Thermoregulation in the female hedgehog, *Erinaceus europaeus*, during the breeding season

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Summary. The body temperatures of 3 breeding and 7 non-breeding female hedgehogs were monitored during 3 years. Lactating females had significantly higher and less variable body temperatures than did pregnant and non-breeding hedgehogs. Breeding females had circadian body temperature cycles that were more biphase than those of non-breeders. Females maintaining higher mean daily body temperatures showed less variability about the mean than those exhibiting lower mean daily body temperatures. The rate at which body temperatures became more variable as mean daily body temperatures fell was 4-6 times more rapid in non-breeding females than in pregnant and lactating hedgehogs. With the exception of a single female in late gestation, hedgehogs readily became torpid under conditions of low ambient temperature and short photoperiod during summer, particularly when their food intake was restricted.

Keywords: female hedgehog; breeding; thermoregulation

Introduction

Gestation length in mammals is thought to be largely controlled by fetal genotype, maternal age (Racey, 1981) and maternal body mass (McKeown et al., 1976). Yet in hibernators estimates of gestation length are often variable and many hibernating animals, including the European hedgehog, *Erinaceus europaeus* (Dmi'el & Schwarz, 1984), are also readily able to become torpid under the appropriate conditions of inanition, low ambient temperature and darkness. It is possible therefore that depressed body temperature (T<sub>body</sub>) during gestation, with a consequent reduction in the rate of fetal growth, is responsible for the variability in estimates of gestation length in heterotherms (Racey, 1981).

Such variation is recorded for the European hedgehog, with estimates of gestation period ranging from 30 to 40 days (Herter, 1938; Ranson, 1941; Morris, 1961, 1966). An observation of hypothermia during gestation in the European hedgehog (Fowler, 1982) indicated that further research into this interface between reproduction and thermoregulation is required.

Torpor is widely regarded as the lowering of T<sub>body</sub> to a variable extent, with the fall in T<sub>body</sub> being less than during hibernation, at regular or irregular intervals (Hudson, 1973; Lyman, 1982). The distinction between adaptive hypothermia and hypothermia per se is that the latter, unlike the former, has the clinical and pathological implications (Hudson, 1973) of a lowered T<sub>body</sub> from which the animal cannot spontaneously recover. Therefore, adaptive hypothermia is an appropriate term to use in discussing lowering of T<sub>body</sub> during breeding as a strategy for surviving unfavourable conditions, as opposed to a pathological state imposed upon breeding females by the environment.

The specific aims of the present study were to investigate thermoregulatory differences between non-breeding, pregnant and lactating hedgehogs, and to determine whether conditions which induce unseasonal torpor in non-breeding hedgehogs would also induce torpor in pregnant females.

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Materials and Methods

Animals. Hedgehogs captured in Aberdeenshire, N.E. Scotland, at 57°N, were housed in outdoor pens at the Cultery Field Station, Department of Zoology, University of Aberdeen. Day-old chicks, cat food and dog meal, and water, were provided ad libitum. Disturbance was kept to a minimum and the animals were exposed to natural photoperiod and ambient temperatures.

Temperature telemetry. Unit A temperature sensing transmitters (AVM Instruments, Ltd, Dublin, U.S.A.) were used to determine $T_{\text{body}}$, and in situ comprised <10% of the hedgehog's body weight. The transmitters were calibrated to 0–1°C accuracy, before and after implantation, and all data from transmitters with significant calibration drift were discarded.

Female hedgehogs were anaesthetized with 5% halothane/O$_2$ (Fluothane: ICI Plc, Macclesfield, U.K.), and the transmitters were introduced into the peritoneal cavity by laparotomy and allowed to move freely. Post-operative treatment involved Terramycin antibiotic spray (Pfizer Limited, Sandwich, U.K.), and Streptopen antibiotic injection (Glaxovet Ltd, Harefield, U.K.). The 10 hedgehogs were housed overnight at 24°C and then returned to their pens.

