Oecologia (1989) 80:562–565

Oecologia

Feeding activity of the northern bat *Eptesicus nilssoni* during pregnancy and lactation

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Summary. Female northern bats emerged at dusk to feed when aerial insect density was 0.1 m^{-3} or higher. A model suggests that this is the threshold level above which foraging may be energetically profitable. Insect density was determined mainly by air temperature, and reached the threshold level at 6–10° C. Mean temperature during early summer in six years was correlated with the date of parturition. This suggests that periods when foraging was not energetically profitable were spent in torpor.

Key words: Insectivorous bats – Energetics – Feeding – Insect activity – Gestation

The northern bat (*Eptesicus nilssoni* Keyserling and Blasius 1839) forages in open habitats using straight or slightly curved flight paths and it feeds exclusively on flying insects (Rydell 1986). It has a pronounced northern distribution (Stebbings and Griffith 1986), and is considered non-migratory (Strelkov 1969).

The reproductive cycle of most Palaearctic bats is adapted to seasonally fluctuating insect densities. Mating takes place in autumn or winter, and spermatozoa are stored in the female reproductive tract until spring, when ovulation and fertilization occur. In northern Europe lactation and weaning take place in July and August, when insects are most abundant, and, hence, the period of pregnancy coincides with relatively low and unpredictable food levels in May and June (Speakman and Racey 1987).

Contrary to most mammals, insectivorous bats living at high latitudes are usually unable to meet the increased energy demands imposed by pregnancy by increasing their food intake or by metabolizing stored energy reserves. Instead, they periodically enter torpor when food shortage is encountered (Racey and Swift 1981). As a consequence, the gestation period varies in length in proportion to the time spent in torpor (Racey 1973).

How bats allocate time and energy will obviously influence their survival and reproductive success (Kunz 1980). I studied feeding activity in a maternity colony of northern bats and its dependence on weather and insect activity to determine how pregnant and lactating females allocate their foraging efforts during periods of low and unpredictable food abundance.

Material and methods

A maternity colony of northern bats, living in a farmland area 300 m a.s.l. northeast of the town of Ulricehamn in southern Sweden (57°45′N, 13°25′E), was observed regularly from 1983 to 1988. The colony consisted initially of 25–27 females but was reduced to 15–17 after the cold winter of 1984–1985.

The roof of four dwelling-houses provided maternity roosts for the colony from early June until late July or early August. The bats were captured at least once each summer by means of mist-nets erected in front of the exit holes. They were checked externally for signs of current reproduction and marked individually on each forearm with metal bands (Lambournes Ltd., Birmingham, U.K.) covered with reflecting tape.

The maternity roosts were situated in a 4 ha park, in which I searched for foraging bats on 338 evening visits between April and October (Table 1). Each visit lasted at least one hour after my arrival at dusk. Foraging bats were located with binoculars and a bat detector (QMC S-100, QMC Instruments Ltd., London, U.K. or D-960, L Pettersson Elektronik, Uppsala, Sweden). Identification of the bats by means of the reflecting tape was made with a halogen head light (Silva Sweden AB, Stockholm). All observations analysed refer to reproducing females. Foraging activity was scored if feeding attempts by at least one female were observed. Feeding attempts were heard in the bat detector as distinct "buzzes", as the echolocation pulse rate increased after detection of a prey item (Griffin et al. 1960).

Temperature, cloud cover, wind speed and occurrence of mist and rain were recorded on every visit. In addition, mean monthly temperatures at a weather station 12 km south of the study area were obtained from SMHI (1983–1988).

Birth dates of the young of the year were determined indirectly by listening from outside the roost for their audible isolation calls. Such calls are heard easily and are emitted from the first day after birth (Gould 1971).

When the bats emerged (or when they were expected to emerge) at dusk, aerial insect densities were estimated in the park surrounding the roost in 23 evenings in May and June 1986. A hand net with 0.25 m^2 area attached to a 4 m pole was swept 100 times through the air 4–5 m above the ground while I was walking slowly forwards. Each sweep was about 4 m long, and each sample therefore represents the occurrence of insects in approximately 100 m^3 of air.

