The influence of body condition on sexual development of male Brown long-eared bats (Plecotus auritus) in the wild

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(With 5 figures in the text)

The relationship between sexual maturity and body condition was examined in a sample of 57 male Brown long-eared bats (Plecotus auritus) captured in autumn 1984 from nursery roosts in north-east Scotland (57°N). A direct relationship was found between reproductive status, which was established by external examination of the genitalia, and body weight. No such relationship was established between reproductive status and forearm length. A strong direct relationship was found between reproductive status and an index of body condition (body weight/forearm length). Three of the males examined had distended epididymides, suggesting they were filled with spermatozoa, and that the bats concerned had recently undergone spermatogenesis.

Reproductive status also varied between maternity roosts. Bats from roosts in areas with a high proportion of tree cover were more sexually developed, and in better body condition, than bats from roosts in areas with less tree cover.

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Introduction

The annual cycle of reproductive events in male bats of the temperate zone is well established (Gustafson, 1979; Racey, 1982). In general, spermatogenesis progresses throughout the summer and copulation occurs mainly in autumn. Spermatozoa remain stored in the cauda epididymides throughout the winter hibernation period. In the tropics and subtropics, reproductive patterns are more diverse (Krishna & Dominic, 1981). In many species, spermatogenesis is seasonal and is followed immediately by copulation, fertilization and pregnancy (Krutzsch, Watson & Lox, 1976; Krishna & Dominic, 1981). In some of these seasonal breeders, sperm storage coincides with an unfavourable, usually dry season; spermatogenesis, once established, is continuous in a minority of species.

Many studies have attempted to determine the age at which male bats achieve sexual maturity, defined as the production of fertile spermatozoa and ability to mate, although there have been few attempts to test whether sperm produced by pubertal bats is fertile. Despite this limitation, estimates of time to reach puberty are comparable between studies (Tuttle & Stevenson, 1982).
In seasonally breeding bats of both the temperate and tropical zones, where bats are born during a favourable period of food supply, the majority of individuals of most species do not reach puberty during the season of their birth. Spermatogenesis commonly occurs during the second favourable season, or first period of six months' good food supply (Racey, 1974). The bats are therefore 9–12 months old at puberty and mate shortly afterwards. One exception is the Greater horseshoe bat (*Rhinolophus ferrumequinum*) in which most males mature during their third autumn (Dinale, 1964).

Male young of aseasonal species generally develop more rapidly. *Myotis nigricans* mature sexually in 2.5–4 months (Wilson & Findley, 1970; Myers, 1977) and Marshall & Corbet (1959) estimated that *Chaerephon* (= *Tadarida*) *hindei* achieves puberty in Malaysia in 2–3 months.

Most seasonally breeding bats are morphologically mature in approximately two months (Orr, 1970; Tuttle & Stevenson, 1982). The long delay before sexual maturity is therefore exceptional for mammals which normally undergo puberty in advance of completing morphological development (Sadlier, 1969). Sadlier (1969) and Frisch (1980) have both emphasized the importance of body condition for the attainment of puberty. A probable explanation therefore of delayed puberty in seasonally breeding insectivorous bats is that they are unable to achieve a target body condition during their birth season before food availability decreases and they begin seasonal hibernation (Racey, 1982).

A further complication in the temperate and subtropical zones may be the light regime. Photoperiod may be a proximate factor which links the sexual cycle to food availability. Bats may fail to initiate spermatogenesis, even in areas where food is plentiful, during the summer of their birth because photoperiod is decreasing, and increasing photoperiod is required for the release of pituitary gonadotrophins. Lecyk (1963) has shown that immature voles (*Microtus* sp.) are unable to become sexually mature in decreasing photoperiod.

This study aimed to assess the importance of body condition on sexual maturity in free-living Brown long-eared bats (*Plecotus auritus*) in north-east Scotland (57°N), close to the northern border of their distribution. In particular, tests of two hypotheses were sought:

(a) Immature male bats in good body condition in the summer of their birth will be more sexually developed than those in poor condition.

(b) Body condition and sexual development will vary spatially between roosts as a result of differing opportunities to forage at different sites.

As a null hypothesis, it might be expected that no development beyond descent of testes and epididymides would occur in the year of birth, and that this state would obtain in all roosts if increasing photoperiod were a necessary proximate stimulus for the release of pituitary gonadotrophins.

