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Rewarming rates and thermogenesis in hibernating echidnas ☆

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Abstract

We measured body temperatures (T_b) in 14 free-ranging echidnas (*Tachyglossus aculeatus*) using implanted data-loggers. An average of 1020±744 days of T_b data was recorded from each animal. The average maximum T_b was 35.3±0.7 °C (n=14), and the lowest T_b was 4.7 °C. Detailed analysis of rewarming events from four echidnas showed rewarming time to be dependent on initial T_b (rewarming time in hours=15.6−0.41$T_{initial}$, n=31) with an average rewarming rate of 1.9±0.4 °C h^{-1}. Based on an hourly sampling rate, the peak rewarming rate was found to be 7.2±0.8 °C h^{-1} (n=12), which was measured at a mean T_b of 26.2±2.4 °C. This rate of heating was calculated to be equivalent to a peak oxygen consumption rate of 1.4±0.2 ml O_2 g h^{-1}, approximately 9 times the basal metabolic rate. We found that a plot of rate of change of T_b against T_b for the entire data set from an individual echidna provided a useful summary and analytical tool.

Keywords: *Tachyglossus aculeatus*; Echidna; Monotreme; Hibernation; Thermoregulation; Rewarming; Maximal metabolic rate; Non-shivering thermogenesis

1. Introduction

When first described in the scientific literature, hibernation in the egg-laying echidna was interpreted as a confirmation that this was a primitive mammal "lowest in the scale of warm-blooded animals" and an incomplete homeotherm that during cold weather "abandons all attempts at homeothermism" (Martin, 1902). Since that time it has become apparent that hibernation is not simply a matter of abandoning the control of body temperature, but is under precise physiological control (Lyman, 1982).

Data from free-ranging echidnas in the wild have shown that hibernation in the echidna closely resembles hibernation in other mammals, with body temperature (T_b) following a pattern identical to that of eutherian mammals (Grigg et al., 1989; Beard et al., 1992; Nicol and Andersen, 1996, 2000). During hibernation body temperature drops to within about 1 °C of ambient (T_a), down to about 5 °C, and the period of hibernation is broken by periodic arousals with euthermic periods lasting about 1 day (Nicol and Andersen, 2000).

In eutherian hibernators the heat for rewarming is generated in brown adipose tissue (BAT), which appears so important for arousal from hibernation that Cannon and Nedergaard (2004) in their review of BAT state "brown fat-derived heat is essential for arousal from hibernation in mammals". However, Hayward and Lisson (1992) after examining tissues from all extant families of marsupials and monotremes concluded that BAT is unique to eutherian mammals, and examination of tissue samples from echidnas has also failed to reveal expression of UCP1 (Kabat and Andersen, unpublished data). Thus all evidence indicates that the echidna, like marsupials, does not have BAT, or BAT-like function, reinforcing the fact that BAT based thermogenesis is not a prerequisite for arousal from torpor (Körtner and Geiser, 2000).

Given the importance of BAT to eutherian hibernators for arousal from hibernation it is of considerable interest to compare warm-up rates of eutherian and non-eutherian hibernators. In a comprehensive study Geiser and Baudinette (1990) compared maximal rewarming rates at T_a of about 20 °C for eutherian and marsupial hibernators and the echidna. They found no difference between marsupials and eutherian mammals, and suggested that rewarming rates for echidnas were no

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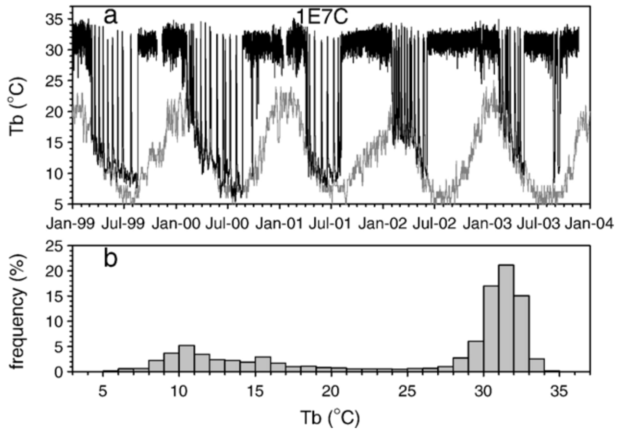

Fig. 1. (a) T_b data (black lines) recorded from an adult male echidna (1E7C, average mass 3.9 kg, mass range 3.2–5.2 kg) from January 1999 until November 2003. Gaps in the record represent the point at which loggers were exchanged, and the recovery period in which the echidna was held in captivity. Grey line shows soil temperature measured at a depth of 20 cm. The lower panel (b) shows the frequency distribution of the entire T_b data set for this echidna.

lower than those for other mammals. Stone and Purvis (1992) analysed a smaller data set from eutherian and marsupial heterotherms showing torpor (minimum T_b of about 20 °C, maximum body mass 230 g) whereas Geiser and Baudinette (1990) found maximal metabolic rate to be positively correlated with basal metabolic rate (BMR). Stone and Purvis (1992) claimed a negative correlation between mean rewarming rate and BMR, but a positive correlation between peak warm-up rate and BMR. Neither study found a difference between rewarming rates of eutherians and marsupials, and both suggested that an absence of brown fat did not affect rewarming ability.