In order to establish the relationship between insect density and the bats' feeding rate, I collected 2–5 min samples of echolocation pulses of foraging bats on 14 occasions in May and June 1986 on tape by means of a bat detector and a Sony TC D5-M cassette tape recorder. Feeding rate was subsequently determined from the number of "feeding buzzes" recorded. When the bat was being recorded, an insect sample was simultaneously taken at the same site by the method described above.

Results

Activity patterns and parturition dates

Foraging females were normally observed for the first time during the first half of May, when evening temperatures reached 7–9° C. Feeding activity was irregular in May and early June, but from mid-June and throughout July females were observed feeding almost every evening (Table 1). The activity became more irregular again in August. Similar activity patterns were observed in each year of the study except in 1987, when unusually cool weather resulted in periods of inactivity throughout the summer (Table 1).

Assuming that the isolation calls indicated the day of parturition, the first young were born between 25 June and 11 July (Table 2), and were observed flying 12–15 days later. In 1987 no isolation calls were heard and no young were yet flying on 4 August, when the observations were terminated. However, one indication that young were nevertheless born that year was a female carrying a young outside the roost on 28 July.

There was a significant negative relationship between the date of parturition and the mean temperature prevailing in May, i.e. young were born earlier in years when May was relatively warm ($r_s = 0.83$, $N = 6$, $P < 0.05$; Fig. 1). The significance of the correlation remains if the June temperatures are included.

A partial correlation analysis suggests that the day of parturition was also related to the frequency of feeding activity during the gestation period ($r = 0.92$, $N = 6$, $P < 0.01$), but not to the day when females were first observed feeding in spring ($r = 0.09$, $N = 6$, $P > 0.05$) (Table 2).

Correlates of feeding activity

The number of days during which feeding activity was observed in May, June and July was influenced by the temperature prevailing each evening. Foraging was observed every evening when temperature was above 10° C, and was never observed when it was below 6° C (Fig. 2). Within the 6–10° C temperature interval, feeding activity was also dependent on wind speed. Thus, it was more frequent on calm or nearly calm evenings than on evenings with moderate or strong wind ($\chi^2 = 4.0$, $df = 1$, $P < 0.05$; Table 3). No forgaing was observed when heavy rain coincided with temperatures below 10° C, but light rain or mist did not seem to prevent feeding activity.

The density of flying insects as measured with a hand net in May and June 1986 was positively correlated with evening temperature ($r_s = 0.66$, $N = 23$, $P < 0.001$; Fig. 3), flying insects being much more numerous in evenings when the bats were feeding than in evenings when they were not observed to feed ($\chi^2 = 19.1$, $df = 1$, $P < 0.001$).

Feeding occurred predominantly in evenings when insect density was 0.1 per m^3 or higher (Fig. 3). This threshold

Table 1. Feeding activity by female northern bats. The table gives the per centage of evening visits to the study area during which bats were observed feeding. Number of evening visits in brackets

Year	April	May	June	July	August
1983	– (0)	56 (18)	96 (27)	100 (15)	20 (5)
1984	27 (11)	72 (22)	100 (24)	100 (29)	25 (4)
1985	– (0)	61 (18)	76 (21)	100 (23)	– (0)
1986	– (0)	50 (12)	83 (23)	100 (25)	100 (3)
1987	0 (2)	25 (8)	0 (3)	64 (11)	100 (2)
1988	– (0)	54 (11)	100 (23)	100 (10)	43 (7)
Total	23 (13)	56 (89)	89 (121)	94 (113)	48 (21)

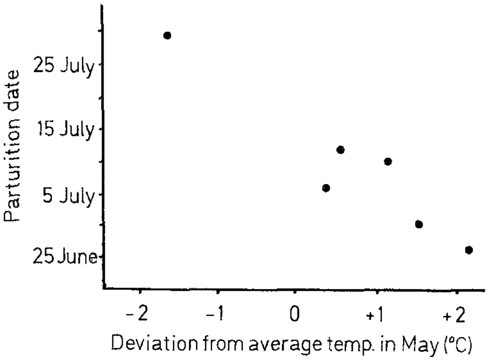

Fig. 1. The day when the first isolation calls were heard in 1983–1988, indicating parturition, in relation to mean temperature in May (expressed as deviations from the average in the period 1931–1960)

