POSITION OF THE PINNAE AND THERMOREGULATORY STATUS IN BROWN LONG-EARED BATS
(PLECOPTUS AURITUS)

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Abstract—The relationship between position of the pinnae and thermoregulatory status was investigated in 13 captive brown long-eared bats (Plecotus auritus L.). Bats with body temperature ($T_b$) in excess of 28°C were endothermic, and those at lower $T_b$ were torpid. The pinnae of torpid bats were generally tightly folded below the forearms, whilst those of endothermic bats were, to a varying degree, erected. There was a significant positive relationship between $T_b$ and degree of erection of the pinnae, ranked on a scale 0-5. A fitted regression, however, only explained 9.3% of the variability in $T_b$. There was also no significant relationship between the elevation of $T_b$ above the ambient temperature ($T_a$) and the degree of erection of the pinnae, for both endothermic and torpid bats.

The absence of a precise relationship between both $T_b-T_a$ and $T_b$, with pinnae erection, in addition to a significant association between pinnae erection and thermoregulatory status suggests that pinnae erection and thermoregulatory status are not functionally related. Folding the pinnae below the forearms is probably incompatible with other behaviours, such as grooming, which involve considerable movement of the forearms. These behaviours occur predominantly during endothermy and it is more likely therefore pinnae would be unfolded during endothermic periods. This latter hypothesis is supported by longitudinal measurements of both $T_b$ and ear position in individual bats at a relatively constant $T_a$. Pinnae position cannot be used to reliably assess thermoregulatory status of individual brown long-eared bats through time.

Key Word Index—Thermoregulation; brown long-eared bat; pinna; torpor; body temperature; Plecotus auritus.

INTRODUCTION

When long-eared bats (Plecotus sp.) are at rest their enormous pinnae are found in a variety of positions. These vary from fully erect, to tightly folded beneath the forearms. In the field it has been frequently observed that long-eared bats with their pinnae tightly folded are torpid, whilst those with their pinnae fully extended have high body temperatures and are active (e.g. Stebbings, 1986). Most records of torpid bats however refer to bats which are in hibernation. Nevertheless, observations of brown long-eared bats (Plecotus auritus L.) in maternity colonies, between May and October, suggest they also frequently hold the ears in the tightly folded position. A relationship between the degree of pinnal erection and thermoregulatory state would represent a powerful tool by which the thermoregulatory condition of free-living or captive Plecotus could be assessed without disturbance. This study aimed to assess the relationship between pinnae position and thermoregulatory status in the brown long-eared bat during the summer and autumn (May–October).

METHODS

Observations were made on six male and seven female $P. auritus$, captured from the wild from maternity roosts in the Dee valley, North-east Scotland (58°N). The bats were housed individually in cages ($30 \times 30 \times 50$ cm, Racey, 1970), subject to a natural photoperiod and temperature cycle, with free access to both food and water. Observations were made predominantly between 0900 and 1300 h, and were restricted to individuals which were hanging at rest. The position of the ears was ranked according to the degree of erection of the pinnae, on a scale 0–5, with 0 referring to flaccid pinnae folded beneath the forearms and 5 being maximally erect (Fig. 1). The ambient temperature ($T_a$) was measured using a probe and digital thermometer 5 cm away from the bat. The bat was then removed from the cage and its body temperature ($T_b$) measured using insertion of a $0.5$ mm external diameter probe $10$ mm into the rectum within $10$ s of capture. Only a single body temperature measurement was made on any individual on any day.

Direct observations of the bats showed they did not respond to the inevitable noises of processing other bats by changing their ear position, although it is possible that there was an anticipatory rise in $T_b$ in response to these noises. There was no evidence to support this latter hypothesis since there was no significant relationship between $T_b$ and order of processing ($r = 0.07, P > 0.05$, not illustrated). In a second series of observations the same measurements were made but more frequently (at 6–9 h intervals) on nine individually caged bats, housed at a relatively constant $T_a$ ($15 \pm 2$°C) in natural photoperiod. One group ($n = 4$) were deprived of food, whilst the other group had free access to live mealworms. All bats had free access to water. It is known the propensity to enter daily torpor varies with many factors (Racey and Swift, 1981) of which one is food supply. By
manipulating food supply therefore a range of thermoregulatory behaviours across individuals was generated. Food deprived bats were observed over 30 h and fed bats were observed over 52 h. During both sets of observations, on occasion, the positions of the two pinnae was not the same. In these asymmetrical cases, which amounted to less than 5% of observations, an average ear position was calculated.