Sharp microcomputer/Fliptrack radio receiver (Sharp Ltd, Manchester, U.K.; AVM Instruments, Ltd, Dublin, U.S.A.) or BBC 'B'/Falcon V radio receiver (Acorn Computers Ltd, Cambridge, U.K.; Wildlife Materials, Inc., Carbondale, U.S.A.) systems were used to collect data at 30-min intervals, over consecutive 24-h periods (09:00–08:30 h GMT). Analysis was carried out on a mainframe computer.

Torpor induction. In June 1983, July 1984 and August 1985, hedgehogs were placed in a cold room for 48-h periods. Overall 6 male and 14 female hedgehogs were used for these trials. In 1983 and 1984 the temperature of the cold room was set at 11°C, and at 5°C in 1985. Feeding was either ad libitum or restricted and lighting conditions were: 24L:00D, 18L:06D or 00L:24D, giving 6 combinations of environmental and dietary conditions under which torpor induction was tested in the hedgehogs. In 1985 7 additional females were subjected to the experimental condition that had been determined during the previous 2 years as that most likely to induce torpor.

Breeding. All animals used in this study were part of a stock maintained at the Cultery Field Station as part of wider studies. The hedgehogs were given every opportunity to breed, and after a period with males females were kept isolated from other hedgehogs to minimize disturbance, thus increasing the likelihood of successful gestation. Similarly, tests for oestrus or pregnancy were not undertaken in order that the females would remain undisturbed. The lack of consistent body mass changes during pregnancy (Fowler, 1986) meant that gestation was most easily determined retrospectively if the young were seen.

Statistical analysis. All comparisons between females in various stages of the breeding cycle were made with females whose $T_{\text{body}}$ were measured at the same time of year. Differences between $T_{\text{body}}$ measurements were tested by analysis of variance (ANOVA) or two-sample $t$ test (Zar, 1984). Fitted least-squares linear regressions were compared by $t$ testing and relationships between variables by correlation coefficients, $r$ (Snedecor & Cochran, 1980). When shown, mean values are quoted with ± s.d.

Results

There were no apparent side effects of transmitter implantation, apart from the growth of fibrous tissue sheaths around the transmitters, upon the females or the fetuses of pregnant females. Three pregnancies were confirmed, and 2 litters were weaned successfully, in 3 females carrying transmitters.

Body temperatures

During 3 years, 1982–1985, $T_{\text{body}}$ data were obtained from 9 of the 10 females implanted with transmitters.

Dividing the breeding season into pre-gestation (including females at all stages of the oestrous cycle), gestation, lactation and post-lactation phases, it can be seen (Fig. 1) that the mean daily $T_{\text{body}}$ of breeding females remained relatively constant during gestation and lactation, beginning to vary significantly only after the young were weaned. However, despite the lower variability of $T_{\text{body}}$ of breeding females, day-to-day changes in mean daily $T_{\text{body}}$ of breeding females followed the same general trends as those of non-breeding females. The year-to-year differences in changes in $T_{\text{body}}$ seen in Fig. 1 reflect differences in environmental temperature, and other conditions, between the years. The short-term depressions in mean daily $T_{\text{body}}$ were most marked when minimum ambient temperatures fell 5°C below mean minimum levels (Fowler, 1986) for the time of year.
Breeding and thermoregulation of female hedgehogs

Fig. 1. Changes in mean ± s.d. daily body temperature of breeding (●) and non-breeding (◯) female hedgehogs during the breeding season in (a) 1983, (b) 1984 and (c) 1985. G = gestation, L = lactation, W = weaning.