Table 2. The day when the first young was recorded in each year of the study, the day when the first females were observed in spring, and the per centage of evenings in which feeding activity was recorded in the period 22 May to 24 June

Year	First young recorded	First female observed	Frequency of feeding activity	
			% of evenings	*N*
1983	5 July	6 May	86.7	30
1984	29 June	24 April	100.0	24
1985	11 July	12 May	76.9	26
1986	8 July	2 May	61.5	26
1987	28 July	22 May	30.0	10
1988	25 June	13 May	95.6	23

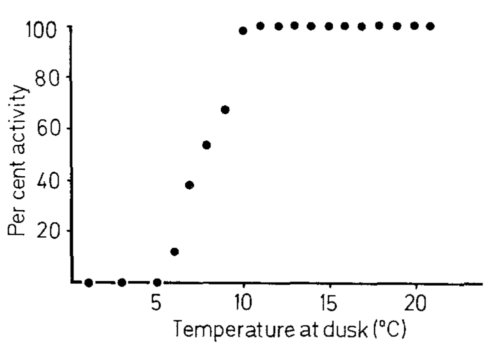

Fig. 2. The per centage of evenings in which feeding activity was observed during the period of pregnancy and lactation in relation to temperature at dusk in 1983–1988 ($N = 208$ evenings)

Table 3. The influence of wind speed on bat feeding activity when temperature at dusk was 6–9° C. The table gives the number of evenings with and without recorded feeding activity

Windspeed	Activity	No activity
Very low	15	7
Low	10	8
Moderate	4	8
High	1	4

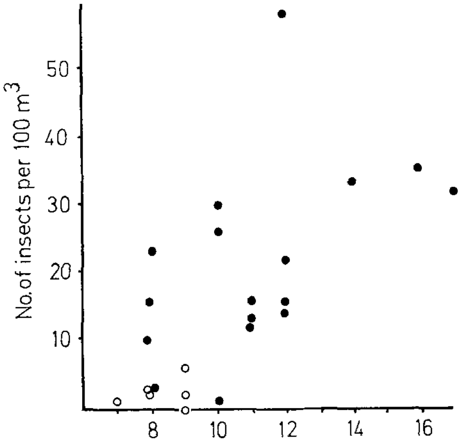

Fig. 3. Number of insects caught with a hand net in approximately 100 m^3 of air in evenings with different air temperatures at dusk in May and June 1986. Filled circles represent evenings when female northern bats were observed foraging, open circles evenings when foraging was not observed

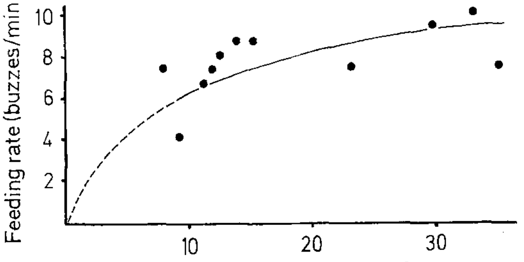

Fig. 4. Regression of attempted feeding rate as a function of insect density in May and June 1986. The regression equation is $y = 11.3\,x/(8.5+x)$

level was reached in all evenings with temperatures above 10° C, but only occasionally when it was cooler. Feeding was observed in two evenings when hand net samples showed insect densities much lower than the threshold level (Fig. 3). In both cases, however, the bats did not use their common feeding sites, but were observed to exploit local patches of insects (moths) that were not sampled with the hand net.

In some of the cooler evenings, when feeding activity was not scored, 1–3 females were nevertheless observed to leave the roost at dusk only to return after 10–20 min.

Feeding rates

Feeding rates increased with insect density, apparently reaching an asymptote at about ten capture attempts per min (Fig. 4). This relationship was significant at low insect densities ($<0.5\ m^{-3}$; $r_s=0.72$, $N=11$, $P<0.01$). The regression for attempted feeding rate on insect density was computed by means of a non-linear least squares model. The feeding rate at the threshold insect density of 0.1 per m^3 was about 6.1 capture attempts per min (Fig. 4).

