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Why Do Brown Long-eared Bats (Plecotus auritus) Fly in Winter?

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Abstract
We investigated the daily food and water consumption of a captive colony of three brown long-eared bats (Plecotus auritus) for 51 d. The bats were kept in a free-flight enclosure exposed to the natural photoperiod and temperature during the winter (January to March 1991) at 57°N. Water was always available, but food was available only on some nights. The mean daily temperature inside a wooden box provided as a hibernaculum was positively correlated with and slightly elevated above (0.6°–2.8°C) the mean daily temperature outside the box in the free-flight enclosure. The mean temperature inside the hibernaculum was 7.1°C and outside was 5.6°C. The mean relative humidity in the hibernaculum was 82% (range 67%–93%). The activity of the bats outside the hibernaculum was monitored by two Doppler radar units. The daily probability of an individual bat emerging from the hibernaculum was between 0.26 and 0.99. Emergence probability increased when there was food available and when it was warmer. The activity of the bats was strictly nocturnal, initial emergence occurring a mean of 64.4 min after sunset (n = 42, SD = 27.0 min). When denied access to food, the bats drank an average of 0.20 mL · bat⁻¹ · night⁻¹ on the nights that at least one emerged (n = 14 nights; SE = 0.05, range = 0.00–0.68). On warmer nights the bats were more active and ate and drank more than on colder nights. We suggest that typically in P. auritus winter flights may not be induced by the onset of starvation (and hence the need to feed) or by the onset of dehydration (and hence the need to drink). Rather, at typical winter temperatures P. auritus may fly frequently, almost daily, to try and ensure that neither energy nor water reserves approach critically low levels. Only during a prolonged cold period (mean night temperature <4°C) might many days pass without a winter flight.

Introduction

As a consequence of low food availability and low ambient temperatures, bats living in temperate regions require adaptations to survive the winter.

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In response to these problems some species migrate in winter to warmer regions (Strelkov 1969) while other species hibernate in situ. Hibernation is a seasonal event during which the body temperature drops from eutermic levels and is maintained slightly above ambient temperature (Nedergaard and Cannon 1990), causing a decrease in metabolic rate and hence energy conservation (Hock 1951; Speakman, Webb, and Racey 1991).

Hibernation torpor is, however, not continuous. Bats arouse at intervals ranging from a few days to many weeks (Menaker 1964; McManus 1974; Brack and Twente 1985; Twente, Twente, and Brack 1985) and may then fly (Ransome 1968; Avery 1985). However, the primary function of winter flights is unclear. Bats may feed during winter flights (Ransome 1968; Avery 1985) and drink (Davis 1970). Establishing whether the more important stimulus for winter flights is to feed or to drink is problematical since both behaviors may be performed. Some authors (Avery 1985; Brigham 1987) suggest that the need to feed is the primary stimulus for winter flights. Recently, however, Speakman and Racey (1989) suggested that the primary function is to drink, and that, even though a bat may feed while flying in winter, this feeding may simply be to cover the cost of flying out to drink, with drinking being the primary stimulus initiating the flight.

To further investigate the function of winter emergence we examined the daily food and water consumption and the individual probability of emergence of a captive colony of brown long-eared bats (Plecotus auritus) exposed to natural photoperiod and environmental temperature but with varying conditions of food availability.

**Material and Methods**

**Animals**

We used a captive colony of three female long-eared bats (Plecotus auritus). The bats had been captured during the preceding summer in Grampian region, northeast Scotland (approximately 57°N). Observations were made between January and March 1991. The bats were maintained in a large (approximately 5 m × 3 m × 2 m) outside free-flight enclosure at Aberdeen, where they were exposed to the natural environmental photoperiod and temperature. A small (700-mL) wooden box, in which the bats could hang, was positioned on one of the walls of the free-flight enclosure to serve as a hibernaculum. On the five occasions that the bats were weighed, all three bats were found in the box, suggesting they routinely roosted there.
Environmental Measurements

Air temperature and humidity in the box and air temperature outside the box in the free-flight enclosure were monitored at 10-min intervals using temperature and humidity probes linked to a data logger (Grant’s “Squirrel,” Grants Instruments).