Because it is very difficult to induce echidnas to hibernate in the laboratory, we have for the last 10 years concentrated on studying hibernation in echidnas in the field, by using implanted temperature data-loggers in free-ranging echidnas (Nicol and Andersen, 1996, 2000, 2002; Nicol et al., 2004) and we have so far collected more than 39 echidna years of data from 14 animals. These data include a large number of arousals, and the principal aim of this paper is to investigate the rewarming rates of free-ranging animals under natural conditions and to compare these with published data from laboratory measurements. A data set of this size is also amenable to analyses that could not be carried out by collecting T_b data manually, and we thus asked the question: “Is it possible to make inferences about the nature of thermogenesis in echidnas from this data?”

2. Materials and methods

Fourteen echidnas (*Tachyglossus aculeatus*, 9 adult female, 4 adult male and one juvenile male) were caught by hand at our field study site in the southern Tasmanian midlands, and brought to the University of Tasmania. Temperature data-loggers (Stowaway Tidbit, Onset Computer Corporation) were implanted intraperitoneally under halothane or isoflurane anaesthesia, and a tracking transmitter was glued to the spines on the lower back. After a recovery period the echidnas were returned to their site of capture.

The loggers have a measurement range of −5–37 °C, a stated accuracy of ±0.2 °C, and resolution of 0.16 °C. Loggers were coated in a wax-polymer compound (Elvax, Dupont) to improve water resistance and prevent tissue reactions. The final package (mass approximately 25 g) was slightly larger than the 30×41×17 mm logger, and the 95% response time of the packaged logger to a step change of 10 °C was about 7 min in a stirred water bath and 8 min in an unstirred bath. Initially 8K loggers were used but for later measurements we used 32K loggers capable of recording T_b hourly for 3.7 years. To extend the recording period for the 8K loggers the sampling interval for field recording was set to 96 min in some cases, but for the majority of the recordings the sampling interval was 1 h. Loggers were calibrated before implantation and after removal. In only one case did we find a significant deviation from the specified calibration that required correction. One echidna (male 1E7C) was subsequently fitted with an activity logger (Minimitter Actiwatch) (Nicol et al., 2004), giving 6 months of concurrent T_b and activity records. Meteorological data, including soil temperature data (T_{soil}) measured at a depth of 20 cm, was obtained from an Australian Bureau of Meteorology observation station on the field site within a few km of the animals.

3. Results and data analysis

Details of the timing and patterns of hibernation based on some of these data have been published previously (Nicol and Andersen, 2002). Figs. 1 and 2 show two of the largest T_b data sets. Fig. 1 shows T_b data recorded from an adult male echidna (1E7C, average weight 3.9 kg, weight range 3.2–5.2 kg) from January 1999 until November 2003, representing a total of 35,763 T_b data points or 1962 days of data. Gaps in the record represent the point at which loggers were exchanged, and the recovery period in which the echidna was held in captivity. Fig. 2 is a recording from a female echidna (5D5E, average weight 3.8 kg, range 3.5–4.2 kg) from January 1997 until November 2001 (37,389 data points, 1697 days). Also shown

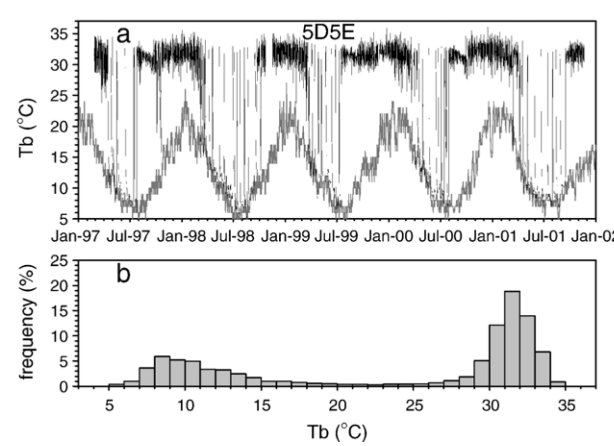

Fig. 2. T_b of a female echidna (5D5E, average mass 3.8 kg, range 3.5–4.2 kg) from January 1997 until November 2001. Other details as in Fig. 1.