**Methods**

Bats were captured from 9 maternity roosts. One was in the valley of the River Spey, the remainder were in the valley of the River Dee, in north-east Scotland. All the roosts on Deeside were within 20 km of Aboyne. At least 2 visits to each roost were made in late August and early September 1984 between 10.00 h and 13.00 h. All bats were captured by hand or hand-net, placed in cotton bags and examined within half an hour of capture. Although there is a diurnal cycle of weight change in insectivorous bats (Kunz, 1980), and bats may lose weight rapidly whilst held briefly in captivity (Stebbings, 1966), the timings of capture in different roosts and the order in which bats were examined were unlikely to be biased with respect to sexual development of immature bats in the sample.
Female bats were separated into 2 classes after examination of their nipples (after Racey, 1974). Nulliparous females had rudimentary nipples, and included immature females born in 1984 and possibly older bats which had not given birth in 1984. Parous females were mostly in late lactation and had probably all given birth in 1984.

Males were divided between 6 classes after examination of their external genitalia (generally after Racey, 1974):

Class I: epididymides not descended to inguinal area
Class II: epididymides descended—black tunica vaginalis, testes diminutive
Class III: as II but testes small (< 2 mm)
Class IV: as III but testes medium-sized (2-4 mm)
Class V: as III but testes large (> 4 mm)
Class VI: distended cauda epididymides, tunica vaginalis speckled (as a result of dispersion of the pigment cells).

Examination of the wing membrane texture and pelage colour of these male bats suggested they had all been born 6-8 weeks previously; classes I to V inclusive correspond with the term ‘immature’ in the terminology of Racey (1974), whilst class VI correspond with the term ‘adult’. The body weight and forearm length of all bats were measured using a Pesola spring balance (±0.1 g) and vernier caliper (±0.1 mm), respectively. Since classifications were made prior to body measurements, the classifications were not biased by any information on body condition.

Results

A total of 85 bats were captured and examined. Of these 57 were males and 28 were females, of which 18 were parous.

The sex ratio of males to nulliparous females was biased towards males. The observed ratio (5.7:1) differs significantly from an expected foetal ratio of unity ($\chi^2 = 32.97, P < 0.01, d.f. = 1$). There was no evidence, however, that significant neonatal mortality had occurred within the roosts since no dead neonates were found.

Body weight and forearm length of the male bats were both unimodally distributed (Fig. 1). There was a positive relationship (rank $r_s = 0.50, P < 0.01, n = 57$) between the reproductive condition of male bats (classed I to VI) and body weight (Fig. 2a). Heavier bats were more likely to be ranked higher in reproductive status. The mean weight of all male bats (7.33 g) was significantly lower than the mean for nulliparous females (7.78 g, $t = 3.33, P < 0.01$). Both males and nulliparous females were significantly lighter than parous females ($\bar{x}$ weight 8.54 g, $t$ (male vs. parous females) = 8.0, $P < 0.01$, $t$ (parous vs. nulliparous females) = 4.39, $P < 0.01$).

There was no significant relationship between forearm length and reproductive condition ($r_s = -0.11, P > 0.05$) in male bats (Fig. 2b). On average, male bats had significantly shorter forearms than nulliparous females ($t = 4.38, P < 0.01$) and parous females ($t = 4.31, P < 0.01$). There was no difference in forearm length between parous and nulliparous females ($t = 0.48, P > 0.05$).

If different individuals have equal body sizes along some biometric variable other than weight, for example, forearm length, then different body weights between these individuals are likely to represent differences in body condition. Heavy individuals are likely to have more energy reserves than lighter individuals of the same size. A body condition index (BCI) was calculated as the body weight/forearm length. There was a highly significant positive relationship between body condition (BCI) and sexual development ($r_s = 0.544, P < 0.01, n = 57$) in males (Fig. 3). In both
females and males, the distribution of BCI was unimodal (Fig. 4). On average, however, the immature/nulliparous females had significantly lower BCIs than parous females ($t = 5.68$, $P < 0.01$). Males had significantly lower BCIs than parous females ($t = 4.84$, $P < 0.01$) but did not differ significantly from nulliparous females ($t = 1.12$, $P > 0.05$).

