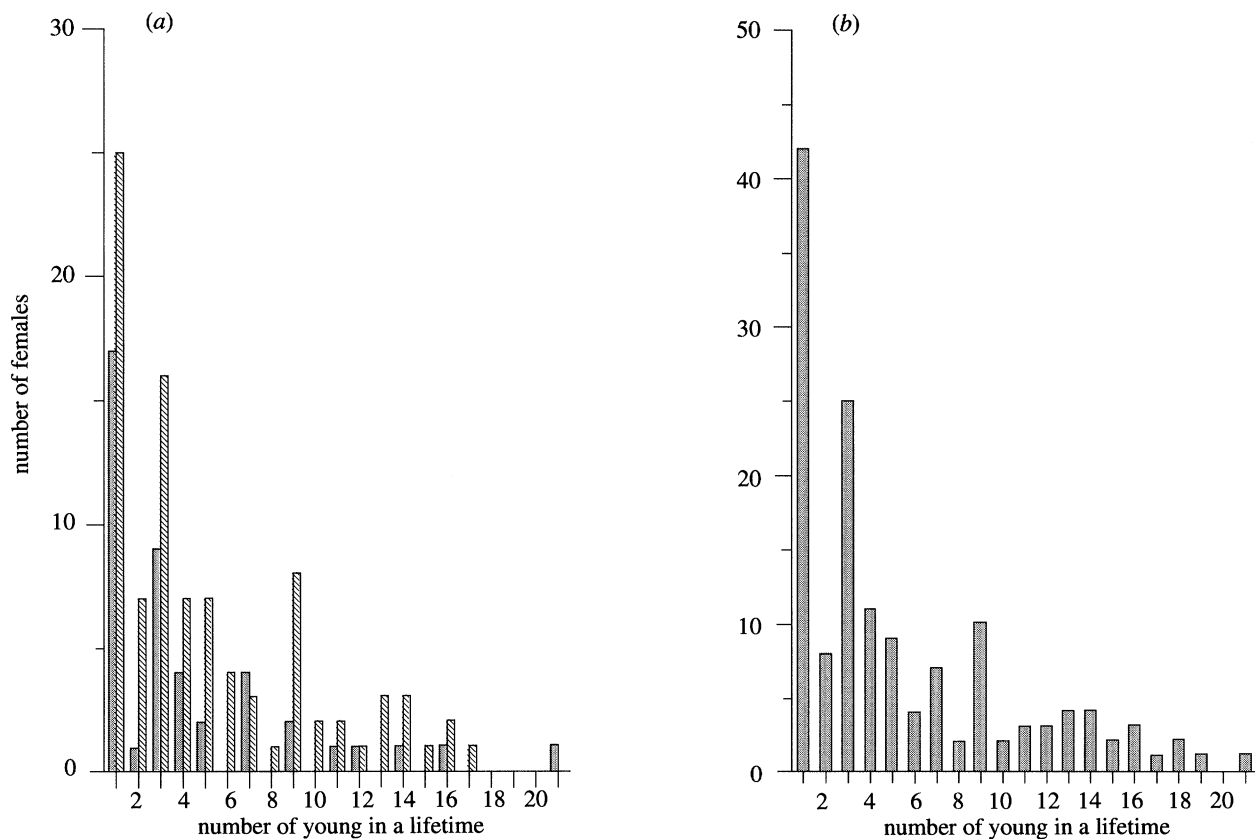


Figure 2. Lifetime reproductive success (LRS) of female bats born to cohorts from 1958–1962 and 1975–1983. Note that certain individual females are still alive and may produce further young. They are two that have had 14 young, one ten young, two nine young, and one five young. Productivity was seriously reduced by a major population decline in 1986 caused by climate. (a) LRS by age of first breeding. Data for early breeders are given in the first (darker) column. (b) Total LRS for all breeding females, including seven whose age of first breeding was unknown and therefore were omitted from graph (a).

whole study period was 4.4 ± 4.6 (44), compared with 5.1 ± 4.4 (93) for LB ($t_{81} = 0.38$, n.s.). Productivity varied among cohorts, but was highest in the 1975–1978 group, which had early mean birth dates and experienced warm springs and summers in its early years (table 1). EB were more productive than LB during this period, though not significantly so.

Breeding females showed great variability in their LRS (figure 2). Lifespan explained 99.2% of variation in the LRS of EB ($F_{1,43} = 5401$, $p < 0.001$) and 96.2% in the LRS of LB ($F_{1,92} = 2310$, $p < 0.001$).

