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**Inter- and intra-individual variation in wing loading and body mass in female pipistrelle bats: theoretical implications for flight performance**

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**Introduction**

Flight performance is critically dependent on body mass and on the ratio between body mass and wing area, commonly known as the wing loading. For instance, the minimum theoretical flight speed is directly proportional to the square root of wing loading; the minimum theoretical radius of a banked turn is directly proportional to wing loading; and, when the aspect ratio and wing span are constant (for example in a fully grown individual), then the minimum theoretical power requirement for flight is proportional to (body mass)\(^{3/2}\) (Norberg, 1987).

Variation in wing form between different species of bat has been interpreted as having an adaptive basis (e.g. Norberg, 1987; Norberg & Rayner, 1987). However, measures of wing form
and body mass are usually based on relatively few individuals, taken at a single point in time. Little attention has been focused on the extent of inter- and intra-individual variation in body mass within bat populations, and how this variation will in turn lead to inter- and intra-individual variation in wing loading and hence in flight performance. It is often suggested that the theoretical effects of body mass on flight performance, and hence foraging success, may be a constraint on litter mass (e.g. Kurta & Kunz, 1987). However, this argument is at odds with data on neonatal litter mass which shows that litter mass of bats in relation to female mass compares closely with that in other eutherians (Kurta & Kunz, 1987). If wing loading is a limiting factor on litter mass, then there should be a detectable limit for wing loading of bats in the wild, above which they would be unable to forage successfully.

We examined a population of female pipistrelle bats (Pipistrellus pipistrellus) from north-east Scotland, first to assess the extent of inter-individual variation in wing loading at a single point in time, to predict the consequences of this variation for inter-individual variation in flight performance; and secondly to assess the extent of seasonal variation in body mass and wing loading by comparing predictions of minimum lean body mass during the winter with measurements of body mass taken in late pregnancy.

Fifty-one pregnant female pipistrelles were caught under licence from the Nature Conservancy Council, on emergence from a maternity roost in north-east Scotland on 5 June 1990. The bats were retained overnight in a wooden box, in which water was freely available, and, on the morning of the following day, were each weighed to the nearest 0·01 g, had their left wing traced on to paper to determine wing area, and their left forearm length measured as an indicator of body size. Twenty-five of the bats were released that night and the remaining 26 were retained in captivity and trained to feed on mealworm larvae (Tenebrio species). The captive bats were checked once a day to determine when each gave birth, and were reweighed once every 2–3 days. In this way the body mass of seven of the bats was obtained on the day immediately before they gave birth.

Data showing the inter-individual variation in body mass, wing area and wing loading of the 51

| TABLE 1 |
| Summary of results |
|-------------|--------|------|------|------|
| Measurements made on the morning after capture (6/6/90): |
| Body mass (g) | 7·19 | 0·74 | 4·76 | 8·80 | 51 |
| Wing area (cm\(^2\)) | 67·73 | 5·10 | 55·98 | 78·59 | 51 |
| Wing loading (N·m\(^{-}\)) | 10·52 | 0·91 | 7·38 | 12·51 | 44 |
| Forearm (mm) | 32·2 | 0·74 | 30·2 | 34·1 | 46 |
| Birth date | 17/6 | 4 days | 8/6 | 25/6 | 25 |
| Measurements made on the day before birth (mean date = 17/6/90): |
| Body mass (g) | 7·45 | 1·14 | 5·67 | 9·08 | 7 |
| Wing area (cm\(^2\)) | 64·67 | 3·22 | 59·76 | 68·67 | 7 |
| Wing loading (N·m\(^{-}\)) | 11·33 | 1·62 | 8·55 | 13·84 | 7 |
| Predictions for a bat of minimum body mass (see text): |
| Body mass (g) | 4·03 | | | | |
| Wing area (cm\(^2\)) | 67·63 | | | | |
| Wing loading (N·m\(^{-}\)) | 5·87 | | | | |
FIG. 1. The relationship between wing loading and body mass in pregnant female pipistrelles on the 6/6/90, a mean of 11 days before parturition. Body mass explained 53% of the variation in wing loading: $y = 4.08 + 0.90x$, $r^2 = 0.53$, $F[1,42] = 47.0$. Bats that produced singletons (○), bats that produced twins (●), bats for which the number of young produced was not noted (□).

adult females on the morning after capture are summarized in Table 1. Combining these data with Norberg's (1987) theoretical relationships predicted that the highest individual values for minimum flight speed, minimum radius of a banked turn, and minimum power requirement for flight within the female population at this time were 1.30, 1.70 and 2.51 times the lowest individual values, respectively. These data highlight the large amount of potential variation in flight performance between individuals within the population at any given time, and hence the necessity of measuring relatively large numbers of bats to obtain accurate means. On its own, body mass explained 53% of the inter-individual variation in wing loading (Fig. 1), whilst only 2% was explained by wing area alone (Fig. 2). This implies that bats with a higher wing loading, and hence a lower theoretical flight performance, had greater mass rather than wings of smaller area.

