Cooling rates and body temperature regulation of hibernating echidnas (*Tachyglossus aculeatus*)

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Summary

Echidnas (*Tachyglossus aculeatus*) are amongst the largest deep hibernators, but it is difficult to get them to hibernate normally under laboratory conditions. We measured body temperature (T_b) in 14 free-ranging echidnas using implanted data-loggers. Cooling during entry into hibernation bouts followed a Newtonian cooling curve, and conductances calculated from cooling curves were identical to those observed in cold exposed euthermic echidnas. Comparison with a reference soil temperature demonstrated that echidnas showed behavioural thermoregulation during hibernation; early in the hibernation season echidnas preferred to hibernate in cool areas, while during the coldest months they moved to warmer hibernacula, giving a preferred T_b in the range 8–10°C. Thermal buffering against excessive variation in T_b may be as important as maintaining a low T_b.

Key words: echidna, monotreme, hibernation, cooling, thermoregulation, conductance.

Introduction

Although hibernation was once believed to represent an abandonment of control of body temperature (T_b), it is now known to be a precisely controlled physiological process (Lyman, 1982). When an endotherm enters hibernation there is a drop in metabolic rate (MR) and T_b, and as long as ambient temperature (T_a) is not too low, T_b will fall to a value typically 1–3°C above ambient. If T_b falls below a critical value, MR will increase, but when a hibernating endotherm is undisturbed and its T_b is above the critical value, T_b will passively follow T_a, i.e. it will thermo-conform (Geiser, 2004).

When first described in the scientific literature, hibernation in the egg-laying echidna (*Tachyglossus aculeatus*) was interpreted as a confirmation that the echidna was an incomplete homeotherm (Martin, 1902). Since that time it has been demonstrated that hibernation in the echidna closely resembles that of other mammals (Grigg et al., 2004; Nicol and Andersen, 2002), although with an adult body mass of 2–7 kg the echidna is one of the largest species to enter deep hibernation (Geiser, 2004; Nicol and Andersen, 2007a). Over the last 10 years we have studied hibernation in free-ranging echidnas in the field using implanted T_b data-loggers, and have collected a very large data set of more than 39 echidna years of data from 14 animals. We have previously analysed parts of this data set data to examine the relationship between T_b and hibernation bout length (Nicol and Andersen, 2000), the timing and patterns of hibernation (Nicol and Andersen, 2002), and rewarming rates and thermogenesis (Nicol and Andersen,

2007b). These data show that during the hibernation season T_b appears to follow T_a quite closely. In the laboratory, we noted a slight increase in T_b, MR and ventilation when T_a fell below 5°C (Nicol and Andersen, 2003; Nicol et al., 1992), and if the low T_a was sustained, or if cooling was too rapid, the echidna would arouse from hibernation. In this paper we make a detailed analysis of T_b in hibernating echidnas. Is there any evidence that echidnas under natural conditions regulate T_b when T_a falls below a certain level?

Our data set includes a large number of cooling episodes as echidnas enter bouts of hibernation. The physiological changes associated with entry into hibernation and torpor have been the subject of considerable debate, particularly with respect to the causal relationship between the reduction in T_b and MR, and the relative timing of these changes (Geiser, 2004; Heldmaier and Elvert, 2004). Although our data do not include measurements of MR, we are able to make some estimates of thermal conductance (C), which in turn allows some inferences to be made about MR. It has been argued, for example, that entry into hibernation and torpor is associated with an initial increase in C, which is then reduced to levels below the euthermic minimum (Snyder and Nestler, 1990). Conductance can be calculated from thermal time constants calculated from cooling curves (Robertson and Smith, 1981), and this approach has been used extensively in studies on the thermal properties of ectothermic animals (Bakken, 1976; McNab, 2002). Cooling constants are independent of T_a and T_b, and are preferable to measures such as the time required

to reach a specific temperature, or rates of change of temperature, as these will vary with the difference between T_b and T_a. This approach has had only limited use with endotherms; it has been used to calculate C of torpid dormice (Wilz and Heldmaier, 2000) and to characterise the entry of humming birds into torpor (Lasiewski and Lasiewski, 1967). Because echidnas normally bury themselves in the substrate before entering hibernation they are sheltered from convective and radiant heat exchange with the environment. Under these circumstances Newton's Law of Cooling should be applicable, and in the second part of this paper we investigate the use of this model to characterise cooling in echidnas entering hibernation, and to estimate C.