Experimental Protocols

The bats were subjected to two experimental treatments (both food and water available and only water available) occurring over four experimental periods. The bats had 11 d with access to water only, then 14 d with access to food and water, then 11 d with access to water only, and finally 15 d with access to food and water again. The bats were weighed (±0.01 g) at the start and end of each experimental period but were otherwise left completely undisturbed.

When food was made available, the bats were fed live mealworm larvae, *Tenebrio molitor*, from a lipped pot that prevented the mealworms escaping. We calculated food consumption in terms of the dry mass of mealworms consumed per day. Each day we took a sample of approximately 40 g of mealworms, which was then subdivided. Approximately 10 g was weighed with a precision of 0.001 g with a pan balance (Sartorius Ltd.) and then dried to constant weight (4 d at 60°C) to calculate a dry weight to wet weight ratio for the sample. The remaining fresh mealworms were weighed to 0.001 g and placed in the feeding pot. We used the dry: wet weight ratio for the sample to calculate the dry weight of the mealworms placed in the feeding pot. The next day any uneaten mealworms were removed and dried to constant weight, hence allowing the dry weight of the mealworms consumed by the bats to be calculated. More mealworms were provided than the bats ate, so that food consumption was not limited by food availability.

Daily water consumption was calculated by weighing a water pot (approximately 6-cm diameter, 1.5-cm lip height) each day with a precision of 0.001 g, along with a control pot used to correct for evaporative water loss. The control pot was covered with a wire mesh (approximate mesh size 5 mm × 5 mm) to prevent the bats’ drinking from it and was placed adjacent to the uncovered drinking pot. Direct observation indicated that spillage during drinking did not occur and also that the bats did not walk in the drinking pot, that is, water was not lost from the pots on the fur or the feet of the bats. The feeding and drinking pots were placed approximately 2 m apart, with each pot being positioned in the same place each day.

We recorded whether any bats emerged each day by using two Doppler radar units (RS Components, RS 8960) interfaced to a BBC microcomputer...
(Acorn Computers Ltd.) that logged when the radars were triggered. One radar was positioned to monitor when the bats went to the feeding pot, and the other was positioned to monitor when the bats went to the drinking pot. We operated the radars for 11 d without any bats in the free-flight enclosure to establish the level of “false triggers,” that is, triggers that were not attributable to the bats. We assumed that, if the observed number of triggers on either radar had a <1% probability of being entirely due to false triggers, then at least one bat had emerged from the hibernaculum and had attempted to either feed or drink. We could not establish situations where the bats emerged but did not attempt to feed or drink. The radars did not identify individual bats but rather gave an integrated value for the level of bat activity.

Data Analysis

Regression equations (least squares fit) and the associated $F$ values, df and $P$, and Student’s $t$ tests were calculated with Minitab Statistical Software (Minitab Inc.); $G$ values were calculated according to Sokal and Rohlf (1981).

Results

Complete temperature data inside and outside the hibernaculum were recorded on 41 of 51 d and relative humidity inside the hibernaculum on 22 of 51 d. The mean daily (1200 to 1200 hours the next day) temperature inside the hibernaculum was 7.1°C (range 3.4°–12.4°C, SD = 2.2°C) and outside was 5.6°C (range 2.1°–9.6°C, SD = 1.8°C). Relative humidity in the hibernaculum averaged 82.0% (range 66.3%–93.3%, SD = 7.1%). The mean daily temperatures inside and outside the hibernaculum were positively and linearly correlated ($F$ = 684, df = 1,39, $P < 0.01$, $r^2 = 0.95$) with the temperature inside the hibernaculum exceeding that outside by 0.6°–2.8°C (fig. 1).

