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HIBERNATION IN A MONOTREME, THE ECHIDNA (*TACHYGLOSSUS ACULEATUS*)

Abstract-1. The body temperatures of five echidnas in Australia's Southern Alps were monitored by radio telemetry from February to December 1987.

2. All five hibernated throughout the winter, showing very low body temperatures (4-9°C, close to ambient) when torpid, compared with 28-33°C in a typical day during the active season.

3. Spontaneous arousals from hibernation occurred every 2-3 weeks, during which body temperatures rose rapidly to over 30°C for several hours before dropping to be close to ambient again.

4. The identification of "classical" hibernation in a monotreme, with a similar pattern to that seen in Eutheria and in an animal as large as the largest eutherian hibernator, has important implications for current ideas about the evolution of endothermy.

INTRODUCTION

The echidnas (*Tachyglossus aculeatus* and *Zaglossus bruijni*) and the platypus (*Ornithorhynchus anatinus*) are the only surviving monotremes and the only egg-laying mammals. The short-beaked echidna (*T. aculeatus*) occurs throughout Australia and in parts of Papua-New Guinea and is the only native mammal in Australia whose distribution may be said to be continent-wide (Griffiths, 1968), a distribution that implies great adaptability to habitats as diverse as hot inland deserts, mild coastal woodlands and cold alpine meadows. Echidnas have long been known to be heterothermic (Martin, 1902; Schmidt-Nielsen et al., 1966; Augee and Ealey, 1968) yet there has been no previous study of their thermal relations under field conditions.

Controversy has existed for years about the thermal status of echidnas in winter. Martin (1902) referred to them undergoing 4 months hibernation during winter, but gave no data to support his statement. Wardlaw (1915) reported periods of torpor lasting 1-7 days in captive animals, but most of his animals died, some without re-warming. In the field, there is an anecdotal account of an echidna being found "torpid" in winter (Augee, 1969), while Griffiths (1978) reported torpor in a juvenile. Green et al. (in preparation) measured a dramatic fall in winter in rates of ²²Na turnover (as an indication of food intake) and ³H₂¹⁸O turnover (measuring carbon dioxide production and water influx) in echidnas on Kangaroo Island, near Adelaide, South Australia, which has a mild climate.

However, in a comprehensive review of the thermal relations of echidnas, Augee (1978) concluded that echidnas are heterothermic endotherms which depend upon shivering thermogenesis and/or exercise as a source of body heat, which will enter torpor only reluctantly, in response to starvation. He concluded that they are not hibernators.

Until now, there have been no data on diurnal and seasonal changes in body temperature of echidnas in the wild. We were stimulated to pursue the question because of reports of echidnas being seen above the snowline in late winter and early spring in Kosciusko National Park, even near the summit of Australia's highest mountain, Mt Kosciusko (2228 m). To be there at that time, echidnas would have to have either traversed several kilometers of snow or, alternatively, have spent winter in a burrow under the snow, probably in a torpid state. To resolve the controversy, we employed radiotelemetry to monitor the locations and body temperatures of echidnas above and below the snowline, before, during and after the period of winter snow.

MATERIALS AND METHODS

We implanted calibrated temperature-sensitive radio transmitters (J. Stuart Enterprises or Austec Electronics) in the peritoneal cavities of five echidnas (three male, two female). Surgical procedures were performed under halothane anaesthesia, following guidelines approved by The University of Sydney's Animal Care Committee. Four echidnas were released during February, each at its capture point. The fifth (No. 12) was transported into the study area from its capture site in a similar habitat 20 km away and released in April. Radio signals were monitored with a Telonics VHF Receiver, pulse intervals (indicative of body temperature) being determined with a stopwatch or electronically. Recorders, switched on at predetermined intervals by automatic timers, enabled us to monitor body temperatures and relevant ambient temperatures every few hours during our absences from the study area.

RESULTS

Data were obtained from February to December 1987, i.e. from late summer, through the southern winter and into the following summer. Echidnas 10 and 12 remained in sub-alpine habitat at Prussian Plain (1815 m). Numbers 11 and 13 remained in dry sclerophyll forest at Waste Point (920 m), below the normal winter snowline. Echidna 15, from sub-alpine habitat at Rennix Gap (1560 m), moved 6 km across a mountain range in April, spending the winter in dry sclerophyll forest near Island Bend (1370 m). It moved back to Rennix Gap in December. The other animals all remained within 2 km of their release sites.