Materials and methods

Fourteen echidnas *Tachyglossus aculeatus* Shaw (nine adult female, four adult male and one juvenile male, mass range 2.3–5.5 kg) 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, Wilmington, DE, USA) 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 to –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, Pocasset, MA, USA) to improve water resistance and prevent tissue reactions. The final package (mass approximately 25 g) was slightly larger than the $30{\times}41{\times}17$ 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 and after implantation. In only one case was there a significant deviation from the specified calibration that required correction.

Meteorological data including soil temperature measured at depths of 10, 20 and 50 cm, were obtained from an Australian Bureau of Meteorology (BoM) observation station (Melton Mowbray, 147°11′44″E, 42°29′35″S, elevation 218 m) approximately 4.5 km from the centre of the field site. These data were recorded daily to the nearest 1°C at 09:00 h and in some years at 15:00 h. To check the applicability of the BoM data to the field site itself, soil temperatures were measured at several points in the field site for periods of up to 8 months.

Data analyses were carried out using the statistical packages statistiXL (statistiXL, Kalamunda, Western Australia) and Statistica 6.1 (Statsoft Inc, Tulsa, OK, USA), and all results are shown as means ± s.d.

Table 1. T_b *and environmental temperatures for the 14-day hibernation period between arousals 4 and 5 from Fig. 1*

Temperature (°C)	T_b	T_b*	Air	Soil10	Soil20	Soil50
Range	9.5–11.8	9.6–11.6	6–25	4–7	6–8	9–10
Average	10.8	10.7	5.4	6.0	7.4	9.4
Variance	0.40	0.44	12.4	0.92	0.42	0.26
N	203	14	14	14	14	14

*09:00 h only.

T_b was measured at 96 min intervals, and soil temperatures were measured only at 09:00 h during this period. Air temperature was measured twice daily but statistics are given for 09:00 h temperatures only. For comparison column 2 shows statistics for T_b values measured at the same time as the other variables. Soil temperature was measured at 10, 20 and 50 cm. All environmental temperatures are from a Bureau of Meteorology observation station approximately 4.5 km from the field site.

Results and data analysis
Body temperature during hibernation

Details of the timing and patterns of hibernation based on some of these data have been published previously (Nicol and Andersen, 2002), as has an analysis of rewarming (Nicol and Andersen, 2007b). A comparison of the T_b records with the various environmental measures obtained from the BoM station (air temperature and soil temperature at 10, 20 and 50 cm) showed that, during hibernation, T_b varied in parallel with soil temperature at 20 cm, although the absolute difference between the records would sometimes change. Air temperature and soil temperatures at 10 cm showed a much greater variance than T_b, while soil temperature at 50 cm had a lower variance than T_b (Table 1). Recordings of soil temperature at several locations in the field site were found to correspond closely with the BoM data: a 4-month recording of soil temperature in what we judged to be the coldest part of the field site, when plotted against the BoM data, yielded a regression line with a slope of 1.04±0.04, and an intercept of –4. Thus although the absolute values of soil temperature varied around the field area, as would be expected, the BoM data accurately reflected the pattern of temperature change. Hence the BoM soil temperature measurements at 20 cm have been used as a reference substrate temperature (T_{ref}). In the nine winters over which we collected T_b data (1997–2005) T_{ref} fell below 5°C on only 23 days, and only once fell below 4°C. Fig. 1 shows the T_b and T_{ref} records for an echidna (male 4572) over the 2000 hibernation period, demonstrating the remarkably close correspondence between the two temperatures. Fig. 2 shows T_b records from early in hibernation for echidna 4572, as well as three other echidnas (females 2753 and 006F and male 1E7C), all hibernating at different locations, up to about 2 km apart. Each animal appears to track the changes in T_{ref} although the absolute temperature varies between echidnas.