The number of false triggers on the two radars was small, averaging 0.18 d$^{-1}$ ($n = 11$ d, SD = 0.60) for the radar covering the feeding pot and 1.55 d$^{-1}$ ($n = 11$ d, SD = 3.30) for the radar covering the drinking pot. This equated to an average of 0.06% of the mean daily number of triggers for the radar covering the feeding pot and 1.6% of the mean daily number of triggers for the radar covering the drinking pot. Since the level of false triggers was so low and the first triggers on any day always occurred in a batch (>5 triggers in the first minute of activity) we used the timing of the first triggers to record when the first bat emerged each day. The timing of initial activity was positively correlated ($F = 42.1$, df = 1,40, $P < 0.001$, $r^2 = 0.51$) with
time of sunset, with the first bat emerging a mean of 64.4 min ($n = 42$, $SD = 27.0$ min) after sunset (fig. 2). Activity was strictly nocturnal, with >99% of all the radar triggers occurring between 1600 and 0700 hours. We therefore defined the mean temperature at night as the mean value recorded between 1600 and 0700 hours.

Bats did not emerge on significantly more nights when there was no food available (no emergence on 8 of 22 nights) than when there was food avail-

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**Fig. 1.** The relationship between the mean daily temperature inside and outside the artificial hibernaculum. The line of equivalence (inside temperature = outside temperature) is shown.

**Fig. 2.** The time of the first activity each evening plotted against the date. The solid line represents the time of sunset (calculated using predictor software [Telonics TSP] as the time of $0^\circ$ sun elevation above the horizon).
able (no emergence on 1 of 29 nights) \((G = 9.43, \text{df} = 2, P < 0.01)\). When food was available, the mean daily temperature in the free-flight enclosure \((\text{mean} = 6.50^\circ\text{C}, n = 20, \text{SD} = 1.53)\) was significantly \((\text{Student’s} \ t\text{-test}, t = 3.75, \text{df} = 38, P < 0.001)\) warmer than on the days when no food was available \((\text{mean} = 4.68^\circ\text{C}, n = 21, \text{SD} = 1.57)\).

If the probability of one bat emerging was not influenced by the probability of another emerging, the daily probability of an individual not emerging was \((9/51)^{1/3} = 0.56\), and, hence, the probability of an individual emerging was \(0.44\) \((95\% \text{ level of certainty} = 0.26–0.54)\). If, however, the emergence of one bat precipitated the emergence of the other two, then on 42 d all three bats would have emerged, giving the daily probability of emergence as \((42/51)^{1/3} = 0.94\) \((95\% \text{ level of certainty} = 0.85–0.99)\).

At the onset of the experiment the bats weighed 8.99 g, 9.86 g, and 10.71 g. The mealworms provided as food consisted, on average, of 59.3% water \((n = 29 \text{ samples}, \text{SD} = 0.88\%)) when there was no food available, the mean mass loss was \(0.078 \text{ g} \cdot \text{bat}^{-1} \cdot \text{d}^{-1}\) \((n = 6, \text{SD} = 0.022)\).

Food consumption was significantly and positively correlated with the mean temperature at night in the free-flight enclosure \((F = 42.1, \text{df} = 1.18, P = 0.027, r^2 = 0.24)\) \((\text{fig. } 3a)\). None of the residual variation in food consumption was explained by the number of days since food deprivation had ended \((\text{stepwise regression}, P > 0.05)\). We used the total number of radar triggers to give an indication of the overall level of bat activity \((\text{fig. } 3b)\). When food was not available, activity was low and independent of the mean temperature at night in the free-flight enclosure \((F = 1.3, \text{df} = 1.13, P = 0.274)\), but when food was available there was more activity and activity increased with temperature \((F = 8.4, \text{df} = 1.18, P = 0.01, r^2 = 0.32)\).