In late summer, all animals showed similar patterns of considerable daily heterothermy (Fig. 1). These results, the first from echidnas free-ranging in their natural habitat, confirm the findings of studies on captive animals (Schmidt-Nielsen et al., 1966; Augee and Ealey, 1968). The animals were active from late morning for most of the day and, sometimes, into the night as well. During activity, body temperatures were typically in the range 31-33°C, regardless of ambient temperature. At rest, body temperatures fell to 27-29°C or lower, the daily minimum depending upon the length of the period of inactivity and ambient temperature.

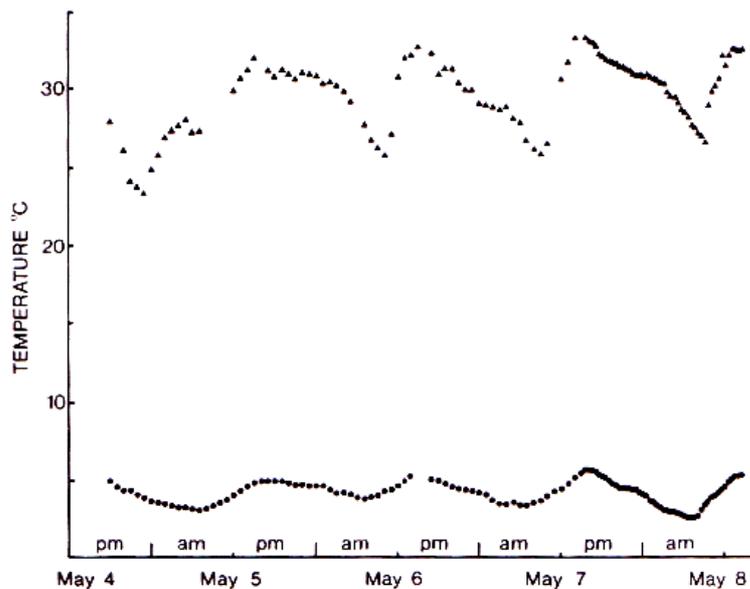


Fig. 1. Daily variation in body temperature (solid triangles) in a free-ranging echidna (No. 12) on Prussian Plain (1815 m), Kosciusko National Park, Australia, towards the end of the active season. Ground temperature is shown as solid circles.

All five animals were captured and weighed approximately 6 weeks after their release. All had put on weight: Nos 10, 12 and 15, in the sub-alpine habitat by 6, 6 and 3% respectively, and Nos 11 and 13, at Waste Point, by 23 and 25%.

In early winter (19 April), before the first snow, echidna 10 was located in the base of a hollow tree stump approximately 1800m above sea level, about 300 m from its release point 2 months earlier. Its body temperature was 9.5°C at 10:45 hr. Air temperature was 11°C and the weather was fine and sunny. The following day (also fine), its body temperature was 31.0°C at 08:45 hr ($T_a = -0.7^\circ\text{C}$). This was the first evidence that echidnas enter profound torpor in natural circumstances, and the first indication that a period of torpor may be followed by a rapid arousal. The animal subsequently moved approximately 150 m to a different retreat. Here it dropped its body temperature to 8.5°C and remained in the same location after the snows fell, experiencing body temperatures as low as 3.5°C, until 18 August when we unearthed it, very sluggish, from a burrow beneath the snow after its radio transmitter failed.

All animals were in torpor by mid June, retreating to underground cavities or hollow tree stumps. The temperature data are clear and striking (Figs 2 and 3). Body temperatures of echidnas in torpor were low and stable, ranging from 3 to 9°C, just above ground temperatures. The periods of torpor were, however, punctuated every 2-3 weeks by spontaneous arousals in which body temperature rose within about 12 hr to a plateau of 30-32°C for 12-24 hr before the animal cooled again, almost to ambient, over the next 24-48 hr (Fig. 2). Sometimes an animal would move to a different retreat while warm, then re-enter torpor (Fig. 3). In late winter or early spring, the final arousal signaled the re-commencement of the summer pattern of behaviour.

Dates of entry to and exit from this thermoregulatory pattern are shown in Fig. 3. Note that the animals from lower elevations began it later and ended it earlier than those at higher elevations.

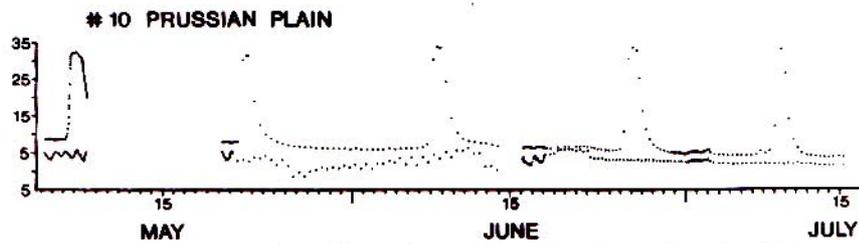


Fig. 2. Body temperature (upper trace) in a hibernating echidna (No. 10) on Prussian Plain over 10 weeks in winter, showing five arousal events. The lower trace is ground temperature.