RESULTS

There was a bimodal distribution of \( T_b \) (Fig. 2). There was a significant positive relationship between \( T_a \) and \( T_b \) for those measurements in the lower distribution (< 28°C) (Fig. 3). The constant of the fitted regression (4.36) was significantly greater than 0 (\( P < 0.01 \)), but the coefficient (0.92) was not significantly different from 1.0 (\( P = 0.24 \)). These data are consistent with bats which are regulating their \( T_a \) but at a low and relatively constant interval above \( T_s \). Elsewhere we have shown these bats have very low endogenous heat production (Speakman and Racey, 1987). Hereafter such bats are termed torpid. The \( T_b \) of bats from the upper distribution was less dependent on \( T_a \) (\( y = 33.6 + 0.12x, r = 0.34, P < 0.05 \)). Measurements of \( T_b \) in the upper distribution were

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Fig. 1. Resting brown long-eared bats hanging posterior uppermost showing the pinnae varying from tightly folded (0) to fully erect (5). All drawings from life (f = foot; ds = dorsal surface; fa = forearm; p = pinnae; t = tragus).

Fig. 2. Frequency distribution of body temperatures recorded from thirteen brown long-eared bats between 0900 and 1300 h (\( n = 137 \)).
therefore from bats which were regulating $T_e$ at a relatively constant level which was significantly greater than $T_b$. We have shown elsewhere that endogenous heat production in these bats is very high (relative to the predicted Basal Metabolic rate: Kleiber, 1961) (Speakman and Racey, 1987). These bats are hence termed endothermic.

There was a significant association (Table 1) between torpidity and having the pinnae tightly folded (classes 0 and 1), and endothermy and having the pinnae erect (classes 2–5). This association is reflected by a significant positive relationship between $T_b$ and ear position (Fig. 4). The variability in $T_b$ explained by differences in ear position (or vice versa) was however only 9.3%. This low predictability occurred because some of the torpid bats had their ears extended whilst some of the endothermic bats had their ears folded.

The absence of a clear relationship between $T_b$ and ear position may reflect differing functions of pinnae erection between each of the two thermoregulatory groups. Amongst the endothermic group extended pinnae may elevate heat loss, hence endothermic bats at lower $T_b$, but with higher elevations of $T_b$ above $T_a$, would be expected to fold their ears more frequently. In contrast amongst torpid bats pinnael erection may serve to enhance heat uptake as an aid to arousal. Since torpid bats had on average lower $T_b$ than endothermic bats (Fig. 2) a plot of $T_b$ alone against ear position may be insufficient to elucidate these functional aspects. There was however no relationship between elevation of $T_a$ above $T_b$ and ear position for either endothermic or torpid bats (not illustrated). Although these data failed to indicate any clear functional relationship between ear position and thermoregulatory status, there were evident differences in the probability of a bat being of a given thermoregulatory state as position of the ears changed (Fig. 5) for measurements made during the period 0900–1300 h. A bat with its ears in position 0 had a probability of 0.73 (SD = 0.05) of being torpid. A bat with its ears in position 3 had a probability of 0.97 (SD = 0.015) of being endothermic.

Longitudinal measurements of both $T_b$ and ear position, made at a more frequent rate, for nine individual bats are shown in Fig. 6(a–i). All bats which had been food deprived entered diurnal torpor. In contrast four of the five bats which were fed remained continuously endothermic. Amongst the food deprived bats there was some evidence of an association between thermoregulatory status and ear position in all of the bats. However the coupling of ear position to $T_b$ (and hence $T_b-T_a$) was imprecise and also variable between individuals. Hence during

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**Fig. 3.** Body temperature ($T_b$) plotted against ambient temperature ($T_a$) for bats from (○) the lower and (●) the upper distributions shown in Fig. 2. The least squares fitted regressions and curves of temperature equivalence ($T_{pe} = T_b$) are shown as broken and solid lines respectively. $T_b$ was highly dependent on and positively related to $T_a$ in (○) whilst in (●) the $T_b$ was almost constant and less dependent on $T_a$. The least squares fit regression equations are: (○) $T_b = 4.36 + 0.92 T_a$, $r = 0.80$, $n = 29$, $F = 48.6$, $P = 0.001$; (●) $T_b = 33.6 + 0.12 T_a$, $r = 0.34$, $n = 108$, $F = 13.8$, $P = 0.001$.

**Fig. 4.** Body temperature ($T_b$) plotted against ear position for all bats. There was a significant positive relationship, $T_b = 27.2 + 1.9$ (ear position), $r = 0.30$, $n = 137$, $F = 13.9$, $P < 0.001$.