Fig. 1 shows that for an individual echidna the relationship between T_b and T_{ref} may change during the course of a hibernation season, and that these changes occur during
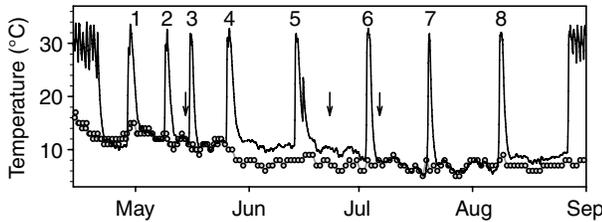
Fig. 1. T_b of male echidna 4572 during the 2000 hibernation season (solid line) and reference soil temperature (T_{ref}; circles). T_b was measured at 96 min intervals by an implanted data logger. T_{ref} data were measured at a depth of 20 cm at a Bureau of Meteorology station about 4.5 km from the centre of the field site, and recorded daily at 09:00 h. Note the changes in relationship between T_b and T_{ref} that occur at arousals 4, 6 and 8. The location of the hibernating echidna was checked at the times marked by the arrows; it had moved 120 m between the first and second observations, and 430 m between the second and third.

arousals. In the initial bout of hibernation, before arousal 1, T_b is lower than T_{ref}. Between arousals 1 and 4, T_b is very close to T_{ref}, and between arousals 4 and 6, T_b was about 4°C above T_{ref}. Between arousals 6 and 8, T_b was again very close to T_{ref}, and then from arousal 8 until the final arousal, T_b was about 1°C above T_{ref}.

In order to analyse the relationship between T_b and T_{ref} further, Fig. 3 shows plots of hibernating T_b against T_{ref} for two echidnas for which we have several years of data. ANOVA showed the relationships between T_b and T_{ref} to be essentially identical for the two animals (comparison of slopes: $F=0.17$, $P=0.68$, common slope=0.63; comparison of intercepts: $F=0.99$, $P=0.32$). In Fig. 4 the frequency distribution of T_b for six echidnas (five female and one male) is compared with the distribution of T_{ref} for the months of May and July. In May the majority of T_{ref} readings (70%) were in the range 9–12°C, as were 70% of T_b readings, but T_b values less than 9°C are under represented (4%) compared with T_{ref} (17%). In July the distribution of T_b values is offset significantly compared with T_{ref}. 58% of recorded T_{ref} values were between 6 and 8°C, but 62% of T_b values were between 8 and 10°C.

Entry into hibernation and calculation of cooling constants

At each entry into hibernation, T_b fell until it was in equilibrium with the substrate temperature. Cooling constants were calculated for cooling intervals in which there was minimal change in T_{ref} during the cooling period, such that T_b fell smoothly and continuously towards the equilibrium T_b. Twenty eight cooling periods from 11 echidnas (seven female, four male) met these criteria. The starting point for each cooling curve ($T_{b(0)}$) was the highest T_b from which T_b fell continuously. The final point in the cooling curve, or equilibrium T_b ($T_{b(eq)}$) was the lowest T_b. If the same T_b was recorded for more than 7 h before falling further, this value was taken to be $T_{b(eq)}$. Each T_b value was then adjusted by subtracting $T_{b(eq)}$, so that the adjusted $T_{b(eq)}$ value became 0. A linear regression was calculated for the natural logarithm of the
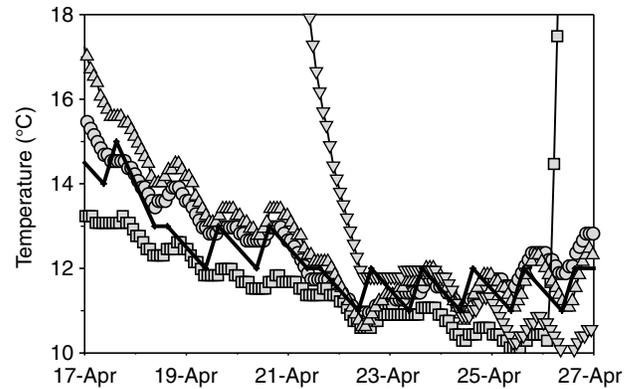

Fig. 2. T_b data from four echidnas early in the 2000 hibernation season, illustrating how during hibernation T_b tracks T_{ref} (solid black line). One echidna (male 4572, down-triangles) enters hibernation for the first time in the season on April 21, while another (female 006F, squares) shows her first periodic arousal on April 27. Echidnas 006F and 1E7C (male, circles) entered hibernation on February 12, while 2753 (female, up-triangles) entered hibernation on March 7. All echidnas were hibernating in different locations up to 2 km apart.

adjusted T_b values against time in hours since $T_{b(0)}$, and the slope of this regression line is the cooling constant. Fig. 5 shows as examples arousal events for two echidnas with subsequent re-entry into hibernation, along with semi-log plots of the cooling curves. The mean T_b interval ($T_{b(0)}$–$T_{b(eq)}$) over which the 28 regressions were calculated was 21.4±2.0°C, and mean time interval was 61±13 h. The average r^2 value for the regressions was 0.97±0.03. Analysis of variance showed that the between-individual variance was less than the within-individual variance ($F=1.0$, $P=0.5$), and there was no discernable relationship between the slope of the regression line and mass or sex. The mean slope of the 28 regression lines was −0.079±0.010 h^{-1}.