The difference in $T_{\text{body}}$ between non-breeding and post-lactating females (+0.9°C, ANOVA, $P < 0.01$) was greater than that between non-breeding and lactating females (+0.6°C, ANOVA, $P < 0.001$), although the statistical significance of the former was reduced by the greater $T_{\text{body}}$ variability of non-breeding females at this time of year (Fig. 2). Variation (s.d.) of $T_{\text{body}}$ about mean daily $T_{\text{body}}$ was 0.5°C (ANOVA, $P < 0.001$) and 1.4°C (ANOVA, $P < 0.001$) greater in non-breeding than lactating and post-lactation females respectively.

In all females there was a significant relationship between variability of $T_{\text{body}}$ about mean daily $T_{\text{body}}$ and declining $T_{\text{body}}$. However, the rate at which the variability of $T_{\text{body}}$ increased was 4.6 times greater in non-breeding (0.828 rise in s.d./°C drop in $T_{\text{body}}$) than breeding females (0.179 rise in s.d./°C drop in $T_{\text{body}}$).

Examples of circadian $T_{\text{body}}$ cycles observed in non-breeding eutermic hedgehogs (Fowler, 1986) are shown in Fig. 3. This circadian cycle was perturbed in breeding hedgehogs, particularly in lactating females, and took the form of an apparent disconnection of circadian changes in $T_{\text{body}}$ from photophase. Breeding females tended to exhibit two daily periods of peak $T_{\text{body}}$, rather than one (Fig. 3), and also showed less variation of $T_{\text{body}}$ about the daily mean during late summer and autumn. The second peak in $T_{\text{body}}$ tended to occur around 12:00 h GMT, and when mean daily $T_{\text{body}}$ was subtracted from mean $T_{\text{body}}$ between 11:00 and 13:00 h GMT, a significant (ANOVA, $P < 0.05$) difference between breeders and non-breeders emerged. In the former, mean daily $T_{\text{body}}$ was 0.1 ± 0.3°C higher than $T_{\text{body}}$ from 11:00–13:00 h, but 0.4 ± 0.4°C higher in the latter. In Fig. 4 the female weaning her young did not undergo test drops (steep and transient reductions and recoveries in $T_{\text{body}}$ characteristic of hedgehogs before hibernation) until the end of September, unlike the non-breeding female.
Fig. 2. Mean ± s.d. daily body temperatures of breeding (●) and non-breeding (○) female hedgehogs during the pre-gestation (PG), gestation (G), lactation (L) and post-lactation (PL) phases of the breeding season. ***P < 0.001, **P < 0.01 (ANOVA).

Fig. 3. Examples of individual circadian body temperature cycles in (a) a lactating and (b, c) 2 non-breeding female hedgehogs.
Fig. 4. Day-to-day body temperature changes in a lactating (-----) and a non-breeding (-----) female hedgehog during late summer.

Table 1. Incidence of hedgehogs becoming torpid (no./total no. in trial), after 48 h, under 6 experimental conditions during summer months (data from all 3 years and both cold room temperatures are combined)

<table>
<thead>
<tr>
<th>Photophase</th>
<th>Ad libitum</th>
<th>Males</th>
<th>Females</th>
<th>Total</th>
<th>Restricted</th>
<th>Males</th>
<th>Females</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>24L:00D</td>
<td></td>
<td>1/3</td>
<td>1/4</td>
<td>2/7</td>
<td>2/3</td>
<td>3/5</td>
<td>5/8</td>
<td></td>
</tr>
<tr>
<td>18L:06D</td>
<td></td>
<td>2/4</td>
<td>2/4</td>
<td>4/8</td>
<td>4/4</td>
<td>4/4</td>
<td>8/8</td>
<td></td>
</tr>
<tr>
<td>00L:24D</td>
<td></td>
<td>2/4</td>
<td>3/4</td>
<td>5/8</td>
<td>6/6</td>
<td>12/13</td>
<td>18/19</td>
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*The only hedgehog not to become torpid under these conditions gave birth 3–6 days after the experiment.