**Fig. 5.** Probability of a bat being endothermic as a function of its ear position. Error bars equal standard deviation. Where error bars not shown they are smaller than dimensions of point. Different ear positions were associated with significantly different probabilities of being endothermic.
Fig. 6. Longitudinal measurements of both $T_e$ (•) and ear position (EP: ○) for bats which were food deprived (a–d inclusive) and bats which were fed ad lib (e–i inclusive). $T_e$ was relatively constant at 15 (±2°C). For those bats which were food deprived there was an apparent association between folding of the ears and torpor. However, the coupling in time was imprecise. For those bats which had free access to food, and hence remained almost continuously endothermic, there was still a daily cycle apparent in the erection of the pinnae, in four of the five individuals observed.
entry to torpor, one individual (Fig. 6a) decreased $T_b$ several hours in advance of folding the ears, whilst for others (Fig. 6b and d) the converse was true. In another individual (Fig. 6c) the coupling of ear position to $T_b$ during entry to torpor appeared to be quite precise. During arousal from torpor all the bats elevated $T_b$ before opening the pinnae, and in one case (Fig. 6d) the pinnae were still folded at the end of the experiment although arousal had occurred about four hours previously. Despite remaining almost continuously endothermic there was still a daily cycle of erecting and folding the pinnae in four of the five bats which were fed ad lib.

**DISCUSSION**

The significant association between tightly folded pinnae and diurnal torpor and between more erect pinnae and endothermy (Table 1), supports the more general and anecdotal field observations. The association is however statistical and not absolute, as is emphasised by the poor relationship between erection of the pinnae and $T_b$ (Fig. 4), and the absence of relationships between the elevation of $T_b$ above $T_c$ and ear position for both thermoregulatory groups. These data suggest the changing position of the pinnae do not reflect an aspect of the bats thermoregulatory state and position of the pinnae. The problem remains therefore as to how this association arose.

The lower critical temperature for brown long-eared bats exceeds 30°C (Speakman and Racey, 1987). If the pinnae do act as heat conductors then it might be considered disadvantageous, in terms of enhanced heat loss, to erect the pinnae at any time during endothermy when $T_b$ is less than 30°C (98% of the current data set). Whilst bats are endothermic however they engage in a variety of behaviours, even when they may be considered to be hanging predominantly "at rest", e.g. grooming and adjustment of hanging position. These behaviours involve extensive movements of the forelimbs. In long-eared bats, retaining the pinnae below the forelimbs is probably incompatible with these other behaviours. Long-eared bats may fold their pinnae to conserve heat, but fail to keep them folded because of grooming and adjustment of the hanging position. Since torpid bats seldom move or groom this may render them more probable to keep the ears folded. Ear position probably depends most critically on which behaviours have been performed in the immediately preceding period. A statistical association probably occurs because endothermic bats are more likely than torpid bats to engage in the activities which are incompatible with folded ears.

This suggestion is supported by the longitudinal measures of both $T_b$ and ear position in individual bats (Figs 6a–i). In those bats which entered a diurnal torpor the observed linkage between $T_b$ (and hence thermoregulatory status, since $T_b$ was almost constant) and erection of the pinnae was imprecise. This is consistent with the suggestion that the pinnae are erected when activities predominantly performed during endothermy mean retaining them below the forearms is not feasible.

In those bats which did not enter torpor (Fig. 6e–i) the position of the ears continued to follow a diurnal cycle in four of the five bats studied, despite the continuously high $T_b$. This cycle in ear position probably reflected the diurnal cycle of activity, which is sustained in bats kept in captivity (Erkert, 1982). Further support is provided by the observations of asymmetry in ear positions. Commonly these involved only differences of 1 or 2 divisions on the position scale (Fig. 1) however exceptionally some individuals were observed with one pinna fully folded and the other fully erect. Measures of $T_b$ adjacent to both pinnae in these bats were always identical. These asymmetrical observations may reflect differences in forelimb activity but are difficult to explain by any functional interpretation of pinnal erection.

As the relationship is probably not functional, ear position cannot be reliably used to assess the thermoregulatory status of individual bats through time. However, during part of the daily cycle corresponding to the time observations were made in this study (0900–1300 h), some ear positions may give a general indication of thermoregulatory condition (Fig. 3).  

**REFERENCES**


**Table 1. Numbers of bats that were torpid and endothermic and their ear positions. Tightly folded ears were associated with torpidity whilst more erect pinnae were associated with endothermy**

<table>
<thead>
<tr>
<th>Pinnae position</th>
<th>Torpid</th>
<th>Endothermic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tightly folded</td>
<td>18</td>
<td>11</td>
</tr>
<tr>
<td>Extended</td>
<td>17</td>
<td>91</td>
</tr>
</tbody>
</table>

The distribution differs significantly from random (Chi squared = 25.8, df = 1, $P < 0.001$).