Discussion

At what insect density should a pregnant northern bat emerge to feed instead of remaining in the roost and enter torpor, which presumably is the alternative strategy? The problem has been analysed for winter-feeding pipistrelle bats (*Pipistrellus pipistrellus*) by Avery (1985), who constructed a simple energetic model. Assuming that the bats respond to daily changes in food availability, and that net energy intake is correlated with fitness, then the bats should consider the expected costs and benefits in terms of energy of the alternatives before making a decision. Feeding is energetically more profitable than torpor when

$$G_f - C_f > G_t - C_t \tag{1}$$

where G and C are gains and costs in terms of energy and f and t are foraging and torpor, respectively. Since the gain expected from torpor is zero:

$$G_f > C_f - C_t \tag{2}$$

The mass of a female northern bat increases from about 8 to 12 g during pregnancy (J. Rydell, unpublished results) and 10 g may be a reasonable average. A minimum flight cost estimate, assuming that the energetic costs of foraging equals that of straight flight, was calculated from equations in Norberg (in press), and suggests that C_f is about 7.1 kJ h^{-1}. C_t is about 14.0 J h^{-1} at 10° C (Hock 1951).

The gain from foraging, G_f, depends on feeding rate, F, mean energy content of prey items, E, and assimilation efficiency, A, which is assumed to be 0.91 (O'Farrell et al. 1972). Energy content of insects is about 22 J mg^{-1} (Krebs and Avery 1985). Faecal analysis suggests that the northern bat only catches insects longer than about 3 mm (Rydell 1986). The mean dry weight of the insects sampled (90% of which were diptearns) after removal of all individuals shorter than 3 mm was 1.0 mg. Thus,

$$FEA > C_f - C_t \tag{3}$$

or

$$F > (C_f - C_t)/(EA) \tag{4}$$

Since $E = 1.0\ \text{mg} \times 22\ \text{J mg}^{-1} = 22\ \text{J}$:

$$F > (7100 - 14)\,\text{J}/22\ \text{J} \times 0.91 \times 60\ \text{min} \tag{5}$$

$$F > 5.9\ \text{captures per min} \tag{6}$$

or, in other words, the bats should emerge to feed only when they can expect an average feeding rate of 5.9 captures per minute. This feeding rate agrees well with the rate observed at the threshold insect density above which the bats emerged to feed (Fig. 5).

The assumption that the bats fed unselectively on insects longer than 3 mm may not be true, since the chance that the insect will be detected still must depend on its size (Barc-

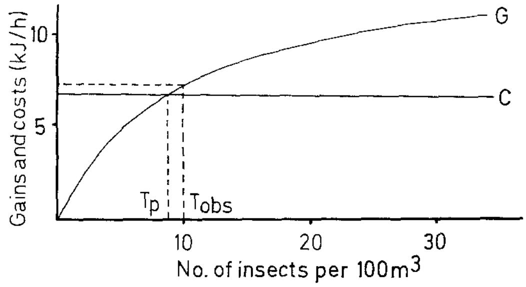

Fig. 5. The threshold insect densities above which the bats were predicted (T_p) and observed (T_{obs}) to feed during May and June 1986. T_p was determined from functions describing costs (*C*) and gains (*G*) of foraging

lay 1985). Therefore, the average mass of the insects captured by the bats was probably underestimated. If this is true, the gain function was higher and, hence, the threshold insect density lower (Fig. 5).

It was also assumed that each capture attempt (feeding buzz) could be regarded as successful. This is probably justified as long as dipterans are the prey items (Griffin et al. 1960). These insects are the dominant prey of northern bats in early summer (Rydell 1986), and are not known to possess any defence mechanisms against bat predation.

The bats apparently left the roost to feed only in evenings when insects were plentiful enough to permit energetically profitable foraging, and probably used torpor as an alternative strategy. The agreement between observed and predicted threshold insect densities suggests that the main determinant of the bats' decisions was daily energy maximization. Other factors, e.g. predation risk, were apparently not important.

How did the bats assess the profitability of feeding? Most cool evenings this could apparently be evaluated indirectly from inside the roost, perhaps on the basis of ambient temperature. However, the observation that in some cool evenings a few bats left the roost but returned shortly afterwards without having fed, suggests that they were not always able to assess insect density by indirect means.

Acknowledgements. I would like to thank R. Gerell, J. Loman and U. Norberg for a lot of help and advice and S. Erlinge and H. Källander for suggestions on the manuscript.

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Received April 9, 1989