Discussion

T_b during hibernation bouts

Echidnas do not construct or dig a hibernaculum, but before entering hibernation they normally bury themselves in the substrate. We have found echidnas hibernating in loose soil, under sandstone slabs, in piles of leaves and bark, in grass tussocks, or in dry decaying wood in hollow logs. Most hibernating sites appear to provide shelter from convective and radiant heat exchange with the environment and from rain, and the principal means of heat loss of a hibernating echidna is likely to be conduction to the substrate in which it is buried. Figs 1 and 2 and Table 1 indicate that echidnas mostly hibernate in conditions that provide an equivalent amount of thermal buffering to approximately 20 cm of soil, and, because they are buried in the substrate, they track substrate temperature quite closely. Unlike the majority of hibernators, echidnas often move to another location during an arousal, and these moves may result in a change in T_b relative to the reference soil
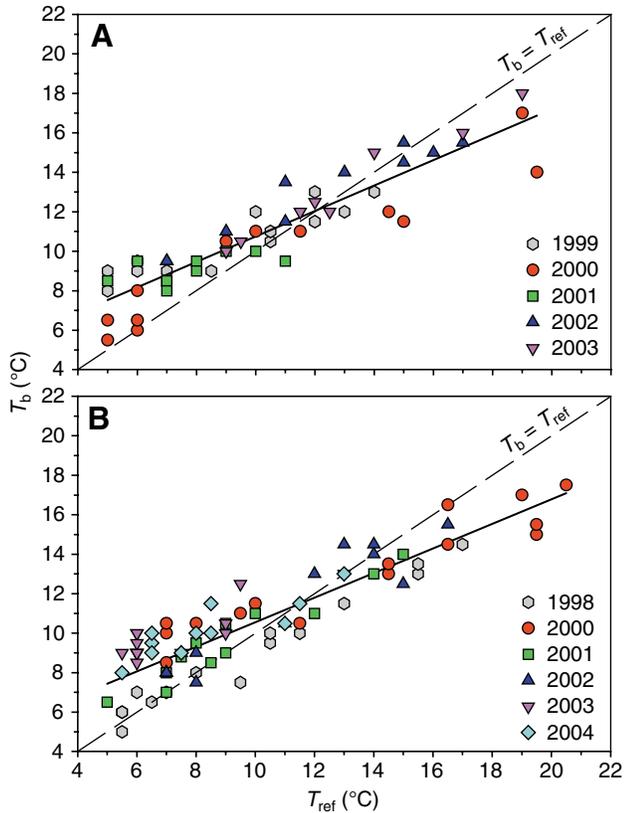
Fig. 3. Hibernating T_b for a male echidna (echidna 1E7C, mass range 3.2–5.2 kg; A) plotted against reference soil temperature at a depth of 20 cm (T_{ref}) for five hibernating seasons, and for a female echidna (echidna 006F, mass range 2.3–3.0 kg; B) for six hibernating seasons. Solid lines are regressions fitted to all data. For echidna 1E7C (A) $T_b = 0.65 T_{ref} + 4.3$, $r^2 = 0.84$; for echidna 006F (B) $T_b = 0.62 T_{ref} + 4.3$, $r^2 = 0.82$. The fact that the slopes are significantly less than 1 shows that at high T_a echidnas seek out cooler areas to hibernate, while at low T_a they move to relatively warmer areas.
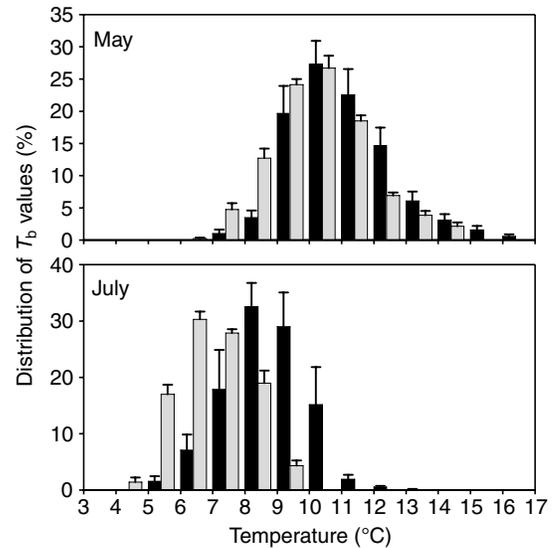

