Reproductive adaptations of heterothermic bats at the northern borders of their distribution

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Pipistrelle, and probably other insectivorous bats breeding at 57°N, sustain an energy deficit throughout reproduction if they remain continuously homeothermic. The bats are unable to meet the changing energy demands of reproduction by changes in food intake. Instead, they resort to extensive compensation to achieve an energy balance by entering daily torpor. The significance of such compensation during lactation for lactogenesis and growth of young has yet to be determined. Thus, the key to bats being able to reproduce successfully in an unpredictable environment at 57°N is their ability to enter torpor at any stage of reproduction. Among mammals such an ability is unique and makes bats an outstanding example of evolutionary adaptation.

There are over 70 species of Palaearctic bats, most of them belonging to the family Vespertilionidae and showing the same reproductive adaptations of autumnal or winter copulations, prolonged storage of spermatozoa, followed by ovulation and fertilization in spring. The number of these species present in Britain declines with increasing latitude. Southern England has 15 species, whereas breeding populations of only three species are found in north-east Scotland, suggesting that the environmental conditions at this latitude (57°N) impose severe constraints on bat reproduction. The species found in north-east Scotland are the pipistrelle, Pipistrellus pipistrellus (6 g), the brown long-eared bat, Plecotus auritus (9 g) and Daubenton's bat, Myotis daubentoni (10 g). At 57°N these bats are close to the northern borders of their distribu-
tions. They arrive at their maternity roosts in the roof spaces of houses during May, from hibernacula that are probably located at more southerly latitudes. On arrival they are generally in the early stages of pregnancy.

Vespertilionid bats are wholly insectivorous and in spring at 57° N, insect densities are less than a tenth of those in late summer (J. R. Speakman, unpublished observations). Aerial insect density is also dependent on short-term variations in ambient temperature, wind speed and humidity, so that periods of high winds, low temperature and occasional sleet and snow will greatly reduce the density of flying insects. In addition, because bats generally forage only in darkness, and the nights get progressively shorter until the summer solstice, a relatively small proportion of the daily cycle is available for foraging. At 57° N, the period of parturition of bats coincides approximately with this solstice.

Our overall aims in studying the ecology and ecophysiology of bats over the last decade have been to investigate how they meet the energy demands of reproduction in conditions that are often unpredictable and sometimes hostile. The questions we asked were: when, where and on what do bats forage, and more importantly, are there any differences in these parameters that reflect the increased energy demand from pregnancy to lactation that characterizes mammalian reproduction? Having answered these questions, and identified the extent to which bats are able to respond to hostile environmental conditions during pregnancy, we then embarked upon an investigation of the energetics of pregnancy and lactation.

When do bats forage?

Direct observations revealed that pipistrelle bats emerge from their roosts to feed at a constant interval of about 35 minutes after sunset. During pregnancy, females undertook a single foraging flight, and the activity pattern of the colony was unimodal. During lactation, mothers returned to the roost in the middle of the night, after their first foraging flight, presumably to suckle their young. They then left again for a second foraging flight before dawn. When the young were able to fly and forage for themselves, albeit inexperiently, activity reverted to a unimodal pattern. The average time that each female spent outside the roost throughout summer varied by a factor of two, from 154 to 294 min, with a mean of 225 min. This variation was related to weather conditions and aerial insect density, and therefore to foraging success, but showed no increasing trend from pregnancy to lactation.

In an attempt to establish whether bats were foraging continuously when they were away from the roost, transects were walked with an ultrasonic receiver ($100 Bat Detector, QMC Instruments Ltd, UK) along a river bank close to a roost, and bat passes and feeding buzzes recorded. The same pattern of activity was apparent as was observed at the roost — unimodal during pregnancy and bimodal during lactation (Fig. 1). Bats were absent from the foraging area in the middle of the night only during lactation, coinciding with their return to the maternity roost, and there was no evidence that they made use of alternative roosts, such as night roosts. The use of night roosts has been documented at 42° N in *Myotis lucifugus*, a North American species occupying a similar niche to *P. pipistrellus*.