The wire mesh that covered the control water pot reduced evaporative water loss. On the nights that no bats emerged, the water loss from the control pot averaged 88.9% \((n = 8, \text{SD} = 8.6\%)) of that from the drinking pot. We used this mean value of 88.9% when correcting for evaporative water loss to calculate the water consumption. For the nights on which the bats did not have access to food but at least one emerged, the mean water consumption was \(0.20 \text{ mL} \cdot \text{bat}^{-1} \cdot \text{night}^{-1}\) \((n = 14 \text{ nights}, \text{SE} = 0.05, \text{range} = 0.00–0.68)\). The amount of water consumed increased linearly with food consumption \((F = 207.4, \text{df} = 1.37, P < 0.001, r^2 = 0.85; \text{fig. } 4)\). None of the residual variation in water consumption was explained by the mean temperature at night in the free-flight enclosure \((\text{stepwise regression}, P > 0.05)\).

The mass change of the bats was significantly correlated with their mean food consumption \((\text{mass change [g]} = 0.0856 \text{ mean dry g mealworms consumed} \cdot \text{bat}^{-1} \cdot \text{d}^{-1} – 0.0755; F = 17.8, \text{df} = 1.10, P < 0.01, r^2 = 0.64; \text{fig. } 5)\). When the bats did not feed they lost mass, but when they fed they either
lost mass at a slower rate or they gained mass. We used the methodology of Speakman and Racey (1989) to calculate the proportion of time that the bats spent in torpor. The intercept of the fitted regression at $y = 0$ on figure 5, which represents the mean daily food consumption needed to maintain a constant mass, was 0.88 g dry mealworm $\cdot$ bat$^{-1} \cdot d^{-1}$. Assuming a dry mass absorption efficiency of 82.8% and an energy content of mealworms of 26.5 kJ $\cdot$ g$^{-1}$ dry mass (Speakman and Racey 1989), the daily energy requirement was estimated as 19.3 kJ $\cdot$ bat$^{-1}$. The intercept of the fitted
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regression at $x = 0$, which represents the rate of depletion of body reserves in the absence of food intake, was $-0.076$ g · individual$^{-1}$ · d$^{-1}$. Assuming that 69% of this mass loss was due to water and that the remainder was due to fat depletion and assuming an energy content for fat stores of 39.41 kJ · g$^{-1}$ (Speakman and Racey 1989), the bats expended a mean of 0.93 kJ · bat$^{-1}$ · d$^{-1}$ when not feeding.

The proportion of time spent in torpor ($pT$) may be calculated from

$$pT = (E_d - aE_a - E_t)/(E_t - E_t)$$

(Speakman and Racey 1989), where $E_a$ = the energy expended per arousal in raising the body temperature to the euthermic level (37°C), $E_d$ = the daily energy expenditure, $E_t$ = the energy expenditure in torpor, $E_r$ = the energy expenditure when regulating body temperature at the euthermic level, and $a$ = number of arousals per day. Using the mean mass of the bats throughout the study (9.0 g) and the mean temperature inside the artificial hibernaculum (7.1°C), we calculated $E_d$ = 0.729 kJ (from Thomas, Dorais, and Bergeron 1990), $E_t = 117.37$ kJ · d$^{-1}$ when flying (from Speakman and Racey 1991) and 46.54 kJ · d$^{-1}$ when at rest (from Speakman and Racey 1987), and $E_t = 0.454$ kJ · d$^{-1}$ (from Speakman et al. 1991). Using our estimate of the probability of arousal on any day as 0.26 to 0.99 and our estimates of $E_d$ (19.3 kJ · d$^{-1}$ from food the consumption needed to maintain constant weight and 0.93 kJ · d$^{-1}$ from the mass loss in the absence of food), we calculated $pT$ (table 1).
The calculated proportion of time spent in torpor was longer when the bats did not feed \((pT \geq 0.99)\) compared with when they fed \((pT = 0.60-0.84)\). When the bats fed, \(pT\) was lower when it was assumed that the bats were continuously at rest when euthermic and higher when it was assumed that they flew continuously when euthermic. In practice while the bats were euthermic they must have spent part of the time at rest and part of the time flying. The calculated proportion of time spent in torpor