Torpor induction

The results of the 3 series of summer torpor-induction experiments are summarized in Table 1, but data for the 3 years are shown grouped because sample sizes from individual years were small, and the condition of 18L:06D was only used in 1984. Torpor was recorded in some individual hedgehogs experiencing all 6 variations in experimental conditions. There was no significant (ANOVA, \( P > 0.05 \)) difference in the percentage of male or female hedgehogs becoming torpid under each experimental condition.

Setting the cold room temperature at 5°C, rather than 11°C, in 1985 did not affect the percentage of hedgehogs becoming torpid at 00L:24D. Restricted food intake, together with 00L:24D or 18L:06D (natural peak photoperiod at 57°N), were the most effective conditions for the induction of torpor during summer. Only one animal did not become torpid during the 48 h trial; she gave birth 3–6 days later and her 5 young were successfully weaned later that year.

Discussion

Thermoregulatory changes in female hedgehogs, during breeding, were conclusively demonstrated by the present study, as was the ability of hedgehogs to enter torpor readily, under the appropriate conditions, during summer.

Variation in the estimates of the duration of gestation in the hedgehog suggests that adaptive hypothermia can occur in pregnant hedgehogs, the rate of gestation being influenced by environmental conditions affecting metabolic rate and/or \( T_{body} \) (Hanus, 1959). The measurement of \( T_{body} \)
of female hedgehogs experiencing natural photoperiod and ambient temperature showed that day-to-day fluctuations of mean daily $T_{body}$ were similar in breeding and non-breeding females. The influence of environmental factors upon thermoregulation in the hedgehog is indicated by the increase in fluctuations of mean daily $T_{body}$ when minimum ambient temperatures were particularly low for the time of year. Other factors, such as heavy rain at night, could affect the hedgehogs by increasing heat loss from the uninsulated dorsal surface.

Frazer & Huggett (1974) indicate a specific fetal growth rate ($a_w$) for the European hedgehog of 0·11–0·13. This is comparatively rapid for an insectivore: amongst the Soricidae $a_w$ ranges between 0·06 and 0·09 and is 0·09 in the mole Talpa europaea. On the other hand, heterothermic rodents, such as the hamster Cricetus frumentarius, may have an $a_w$ of up to 0·23. Neonatal European hedgehogs (Krol, 1985) are only 62% of the size predicted by Millar’s (1977) study of 95 mammalian species. Non-breeding hedgehogs have a metabolic rate 20% lower than predicted from Kleiber’s equation relating body mass to metabolic rate (Hildwein & Malan, 1970), with a relatively slow fetal growth rate at the start of pregnancy, a period when other heterotherms do not have greatly elevated metabolism (Thompson & Nicoll, 1986), perhaps contributing to the small birth size.

The lack of significant difference, both in mean daily $T_{body}$ and variation about mean daily $T_{body}$, between pregnant and non-breeding female hedgehogs suggests that comparatively little modification of thermoregulation occurs during pregnancy. The dephasing of the circadian $T_{body}$ cycle from photoperiod and the tendency towards a biphasic circadian $T_{body}$ cycle in breeding hedgehogs indicates that a greater proportion of each 24-h period was spent at higher $T_{body}$ which contributed towards the slightly higher mean daily $T_{body}$ during gestation. This is similar to observations of the three-toed (Bradypus tridactylus) and tree (Bradypus griseus) sloths. Pregnant sloths not only had less variable $T_{body}$ than did non-breeding sloths under natural conditions, but they also lowered $T_{body}$ by 5°C less than non-pregnant sloths at ambient temperatures of 15°C (Morrison, 1945).

Most mammals, including hedgehogs (Herter, 1938) and other insectivores such as the tenrec Tenrec ecaudatus (Nicoll, 1985), time parturition so that the most energetically expensive phase of reproduction, lactation, coincides with the most abundant food supply (Bronson, 1985; Bronson & Marsteller, 1985).