High variability occurs among the productivity of cohorts (table 1). Some 81% of this variability is related to the mean birth date of the cohort. More young were born to cohorts whose mean birth dates were early ($F_{1,8} = 29.98$, $p < 0.001$, $y = 70.8 - 2.47x$). The 1982 cohort was excluded from this analysis since for these bats the three crucial years (after the first and third young of EB and the first baby of LB were 1984, 1985 and 1986, which were climatically very severe and triggered a major population crash in 1986. If the 1982 cohort is included the relation is still significant ($F_{1,9} = 8.83$, $p = 0.018$).

4. DISCUSSION

(a) Occurrence and causes of earlier breeding

The age of first breeding rises with increase in lifespan in a wide range of birds and mammals. As it rises, so does the potential for variation in the age of first breeding. Variation is particularly high relative to lifespan in many raptors, sea birds, geese and swans (Newton 1985; Ollason & Dunnet 1988; Bacon & Andersen-Harild 1989; Owen & Black 1989; Saurola 1989; Wooller *et al.* 1989). Newton (1989), reviewing these studies, felt that recruitment to a breeding population was often a competitive process in which foraging skills, experience and social status were all involved. In species subject to annual variation in food availability, early breeding was more likely in good years and in years when population levels were low, since resource competition was reduced. However he felt that, since at any given time some individuals start breeding much younger than others, age was not the only factor giving precedence in recruitment.

Earlier breeding by certain individuals from a cohort may be enhanced by circumstances promoting their growth or accumulation of body reserves. For example birth or laying date could influence AFB by altering the time that is available for maturation during the first summer. Also foraging skills may influence growth and fat deposition during immature years.

The importance of birth or laying date to survival and future breeding success has already been shown (see, for example: Mills 1973, 1989; Albon *et al.* 1987; Le Boeuf & Reiter 1988). Mills (1973) found that a negative relation exists between age and laying date in red-billed gulls, *Larus novaehollandiae scopulinus*, and Mills (1989) showed that females laying early in their first year fledged more young in a lifetime and lived longer. He explained this by suggesting that they were superior at gaining food in competition with others.

Of the three phenotypic factors investigated in the present study, forearm length (reflecting skeletal size), birth date and body condition, only the last was found to be important in influencing AFB. It showed a positive relation to earlier breeding. Furthermore, condition was only significantly related to AFB towards the end of a female's first winter and at the start of her second winter. Condition differences between females of the same age must mainly be due to fat levels, the main body reserves, since they were corrected for size and the gut is virtually empty during hibernation torpor (Saint-Girons *et al.* 1969; R. D. Ransome, personal observation). Higher fat levels are known to promote both the onset and the maintenance of breeding in mammals (Sadler 1969; Frisch & McArthur 1974; Frisch 1980, 1988) and birds (Drent & Daan 1980; Martin 1987).

The ovarian follicles of most bats that hibernate, including greater horseshoe bats, start to develop in late summer (Wimsatt 1944; Oh *et al.* 1985). The connection shown to exist between a higher October condition before their second winter and parturition the following year in EB may result from higher fat reserves promoting follicular development. Higher condition levels shown by EB late in their first winter seem to reflect better control of fat losses through the hibernation period. Such control is complex, involving precise temperature selection within hibernacula, which influences arousal frequency in relation to insect availability and the chances of successful winter feeding (Ransome 1968, 1971). EB control their fat reserves better in winter before breeding, build up larger reserves at the start of hibernation (see below), breed at higher rates and continue lactation in severe summer weather. Hence they may be better, or more highly motivated, foragers than LB, rather than better at selecting the most favourable temperatures for hibernation. This view is supported by the much higher estimated masses of dry faecal pellets produced by EB after dawn foraging in the August before their second winter, at the time follicular development starts.

It could be argued that earlier breeding is triggered by changes in reproductive hormones which motivate increased food consumption in a female's second summer and during subsequent hibernation, leading to superior body condition, rather than vice versa. This explanation is less likely to be correct, as significant differences in condition between future EB and LB already exist early in their first winter, long before follicular development starts in either group (table 2).

If the explanation given above is correct, the occurrence of earlier breeding would be expected to vary among years as population density and climate

affected food availability as suggested by Newton (1989). High density and severe climate should depress earlier breeding, and vice versa. This is supported by the data (table 1; compare periods 1983–1986, when climate was severe and population level was high, with 1987–1990, when climate was mild and population level was low).

(b) *The impact of earlier breeding upon body condition and mortality*

Increases in mean body condition in October with age in the early years of about 2 g per year may reflect improving fat reserves, but could also be due to changes in lean body mass. In April, when reserves are low, an increase of about 1 g per year suggests that lean body mass change is a contributory factor. Since linear skeletal growth is complete within the first summer, most mass changes must occur in the body tissues and organs, as was shown by dissection (Ransome 1968). If it is assumed that all April increases are due to lean body mass, it follows that at least an extra 1 g per year of fat reserves was progressively stored in each October in both breeding groups, even after giving birth for the first time. EB showed higher levels of reserves, however.