### Table 1

Estimated proportion of time that the bats spent torpid calculated from food consumption, (the food consumption required to maintain a constant mass) and fat depletion (the loss of mass in the absence of food), assuming either that the bats flew continuously while euthermic or that the bats were always at rest while euthermic, and using our range of estimates for the number of arousals per day \((a)\)

<table>
<thead>
<tr>
<th></th>
<th>Food Consumption</th>
<th>Fat Depletion</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>(a = .26)</td>
<td>(a = .26)</td>
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<tr>
<td></td>
<td>(a = .99)</td>
<td>(a = .99)</td>
</tr>
<tr>
<td>Flew continuously while euthermic</td>
<td>0.84</td>
<td>0.84</td>
</tr>
<tr>
<td>At rest while euthermic</td>
<td>0.60</td>
<td>0.61</td>
</tr>
</tbody>
</table>

Note. See text for details.
was not greatly influenced by the estimate used for the number of arousals per day.

Discussion

In the wild, *Plecotus auritus* hibernate in a range of sites including buildings, trees, and caves and may hibernate singly, in small groups, and with other species (for review see Swift 1991). The mean relative humidity in the experimental hibernaculum used here (82%) was very similar to that reported in natural *P. auritus* hibernacula by Bogdanowicz and Urbanczyk (1983) (mean 84%, range 55%–100%) and within the ranges reported by Lesinski (1986) (range 75%–95%) and Stebbings (1966) (mean relative humidity 70%, range 51%–97%). The range of temperatures we recorded inside the artificial hibernaculum (3.4°–12.4°C) was also within the range reported for natural hibernacula (range −3°–11°C) (Swift 1991). The relative humidity and temperature in our artificial hibernaculum are therefore in accord with the conditions in natural hibernacula. Similarly, body mass at the onset of the experiment (range 8.99–10.71 g) was similar to the range (8.9–10.3 g) reported for *Plecotus* in January in a natural hibernaculum in England (Stebbings 1966).

In a previous estimate of the probability of emergence in *Plecotus* (probably *P. auritus*) during hibernation, Daan (1970) used a camera triggered by an infrared light beam to photograph bats as they exited and entered a natural cave hibernaculum. Daan (1970) estimated that the mean daily number of emergence flights per bat between December and February was 0.6–2.6. In our study the calculated daily probability of emergence was 0.44–0.94. The implication is that, in both the current study and in the wild, *P. auritus* may emerge frequently in winter.

Calculations of the daily energy expenditure from food intake and mass loss strongly suggest that the bats were not remaining continuously euthermic (table 1). Rather, they were torpid for much of the time, presumably to conserve energy. The length of time that the bats spent torpid was longer when they did not have access to food and shorter when they maintained a constant weight by feeding. Presumably when food was available the bats were able to optimize their energy balance by remaining euthermic and feeding for prolonged periods each night. The mass loss that we recorded when there was water but no food available (0.078 g · bat⁻¹ · d⁻¹) was considerably (4.6 times) more than the mass loss recorded for female *Plecotus* (mainly *P. auritus*) during January to March in a natural hibernaculum in England. This may have been because winter feeding in the wild reduces mass loss, as was the case in our study, and indeed there have been
reports of *P. auritus* feeding in winter in the wild (Stebblings 1966; Roer 1969).