There are three major potential sources for inter-individual variation of body mass in pregnant bats; body size, body fat, and the mass of the foetus plus associated fluid and tissue. There was no significant relationship between body mass and length of forearm, hence body size was not a significant factor. If mass of the foetus was the source of the inter-individual variation in body mass then we might expect heavier bats to give birth sooner, or to give birth to larger young. However, there was no significant relationship between body mass on the morning following capture and that on the day on which parturition occurred, and whilst age explained 82% of the variation in juvenile body mass in the first 10 days of life ($n = 19$ measurements), body mass of adults on the morning following capture did not explain a significant further portion of the variation, indicating that the heavier adults on the morning following capture did not necessarily produce heavier young. These data therefore suggest variation in size of body fat store was the
major source of inter-individual variation in body mass in mid/late-pregnancy. This agrees with previous studies on other species of vespertilionid bat where it has been suggested that adult bats may invest against food shortages during late pregnancy or early lactation by storage of body fat reserves during early pregnancy (Speakman & Racey, 1987). During the course of the present study, food was available to the bats ad lib and therefore any differential growth rate of the young dependent on the fat store of the mother may have been masked.

As well as predicting inter-individual variation in flight performance within the female population at a single point in time (mid-pregnancy), we also predicted intra-individual seasonal variation, from estimates of seasonal maxima and minima of body mass and wing loading. We have already presented estimates for fully pregnant bats (Table I), which were used as the maxima. For the body mass minima we used the predicted mean lean body mass of female pipistrelles in the winter in north-east Scotland (4.03 g) (Speakman & Racey, 1989), which, for a mean wing area of 67.63 cm\(^2\) produced a mean estimated wing loading of 11.33 N·m\(^{-1}\) (Table I).

Our estimates indicate that mean body mass and wing loading of fully pregnant pipistrelles in north-east Scotland were therefore approximately 1.8-1.9 times those in female pipistrelles of minimal body mass. Applying Norberg's theoretical relationships to our data predicts that a female pipistrelle moving over the year, from minimum to maximum wing loading and body mass would, on average, experience a 1.39-fold increase in minimum theoretical flight speed, a 1.93-fold increase in the minimum theoretical radius of a banked turn, and a 2.51-fold increase in the minimum theoretical power requirement for flight.

The magnitude of the theoretical impact of mass increases during pregnancy, on flight performance, might imply an equal impact on foraging success (Ransome, 1990). If this were the case, then we might expect body mass and wing loading in the wild to be constrained against a
detectable upper limit. However, the relationship between wing loading and body mass on the morning following capture was linear (Fig. 1), indicating that a limit to wing loading was not reached within the population at this time (on average 11 days before parturition). Of the seven measurements of wing loading made on the day immediately before parturition, only one exceeded the maximum measurement made on the morning following capture, suggesting that, even at parturition, bats still had not reached the upper limit to wing loading. This suggests that the increase in adult body mass associated with pregnancy may impose no disadvantage in terms of reduced foraging success, despite the large predicted effects on flight performance.

The implication of this result is that wing form is probably adapted to ensure adequate flight performance at times when selective disadvantages of not performing well are most acute. Late pregnancy might be such a critical period. Adaptive interpretations of wing form based on wing loading calculations for samples of animals collected outside these critical periods are unlikely to reflect the true nature of adaptation in wing morphology.

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Roost philopatry in female pipistrelle bats Pipistrellus pipistrellus

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Introduction

Philopatry is defined as the tendency of an animal to remain in its home area, or return to it in the case of migrants (Hale & Margham, 1988). Insectivorous bats are often abundant, long-lived and join large maternity colonies during pregnancy and lactation. They are thus appropriate mammals in which to study roost philopatry and the aim of the present long-term study was to