Earlier breeding virtually prevented an increase in April condition between the second and third years, whereas non-parous LB at the same ages showed further April condition increases, presumably owing to lean body mass changes. This indicates that a growth or body reserve penalty may be incurred by EB, as predicted by life history theory.

Annual mortality was shown to fall in non-parous females as they aged. Hence the rise in mortality shown by both EB and LB after their first parturition suggests that the survival costs of rearing young are substantial. Mortality differences between EB (36%) and LB (19%) aged from 2 to 3 years must be due to breeding since only the former produced young. As EB seem to be superior foragers to LB (see above), we should predict them to have lower mortality if breeding had no longevity costs. A major finding of this study is that earlier breeding significantly reduces lifespan, despite the fact that EB are probably superior foragers. This paradoxical situation is linked to the negative correlation shown to occur between parturition dates and age in female breeders aged 2–8 years and to the positive correlation between parturition date and mortality. The high stress of breeding for the first time in both groups is further increased because young mothers give birth late in July, reducing the time available for postreproductive recovery before hibernation starts.

Lactation continues for about 45 days (Jones *et al.* 1995), so that birth dates late in July mean that young are not weaned until mid September. As the build up of fat reserves for hibernation can occur rapidly in late September and early October in favourable climate (R. D. Ransome, unpublished data), fat accumulation may not be a major obstacle to winter survival in most years. Low fat levels in lactating females at the end of August (Harrison-Matthews 1937; R. D. Ransome, unpublished data) could prevent follicular develop-

ment and lead to a year without breeding as has been shown to occur. Furthermore, skeletal calcium deficiency develops in all bats during pregnancy and lactation and in late hibernation (Kwiecinski *et al.* 1987). Calcium therefore needs to be replenished after lactation but before hibernation starts to cope with the further losses that take place then. As most insects are deficient in calcium (Studier & Sevick 1992), late-lactating females may be unable to restore levels sufficiently before hibernation starts, especially in a poor September climate, and so suffer severe calcium deficiency stress. Barclay (1995) has recently argued that calcium, rather than energy, is more likely to be the major limiting factor for breeding female bats. Faecal pellet analyses suggest that serious iron deficiency also develops in lactating female bats (Studier *et al.* 1994), since most insects are deficient in this element as well. If iron deficiency also occurs in greater horseshoe bat females, its effects will add to the stress of calcium deficiency.

Although first births in both groups failed to limit further increases in October fat reserves, losses during the subsequent winter (10 g) were higher than in any previous year. This may reflect the stressed state of females at that time and be linked to the high mortality recorded after first births. Three factors may contribute to the surprisingly low mortality shown after second births. One is that 21% of the females did not breed the year after their first parturition, and 14% for two years. Consequently many had an extra year or even two in which to recover before their second breeding attempt. Failure to breed can occur at other periods of an individual's lifespan, but is much less synchronized among individuals. Secondly parturition dates for second births, especially after 1 or 2 years without breeding, are earlier owing to the effect of the mother's age. The risk of dying reduces, possibly because time for recovery from stress increases. Thirdly they may benefit from experience gained from their first parturition. Third births usually follow on directly after the second in mothers that miss a year or two after their first birth, while other mothers have three consecutive births. The latter are usually EB. Whichever of these patterns occurs, both groups show high mortality after their third birth, possibly owing to the accumulated effects of reproductive stress (figure 1*b*).

A non-breeding period, especially soon after recruitment, although potentially reducing LRS, may be a fortunate response to severe stress which enables individuals to avoid death and permits future breeding. Non-breeding has been shown to occur in many iteroparous birds that experience annual fluctuations in conditions (see, for example: Wooller & Coulson 1977; Owen & Black 1989; Saurola 1989; Wooller *et al.* 1989). Such a response requires a mechanism to explain how it occurs and why it only happens in certain individuals within a population. As discussed above, a failure to breed in a particular year may be caused by low fat reserves in August suppressing follicle development and vice versa (Frisch 1980). Low fat reserves may occur in young females that give birth late in July and are still lactating in late August or early September and in females that are poor foragers.

Years without breeding occur much more frequently in LB despite their being a year older at the same birth sequence than EB. Since this means LB are likely to have earlier parturition dates, it suggests that LB are less successful foragers than EB.

Overall the evidence presented further supports the view expressed by Drent & Daan (1980), Grafen (1988) and Ransome (1990) that animals have an ability to assess their current physiological state quite accurately, and use the information to modify their behavioural and reproductive strategies. Their assessment capacity seems to include a fuel gauge.

(c) *The effect of earlier breeding upon longevity and LRS*

EB breed 1 year earlier than LB and at higher rates (96% of opportunities cf. 85%). Their mean LRS, measured as number of young born in a lifetime, however, is not significantly different from that of LB, as the mean longevity of EB is shorter by about 2.5 years. Life history theory predictions are therefore supported by the major findings of this study. Shorter mean longevity in EB seems to result primarily from the higher mortality seen after their first and third young, when parturition dates are still late in July, especially after severe springs, rather than an inability to live for many years. One EB lived for 24 years and produced 21 young (figure 2).