Although BCI corrects for differences in size, and hence age while the young are still growing, body condition may vary with age once morphological development is complete. The relationship between body condition and sexual development (Fig. 3) may then reflect the association between each of these variables and age.

To assess the effect of age on body condition and sexual development, the data were divided into five-day classes. Since all bats in the present study were probably born in the last week of June or first week in July, later five-day classes would be expected to include, on average, older bats than earlier classes. The mean body condition and mean reproductive status for bats captured in each five-day period are shown in Table 1. There was no significant difference between
FIG. 2. (a) Body weights and (b) forearm lengths of *Plecotus auritus* captured in nursery roosts in north-east Scotland in late August and early September 1984, against reproductive condition. For details of ranking see text. There was a positive relationship between body weight and testicular development in males, but no relationship between forearm length and testicular development.
Fig. 3. Body condition index of Plecotus auritus captured in nursery roosts in north-east Scotland in late August and early September 1984, against reproductive condition. For details of ranking see text. Body condition index equals body weight divided by forearm length. In males, there was a strong positive relationship between body condition and testicular development.

Table I

Variations in mean body condition index and reproductive status of male Plecotus auritus captured from nursery roosts in north-east Scotland with time of capture. Differences between five-day classes of each variable were not significant.

<table>
<thead>
<tr>
<th>Date class</th>
<th>Body condition index</th>
<th>Reproductive status</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{X}$</td>
<td>S.D.</td>
</tr>
<tr>
<td>5/8-9/8</td>
<td>0.206</td>
<td>0.010</td>
</tr>
<tr>
<td>10/8-14/8</td>
<td>0.201</td>
<td>0.012</td>
</tr>
<tr>
<td>15/8-19/8</td>
<td>0.191</td>
<td>0.009</td>
</tr>
<tr>
<td>20/8-24/8</td>
<td>0.179</td>
<td>0.016</td>
</tr>
<tr>
<td>25/8-29/8</td>
<td>0.195</td>
<td>0.004</td>
</tr>
<tr>
<td>30/8-3/9</td>
<td>0.188</td>
<td>0.013</td>
</tr>
</tbody>
</table>
the five-day classes for body condition (ANOVA, $F = 1.42, P > 0.05$) or sexual development (ANOVA, $F = 1.03, P > 0.05$), suggesting that age was not an important influence on sexual development or body condition in this sample of animals.

The sexual development of bats varied significantly between roosts (Table II ANOVA, $F = 2.97, P < 0.05$). There was a significant positive relationship between the state of sexual development at a roost and the percentage coverage of woodland in four 1 km squares centred on the same roost (Fig. 5). Roosts in heavily wooded areas contained males which were more sexually developed, and in better body condition, than roosts centred in sparsely wooded areas.

**Discussion**

A major factor influencing the sexual development of immature male Brown long-eared bats is body condition (Fig. 3). These data therefore support the hypothesis that most temperate zone
bats do not achieve maturity in the summer of their birth because they are unable to achieve a target body condition to support spermatogenesis before aerial insect availabilities decline (Racey, 1982).

Further support for this hypothesis are data which show spatial variability in sexual development between roosts (Table II), and that these differences are related to the area of woodland around the roost (Fig. 5). Brown long-eared bats forage in woodland (Swift & Racey, 1983) and a large area of woodland around a roost may therefore favour sexual development of the young because it provides more and closer resources for adult females during lactation, and for the young themselves when they fly. Also within a large area, competition for food resources may be reduced. It is unlikely that the increasing area of woodland would produce other significant benefits. For example, changes in the local microclimate may occur but these probably have little effect on sexual development.

<table>
<thead>
<tr>
<th>Roost</th>
<th>Percentage local area covered with trees</th>
<th>Reproductive status of male bats</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>6·4</td>
<td>3·4</td>
</tr>
<tr>
<td>B</td>
<td>8·0</td>
<td>2·0</td>
</tr>
<tr>
<td>C</td>
<td>25·7</td>
<td>2·8</td>
</tr>
<tr>
<td>D</td>
<td>32·8</td>
<td>2·75</td>
</tr>
<tr>
<td>E</td>
<td>35·0</td>
<td>3·0</td>
</tr>
<tr>
<td>F</td>
<td>56·2</td>
<td>3·6</td>
</tr>
<tr>
<td>G</td>
<td>60·6</td>
<td>4·1</td>
</tr>
<tr>
<td>H</td>
<td>69·0</td>
<td>4·35</td>
</tr>
</tbody>
</table>