Fig. 4. Frequency distribution of T_b values from six echidnas (five female, one male, black bars) and T_{ref} (grey bars), in May and July. In May the majority of T_{ref} readings (70%) were in the range 9–12°C, as were 70% of T_b readings, but T_b values below 9°C are under-represented (4%) compared with T_{ref} (17%). In July the distribution of T_b values is significantly offset compared with T_{ref}. 58% of recorded T_{ref} values were between 6 and 8°C, but 62% of T_b values were between 8 and 10°C.

temperature (T_{ref}, Fig. 1). In a number of cases, although there was an abrupt change in T_b relative to T_{ref} at an arousal, the echidna did not actually change locations. Field observations showed that in these cases the echidna had changed its position, or the depth at which it was buried in the substrate. Thus the changes in the relationship between T_b and T_{ref}, which occur at arousals are due to movement of the echidna to a warmer or cooler position. Figs 3 and 4 show that although T_b may track T_{ref} closely during an individual hibernation bout, at high ambient temperatures echidnas seek out cooler places to hibernate, and at low ambient temperatures they move to warmer places. This behavioural thermoregulation is remarkably consistent from year to year and between echidnas. Mountain pygmy possums (*Burramys parvus*) may also move during arousals, with a resultant change in hibernating T_b, and males seek out warmer hibernacula than females, allowing them to maintain higher a T_b than females (Körtner and Geiser, 1998). For echidnas, a comparison of corresponding T_b and T_{ref} values for the last hibernation bout before arousal of

reproductively active males and females showed that at any given T_{ref} there was no difference in T_b between females and males. There were consistent differences between hibernating sites: echidnas hibernating in the middle of piles of logs were extremely well buffered from environmental variation, while the lowest T_b values were observed in echidnas hibernating in grass tussocks.

The lowest T_b recorded in this study was 4.7°C, observed in three echidnas, which is close to the minimum of 4.5°C seen in the laboratory (Nicol and Andersen, 1993). A minimum T_b of 3.7°C was reported at Mount Kosciuszko at a T_a of 0.8°C (Grigg et al., 1992), but this was calculated from the pulse rate of a T_b transmitter recorded on a tape recorder, which is subject to a number of significant potential errors, particularly at low temperatures. Our field data give no indication that echidnas will increase heat production and thermoregulate if T_b falls below some critical minimum value. Nowhere in the 39+ years of T_b records from 14 echidnas is there any indication of a change in the relationship between T_b and T_{ref} occurring anywhere other than during an arousal. Attempts to measure T_a near hibernating echidnas have suggested a higher T_b–T_a difference at low T_a, but the data are inconclusive (Grigg et al., 1992). Similarly laboratory data that showed increased metabolic rate and ventilation at low T_a (Nicol and Andersen, 1993; Nicol et al., 1992) may be the result of transient disturbances in response to the lowered T_a, or the beginning of arousal. In the field, when T_b falls too far, or too fast, echidnas will arouse and move to a warmer location to maintain T_b in
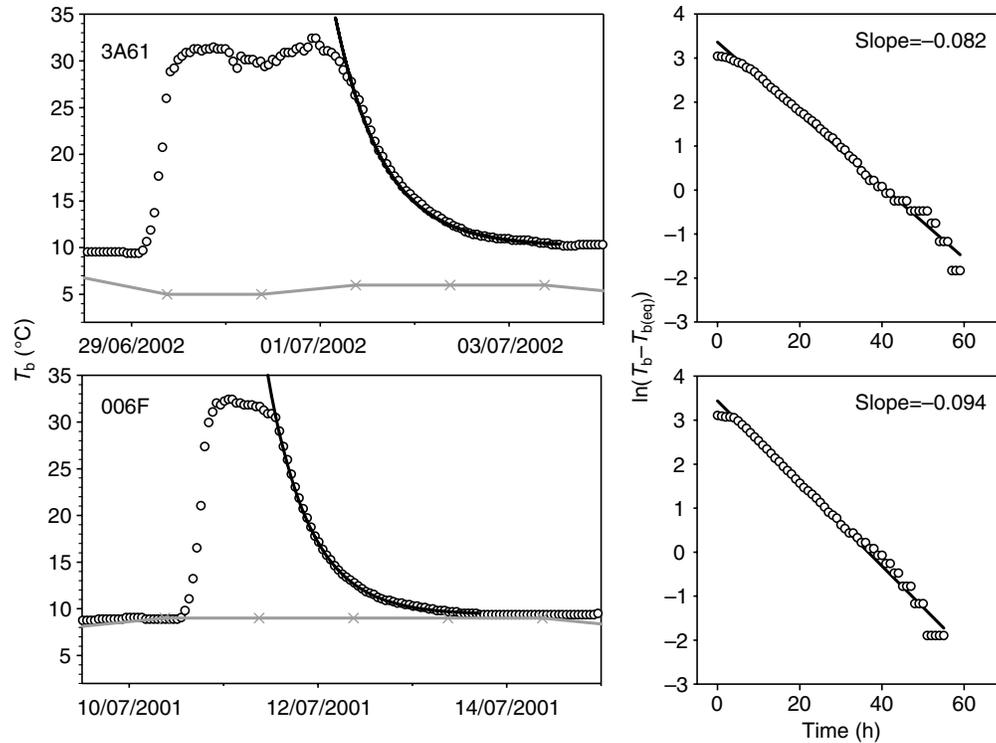
Fig. 5. Arousal events with subsequent re-entry into hibernation for two echidnas (females 3A61 and 006F). (A) T_b (open circles) and T_{ref} (crosses and grey line). Solid black lines are the regression lines calculated from the semi-log plots in (B). (B) Natural logarithm of the adjusted T_b values (T_b minus the equilibrium T_b) plotted against time (h) from the start of the cooling episode. The solid line is the linear regression through these data. $r^2=0.99$ for both regressions. The slope of the regression line is the cooling constant for the animal (h^{-1}) and the reciprocal of the cooling constant is the time constant. For echidna 3A61, the time constant is 12.2 h, giving 36.6 h for 3 time constants or a 95% change. For echidna 006F, the time constant is 10.6 h, or 31.9 h for a 95% change.