Severe climate seems to affect breeding by EB and LB differentially. Since they are able to control autumn and winter fat levels better than LB, probably owing to being superior foragers, EB are more likely to ovulate successfully in spring and/or less likely to abort during pregnancy in years when severe climate occurs in April and May. Low temperatures restrict both the number of feeding opportunities in bats and their success levels (Ransome 1973; Rydell 1989), prolonging gestation (Racey 1973). Ransome & McOwat (1994), in a study of three separate breeding colonies, showed that mean temperature in these months explained between 70 and 93% of variation in mean birth date in July. A drop of 2 °C in mean temperature delayed mean birth date by about 18 days. Ransome (1989) showed that the survival of cohorts of young was negatively correlated with mean birth date. Skeletal growth was also negatively correlated with birth timing, with mean forearm length declining by about 0.1 mm per day. Smaller females, especially those below 54.0 mm in forearm length, rarely survive more than a year or two (R. D. Ransome, unpublished data). Severe nutritional deprivation, during embryonic or juvenile growth, has a long term effect upon the longevity of all members of a cohort. The present study shows that a cohort's mean birth date is negatively related to the productivity of young from those that survive to become breeders. Similar conclusions were reached by Albon *et al.* (1987) for females in a study of red deer, *Cervus elephas*. They showed that the early growth and survival of young affected estimates of female LRS, and argued that female fitness can only be assessed if these aspects are also measured. My own data tend to confirm this view, but are currently insufficient to

present here. They also showed that much of the variation in female breeding success is environmental in origin, and this study supports their findings, especially with regard to climate.

Virgin female hamsters, *Mesocricetus auratus*, deprived of food in the first 50 days of their lives produce during adult life smaller litters and litters with sex ratios biased towards females (the smaller sex), even when subsequently fed *ad lib* (Huck *et al.* 1986). Furthermore their female offspring also show the same effects when they reproduce, despite being on *ad lib* diets throughout their lives (Huck *et al.* 1987). If evidence from these wild and captive studies are combined, one severe summer may influence the growth, fecundity, sex ratios and survival, not only of the cohort born that year, but also of subsequent cohorts produced by any breeding survivors. Such a hypothesis would help to explain the continued decline of greater horseshoe bat populations for several years after severe summers such as those in 1964 (Ransome 1989). Litter size reduction in these bats is not possible, but its equivalent may be extra years without breeding as noted in this study, and it is already known (Ransome & McOwat 1994) that population sex ratios alter after a climate-induced population crash. In this bat the ratios favour males, which is the sex requiring less maternal investment.

Nutritional deprivation in a particular spring and summer, besides curtailing the lifespan of that cohort of young and its future fecundity, seems also to cause the stress-induced death of many mothers within a year. Parturition date is a crucial factor, especially in the survival of young mothers, and further explains how a severe spring climate can cause a long term decline in a population by removing a major part of its future reproductive potential.

Lifespan was found to be the major determinant of LRS in both EB and LB, explaining over 95% of the variation. This high figure is due to births being annual and single, with most females breeding every year, and the use of birth numbers as the measure of LRS. Annual single births are also found in red deer *Cervus elephas* (Clutton-Brock *et al.* 1988) and northern elephant seals *Miroounga angustirostris* (Le Boeuf & Reiter 1988). Both studies show that lifespan is crucial in determining LRS.

In conclusion, this study has supported many of the predictions derived from life history theory. It is one of the few that provides LRS data for a long lived mammal, and the first for any bat species. It also offers mechanisms explaining why superior foragers become EB, as long as the climate is favourable, and why EB, although they are probably superior foragers, may suffer higher mortality rates than LB in severe climate, via higher breeding frequencies, more successful lactation and especially later parturition timing during their early breeding attempts. It provides further detail of the mechanism operating in population regulation by climate of this endangered species. Finally it provides support for the presence of a fuel gauge in bats, as argued by Ransome (1990).

I am grateful to numerous past and present pupils of Rednock School, Dursley, for help with data collection, especially Andrew Hulbert, Robert Swan, David Ransome, Richard Stuckey and Tim Chapman. I thank the

Woodchester Mansion Trust and Miriam Kelly for access to the Mansion, the Royal Society for supporting me for many years and the Leverhulme Trust for recent assistance.

Dr G. Jones gave invaluable help and advice in the preparation of this paper, particularly with statistical analyses. I am also grateful to Professor P. A. Racey and an anonymous referee whose helpful criticisms improved my first draft.

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Received 15 February 1995; accepted 29 March 1995