The proportion of the night which *M. lucifugus* divided between foraging and roosting away from the maternity roost varied nightly and seasonally in relation to the reproductive condition of the bats, prey density and ambient temperature. Energetic advantages are probably derived from clustering together in night roosts when cool ambient temperatures and low insect densities prevent net energy gains from foraging.

The pattern of foraging behaviour observed in *Pipistrellus pipistrellus* correlated with the nightly pattern of availability of flying insects. The flight patterns of nocturnal insects are bimodal with peaks at dusk and dawn, and this pattern was confirmed in our study area. During pregnancy bats exploit only the insect peak at dusk, but during lactation they also forage on the lower dawn peak during the second foraging flight. The restriction of foraging to times when nocturnal insect availability is highest has also been demonstrated in several other temperate-zone bat species, and conforms with the predictions of foraging models, suggesting that in certain conditions the density of food may be so low that the most profitable strategy is to stop foraging completely.

Where do bats forage?

Female pipistrelles caught from their maternity roost in a lowland agricultural river valley about 100 m above sea level were tagged on the dorsal fur with gelatin capsules containing the short-lived chemiluminescent mixture Cyalume (American Cyanamid), and were fitted with numbered forearm bands covered in reflective tape (Scotchlite). Assistants were stationed throughout the study area to report sightings of Cyalume-tagged bats during the first night after tagging. This technique provided an approximate delimitation of the colony foraging area, which was subsequently patrolled with powerful torches to locate Scotchlite-marked bats. In this river valley, with abundant suitable foraging habitat, sightings of marked bats during pregnancy and lactation indicated that they followed the river system and foraged either low over the water or around riparian trees generally at the height of the thickest foliage. The only bats seen further than 100 m from the river were over two large ponds, one about 600 m from the river. No bats were sighted...
where the river passed through open fields that had no riparian trees, nor were they seen in or near plantations of trees on the valley sides. The average direct distance of sightings of marked bats from the roost was 1.8 km before parturition (s.d. 1.3 km, n = 67) and 1.3 km after parturition (s.d. 0.7 km, n = 57) (t = 2.245, P < 0.025). The reduction in the distance that female pipistrelles travelled from the roost during lactation may reflect an increased commuting cost associated with returning to the roost in the middle of the night.

Observations were also made at a roost at an altitude of 350 m a.s.l. in an area of granite hills and moorland, rising to 750 m a.s.l. The area around the roost included a 5-hectare loch surrounded by a conifer plantation, sparse deciduous trees and a river bordered by trees. This area contained trees and water was surrounded by open hills and moorland. Foraging bats covered a smaller area compared with the lowland site and foraged wherever there were trees or water, although they avoided coniferous forests and open hills. The average direct distance of bats from the roost was 1.0 km both before and after parturition. It thus appears that at higher altitude, which is less favourable for flying insects, bats forage in a wider range of habitats.

The average distance pipistrelles travelled from the roost during foraging flights are similar to those established by radiotracking for the larger (20-g) Nearctic *Eptesicus fuscus* and greater than that established for *Myotis mystacinus* and *M. daubentoni*. Such distances, however, may reflect the quality and topography of the foraging area. Thus *M. daubentoni* forage from 2 to 10 km away from their roost, along rivers in central England, up to 2 km from their roost when foraging over ponds in Scotland and only an average of 236 m away from their roosts when foraging over lakes in Finland.

**On what do bats forage?**

An insect suction trap was operated for 18 nights in areas where pipistrelles foraged intensively. Mist nets were set in the same sites, and bats captured while foraging were placed in cloth bags in which they defaecated. The incidence of insects of different families in the traps was later compared to their incidence in the faeces. Pipistrelles fed mainly on Nematocera and Trichoptera, and their diet reflected the availability of these insects over a wide range of abundances. There was no evidence that the bats selected their diet on the basis of insect size. Ephemeroptera and Neuroptera were significantly over-represented in the diet, indicating that these insects were selected, although they never accounted for more than a small proportion of the intake. Nematocera, Coleoptera and Lepidoptera were significantly under-represented. Different diets in were apparent between sexes nor between pregnant or lactating females. The rate at which bats attacked insects was recorded with an ultrasonic receiver and was proportional to insect density until a peak of 10 feeding attempts per minute was reached. Bats did not remain in an area or attempt to forage if the insect density was less than 300 m-3. In general, however, bats fed at the maximal rate, and low insect density affected the rate of attempted feeding on only 4 out of 20 nights on which insects were trapped and bats were flying. The effect of hostile weather conditions on length of gestation