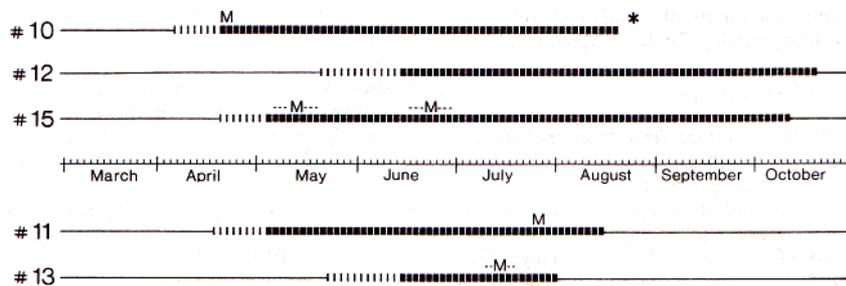


Fig. 3. The hibernation seasons of three echidnas above the snowline (Nos 10, 12, 15) and two below (Nos 11, 13) during 1987. Hibernation is indicated by the black squares. Entry to hibernation is known to have occurred at some time within the cross-hatched section, but the exact date is uncertain. "M" indicates that an individual aroused briefly and moved to a different site. Animal 10 was woken prematurely (asterisk) after failure of the temperature-sensitive transmitter.

DISCUSSION

Whereas torpor in captive echidnas has been reported previously (Martin, 1902; Wardlaw, 1915; Augee, 1969), and torpid echidnas have been found in the field (Augee, 1969; Griffiths, 1978), this is the first time that the pattern and duration of voluntary torpidity has been recorded.

The observed pattern of seasonal torpor punctuated by apparently spontaneous arousals fits exactly the pattern of classical mammalian hibernation (Hudson, 1978).

The discovery that echidnas in Australia's Alps show the classical mammalian pattern of hibernation raises questions about the extent to which the mechanism of hibernation in echidnas is physiologically similar to hibernation in Eutheria. Is monotreme hibernation analogous or homologous to eutherian hibernation? Is this seasonal pattern of temperature changes supported by the same complex adaptive mechanism in both, or is hibernation in echidnas a plesiomorphic state, a retained capability to tolerate low body temperatures resulting when the heat production associated with muscular exercise is turned off by a long period of inactivity? Without the periodic and spectacular arousals, it would be tempting to interpret the observed hibernation as nothing more than an extension of the echidna's daily heterothermic cycle, a consequence of a prolonged period without the heat production associated with muscular activity. The presence of periodic arousals, however, in which the body temperature may rise by 25°C or so in about 12 hr, shows that echidnas have significant endothermic capabilities, as do eutherian hibernators. In this context, it is worth noting that echidnas are as large as the largest eutherian hibernators, marmots, but have only half the resting metabolic rate of marmots. In the later stages of a warm-up, shivering is pronounced, but the source of heat in the early stages is at present unknown. Even though Augee has been unable so far to find brown fat by light microscopy, some form of non-shivering thermogenesis seems probable, as in eutherian hibernators. The weight gain recorded in all individuals prior to entering hibernation also suggests similarities with eutherian hibernation.

Other questions are raised as well. How widespread geographically is hibernation by echidnas? In most of their range they experience only mild or warm winters with hot summers, so aestivation may also be a feature of their lifestyle, especially as they lack significant sweat glands and are known to avoid high temperatures (Griffiths, 1968, 1978; Augee, 1978). Do platypus hibernate? Radiotelemetric work by Grant (1983) in the Thredbo River, also in Australia's Alps, showed no sign of it. Can the idea be resurrected that echidnas may be a model for the evolution of endothermy? It is easy to envisage an intermediate step between ectothermy

and endothermy in which behavioural (ectothermic) heterothermy (typical of Reptilia) is replaced by physiological (endothermic) heterothermy in which facultative endothermic heat production, mainly muscular, but supplemented by shivering (and, possibly, non-shivering thermogenesis), ensures high and stable body temperatures when required, and is turned off when not required. In both their daily heterothermy in the active season and in their winter pattern of hibernation, echidnas fit that model rather well. We are pursuing these questions, but much more work is needed, comparing eutherian and monotreme hibernation qualitatively and quantitatively, before there can be profitable speculation about the significance of these new findings in terms of ideas about the evolution of endothermy and hibernation.

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