Only three of 57 male bats in this study had distended epididymides. Such distension occurs after spermatozoa leave the testis and accumulate in the cauda epididymidis, which acts as a sperm storage organ. This suggests that approximately 5% of immature males in the population studied reached sexual maturity in the summer of their birth. Such an estimate may be biased, however, because there is a possibility of incorrect assignment when reproductive status is assessed by external examination only. In the Pipistrelle bat (Pipistrellus pipistrellus), Racey (1974) has shown that 20% of males classed as adult by external examination were in fact immature when surgically examined. On the other hand, 10% of immatures were in fact adult. There is likely to be a slight bias in favour of misclassifying animals as adult.

In addition, it is possible that some, or all, of the three bats classed as adult (class VI) were not born in 1984, but were older bats which had joined the colony. It is difficult to age bats, once they have achieved adult size and the epiphyses of the finger joints have fused. Nevertheless, the pelage colour and pristine condition of the wing membranes in these animals suggested they had been born six to eight weeks previously, although the reliability of this assessment is unknown. There was no direct evidence, however, that any of the three most mature male bats were of a different year class from any other males. The unimodal distributions of body weight, forearm length (Fig. 1) and body condition index (Fig. 4a) in males may suggest that all the
bats were from a single year class. It is possible that during autumn, older male bats may be indistinguishable from young born in the same year, or if only small numbers of older bats were involved they might be insufficient to produce bimodality. This appears to occur in the unimodal distribution of BCI in females (Fig. 4b) which is composed of two apparently separate distributions, one for parous and one for nulliparous females.

The biased sex ratio in favour of males, in combination with the absence of any evidence of neonatal mortality in the roosts, may support the hypothesis that older males move into the roosts at this time of year. However, we have no data on foetal sex ratios or sex-related differences in dispersal from the roosts in this species, which might equally explain the biased ratio observed.

Even if older mature bats had entered the roosts, they were not in exceptionally good body condition when compared with immature males (Fig. 3), as is observed in the comparison of body condition in nulliparous and parous females (Fig. 3). Our results imply, therefore, either that some male bats in some roosts achieve a body condition compatible with puberty in their
first year, or that the whole top end of the distribution of male body conditions consists of older bats, as in females, which have moved into the roosts, but that not all these older bats become sexually mature.

It is impossible (with the current data) to resolve this problem. Some male Brown long-eared bats may become sexually mature in the year they are born, as has been shown previously in *Plecotus townsendii* (Pearson, Koford & Pearson, 1952) and *Myotis lucifugus* (Myers, 1977), but equally they may show a delay in puberty for several years similar to that observed in *Rhinolophus ferrumequinum* (Dinale, 1964). To further complicate matters, either alternative may apply to *P. auritus*, and time to puberty may vary between nursery roosts. Further observations on bats of known age are required to resolve this problem.

The observed importance of body condition for sexual development suggests that increasing photoperiod is not a necessary proximate stimulus for puberty. In the laboratory, testis growth in immature male pipistrelles fed *ad lib.* is independent of photoperiod (Racey, 1978). In this latter study, however, bats were maintained in constant photoperiods (of 8 h and 16 h light) and, if the stimulus for puberty was increasing photoperiod, it could be argued that no difference would be expected between these treatments but that development would not be complete. Testis size attained by all these bats was, in fact, much smaller than adults, but this was attributed to poor acclimation to captivity. Increasing photoperiod may not be necessary for development, therefore, but may greatly influence the rate and degree of development observed.

The implications of differences in time to reach puberty between roosts for the fitness of male bats are unknown. If early developing males do have longer breeding lives, this may act as a contributory selective pressure on adult females to select roost sites which are most favourable for rapid development, i.e. those situated in woodland. Such sites may be limited and lead to extreme competition between females at roosts in early spring, leading to high site fidelity at 'good' roosts but low fidelity at 'poor' roosts. These hypotheses are currently under investigation.

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**REFERENCES**


SEXUAL MATURITY IN MALE BROWN LONG-EARED BATS