From their lower than predicted birth-size, neonatal hedgehogs grow rapidly and are weaned at twice the size predicted for weaned mammals (Millar, 1977; Krol, 1985). The growth rate to weaning of captive hedgehogs at 57°N was 0·88% of adult body mass/day (Fowler, 1986). Case (1978) collated data for a wide range of mammalian species and for a fast grower, the hare Lepus americanus, growth rate to weaning was 1·04% of adult body mass/day, but only 0·42% of adult body mass/day in a slow grower, a guinea-pig Cavia cutleri. Both these species have adult body mass similar to that of the hedgehog. The rapid growth rate in the European hedgehog is the result of a sustained milk supply, reflected in the significantly higher and less variable mean daily $T_{body}$ of lactating compared to non-breeding hedgehogs. Torpor during lactation would result in discontinuity of the milk supply and affect the growth of the young. Sustained high $T_{body}$ of the dam would also encourage neonate growth due to the maintenance of warm conditions within the nursery nest.

Declining mean daily $T_{body}$ is associated with increased variation in $T_{body}$ (about mean daily $T_{body}$) in the hedgehog. Both the decreasing precision of thermoregulation, about thermoregulatory set point, as $T_{body}$ declines, and the greater amplitude of circadian cycling of $T_{body}$ (within the euthermic range) during autumn are probably major causes of increasing variation in $T_{body}$, quite apart from the increasing frequency of test drops in non-breeders. However, the rate at which $T_{body}$ became more variable with declining mean daily $T_{body}$ was 4·6 times greater in non-breeding than breeding hedgehogs. This figure is similar to a 4-fold increase in the resting metabolic rate of lactating, but not gestating, hedgehogs recorded by Krol (1985).

Since most metabolic processes are thermogenic, increased metabolic rate would inevitably lead to elevated $T_{body}$, or raised heat loss, or both, indicating that the higher and less variable $T_{body}$ and
elevated metabolic rate in lactating hedgehogs are linked. The fact that Thompson & Nicholl (1986) and Nicoll & Thompson (1987) found that mammals with low basal metabolic rate were able to raise metabolic rates significantly during gestation and lactation suggests that the 4-fold increase in metabolic rate and 4-6 times lower rate of increase in $T_{\text{body}}$ variability in the lactating hedgehogs were manifestations of the same adaptation.

The continuation of higher and less variable $T_{\text{body}}$, in breeding females for about 1 month after the young are weaned is probably an adaptation to enable breeding females to accumulate adipose tissue reserves rapidly as hibernation approaches.

Unfortunately the shortage of confirmed pregnant hedgehogs in the laboratory breeding colony prevented a repetition of Fowler's (1982) observation of torpor in a pregnant female hedgehog. The failure of a single hedgehog in late gestation to become torpid, under conditions that caused torpor in all other hedgehogs tested, paralleled observations of the pipistrelle bat, Pipistrellus pipistrellus, which seldom enters torpor in the last days of gestation (Racey & Speakman, 1987) although it does so throughout all other stages of reproduction. The ability of the hedgehog to become torpid under a variety of environmental stimuli during the breeding season has not previously been quantified.

Since 4 out of 14 hedgehogs became torpid after 48 h at 11 or 5°C, even with ad-libitum feeding and at 24L:00D, low ambient temperature is the most important factor in the induction of torpor in the hedgehog. The observation that all hedgehogs became torpid under low ambient temperature when faced with restricted food intake and 00L:24D or 18L:06D indicates that food availability is more important than short-term photoperiod changes in the induction of torpor.

Observations of different gestation periods in bats under natural (Racey & Swift, 1981; Krishna & Dominic, 1982) and laboratory (Racey, 1973) conditions support the concept that adaptive hypothermia explains gestation length variability in other heterothermic mammals. Although further research is required to determine whether gestating female hedgehogs can become torpid under appropriate conditions, this study has clearly demonstrated that non-breeding hedgehogs can readily enter torpor during the breeding season.

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References


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