If *P. auritus* routinely feeds during its winter flights, this begs the question of what food is potentially available. The temperature threshold for flight in insects varies between species (Rainey 1976). For some species this flight threshold is low and might allow frequent winter flights. For example, the moths *Operophtera brumata*, *Agrochola lychnitis*, and *Amphipyra trago-poginis* have flight thresholds of 5°–5.5°C, 6.1°C, and 6.5°C, respectively (Taylor 1963; Alma 1970). These temperatures are in the lower end of the range at which we recorded feeding by *P. auritus* (fig. 3a). However, in addition to catching insects that are flying, *P. auritus* is also able to glean insects off surfaces (Anderson and Racey 1991). In summer, insects that are gleaned may constitute a large proportion of the diet (Swift and Racey 1983; Rydell 1989; Shiel, McAney, and Fairley 1991), although their contribution in winter is unknown. The winter diet may therefore potentially be composed of flying insects captured before they take off and arboreal and terrestrial insects, as well as insects that are flying. When gleanning, *P. auritus* can detect an insect more readily if the insect moves (Anderson and Racey 1991). This has potentially important consequences for winter prey capture by *P. auritus* since wing flapping by insects may occur at temperatures far below those at which the insect may actually take off. For example, Cockbain (1961) found that the aphid *Apis fabae* could fly at a minimum temperature of between 13°C and 15°C but would flap its wings at temperatures as low as 6.5°C. *Plecotus auritus* may therefore be able to glean insects that are preparing for flight, at far lower temperatures than it can capture insects that are flying. In addition during winter *P. auritus* has been shown to capture and consume insects that are diapausing (Roer 1969). To establish the true winter diet will clearly require diet analysis studies in winter of the sort that have been conducted in summer (e.g., Rydell 1989; Shiel et al. 1991).

The strong correlation between the temperatures inside and outside the hibernaculum (fig. 1) would allow the bats to evaluate the external temperature from inside the hibernaculum. Hence they would not need to emerge, which is energetically expensive (Speakman and Racey 1991), to evaluate the external temperature. Such a correlation between internal and external temperatures has been found previously in parts of a natural *P. auritus* hibernaculum (Daan 1973) as well as in natural greater horse-shoe bat (*Rhinolophus ferrumequinum*) hibernacula (Ransome 1968, 1971). For several other species it has previously been demonstrated that winter emergence occurs preferentially on warmer nights, presumably because of a higher abundance of flying insects than on cooler nights (Ransome 1968, 1971; Avery 1985; Brack and Twente 1985; Twente et al.
1985). Similarly, we found that the bats tended not to emerge on nights when it was cold and there was no food. Also when food was freely available, food consumption and activity increased at higher external temperatures (fig. 3). This may have reflected an increased probability of emergence on warmer days, independent of food availability, and/or a greater food intake per individual on emerging when it was warmer.

In the absence of food the bats drank a small amount and were torpid almost all of the time. However, when the bats were able to feed they were euthermic for longer (table 1), were more active (fig. 3), and drank more (fig. 4). This suggests that most of the water consumed was to balance the water loss incurred as a result of staying active and feeding. This is consistent with water loss measurements that have been made for other species. For the bats *Eptesicus fuscus*, *Antrozous pallidus*, and *Leptonycteris sanborni* it has been shown that water loss while flying and while aroused but resting is much greater than while torpid (Carpenter 1969). In addition, urine production in bats may increase markedly after feeding (Bassett and Wiebers 1979).

Traditionally, winter flights by bats have been thought to be feeding trips (Avery 1985; Brigham 1987). Recently, however, Speakman and Racey (1989) inferred that, for hibernating pipistrelle bats (*Pipistrellus pipistrellus*), a bat that does not emerge will die of dehydration before it dies of starvation. For example, a 7.0-g pipistrelle (the approximate mean mass of females at the onset of hibernation) would die of dehydration after about 13 d, but if able to drink would not die of starvation until 38 d. Hence, Speakman and Racey (1989) suggested that the primary function of winter emergence may be to drink. This assumes that a hibernating bat depletes its resources until it is forced to emerge or die. For *P. auritus*, however, it would appear that winter flights may be an almost daily event (Daan 1970; this study). We would therefore suggest that *P. auritus* may not only emerge when there is a physiological need to do so; rather they may also emerge regularly so that this physiological need (to avoid either dehydration or starvation) does not arise. This pattern of frequent winter emergence contrasts with that found in some other species that may remain continuously torpid for several weeks (Menaker 1964; Twente et al. 1985; Twente and Twente 1987). In such cases of prolonged torpor, the bats may be emerging because of some physiological necessity. Such cases of prolonged torpor, although not found in *P. auritus* in this study, might potentially occur in long periods of cold weather and low food availability where the probability of flights is consequently reduced.
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