On cold wet and windy nights during pregnancy, bats did not emerge from their roosts to fly, and the effect of the consequent inanition on the length of gestation was examined. A roost was visited at intervals of two days during the expected times of ovulation and parturition, and at intervals of five days between these events, over two successive years. At each visit, six parous females were caught as they left the roost to forage. Reproductive tracts of bats in early pregnancy were examined macroscopically and histologically, but later in pregnancy, fetuses were removed from the uteri, weighed and the rates of fetal growth calculated using the Huggett and Widdas equation. Samples taken in early May contained females in which the uterus was still distended with spermatozoa, and in which ovulation had not occurred. In subsequent samples, the corpus luteum was evident in one ovary, fertilization had taken place and no spermatozoa were present. In later samples implantation had occurred and the uterine horn of some individuals was swollen (Fig. 2). Thereafter, bats contained dissectable fetuses that could be weighed and measured and the rates of fetal growth compared from year to year. The
presence of blood on the vulva of bats leaving the roost indicated that parturition had recently occurred, and the average gestation period for the colony was estimated as the interval between the first recorded corpus luteum and the first recorded parturition. This interval varied by 10 days in two consecutive years. Early pregnancy in the second year of this study coincided with high winds, rain and sleet. Dusk temperatures and numbers of flying insects were depressed. In these conditions no bats emerged from the roost to forage, and in this state of inanition it is likely that they would have become torpid. Such conditions can be simulated in the laboratory by depriving pregnant bats of food for periods of up to 24 hours. Thermocouple measurements of rectal temperature show that in these conditions it falls cooler to ambient than in controls which are fed. This unique capacity of bats to survive hostile conditions during pregnancy by becoming torpid focused our attention on how they maintain energy balance throughout the entire period of pregnancy and lactation.

Field measurements of daily energy expenditure during pregnancy and lactation

We have made use of a field technique for estimating the daily energy expenditure of free-living mammals directly — the doubly-labelled water technique. This is based on the premise that the oxygen of expired CO\textsubscript{2} is in isotopic equilibrium with the oxygen of body water. So, in an animal given an injection of doubly-labelled water, and released into the wild, the decrease in the concentration of \(^{18}\text{O}\) is a measure of \(\text{H}_{2}\text{O}\) flux only, and the \(\text{CO}_{2}\) flux is obtained by difference. The data obtained to date are shown in Fig. 3 in relation to predictions of the daily energy expenditure of \(\text{M. lucifugus}\) entering daily torpor during pregnancy and lactation, and that of a continuously endothermic bat flying for 225 min each night, and our own estimate of flight cost. Energy metabolism at each stage of reproduction is clearly highly variable between individuals, but some trends emerge from these data. Firstly, most estimates of energy expenditure lie much closer to the line predicted for a bat entering daily torpor, indicating that bats are compensating for the increased energy costs of reproduction by relaxing homeothermy and entering torpor. This happens not only in pregnancy but also in lactation. Secondly, the most significant deviation from the compensation line occurs in late pregnancy when some individuals are clearly increasing their energy consumption and remaining homeothermic. This is evident from the trend for the mean line, which is close to the prediction for a bat entering daily torpor early in pregnancy. It then moves well above this line in late pregnancy and declines in lactation, suggesting extreme compensation in lactation compared with the predicted levels for increased energy consumption. Such compensation during lactation does not correlate with the food supply, which is maximal at this time.

Clearly, more data on energy expenditure during lactation are required to understand the adaptive significance of respiratory compensation during this time. Such a mechanism also has implications for the rate of milk production. In captivity, neonatal bats spend much of their time attached to the mother’s nipple, and this has led to the assumption that mothers are continuously producing milk and the young suckle on demand. However, it seems likely that lactogenesis will increase markedly when the bats are endothermic and in flight. This may also explain why they return to the roost in the middle of the night after an absence of less than two hours — because the mammary glands are engorged with milk.

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