the preferred range. Fig. 4 shows that in the coldest month of the year the preferred T_b of hibernating echidnas is 8–10°C, with 62% of recorded values being in that range. In our study area echidnas appear always to select hibernating conditions that allow them to be thermoconformers.

Cooling during entry into hibernation

In euthermic endotherms below their thermoneutral zone, C is minimal and T_b is regulated by adjusting heat production as described by the familiar Scholander–Irving model (McNab, 2002):

$$\dot{V}_{O_2} = C(T_b - T_a) , \tag{1}$$

where C is total thermal conductance, incorporating evaporative as well as non-evaporative heat loss, and $\dot{V}_{O_2}$ is rate of heat production, expressed as oxygen consumption. During thermoconforming hibernation, this equation can be rearranged with T_b as the dependent variable:

$$T_b = T_a + \frac{\dot{V}_{O_2}}{C} . \tag{2}$$

This is the equilibrium value towards which T_b will fall during entry into hibernation; not T_a, but T_a plus an amount determined by the ratio of hibernating metabolic rate to conductance.

Fig. 5 shows arousal events and the subsequent re-entry into hibernation for two echidnas, with semi-log plots of the cooling phase. The slope of the regression line fitted to these data is the exponent a, or cooling constant, in the equation for Newton's law of cooling (McNab, 2002):

$$T_{(t)} = T_{(0)}e^{-at} , \tag{3}$$

where $T_{(t)}$ is T_b at time t, and $T_{(0)}$ is T_b at time 0, or

$$\frac{dT_b}{dt} = -a \cdot (T_b - T_a) \cdot \tag{4}$$

However, as the equilibrium temperature is not T_a the rate of cooling can more accurately be represented by incorporating Eqn 2 in the following approximation to overall heat transfer, arranged in the form of Newton's law (Bakken, 1976):

$$\frac{dT_b}{dt} = -a \cdot \left[T_b - \left(T_a + \frac{\dot{V}_{O_2}}{C} \right) \right] \cdot \tag{5}$$

In our calculation of cooling constants we have only used those cooling episodes where we could be certain of the equilibrium temperature, as use of the wrong equilibrium temperature can result in significant errors in the calculation of a, the slope of the regression line.

The average value of *a* calculated from 28 cooling curves was -0.079 ± 0.010 h^{-1}. The reciprocal of the cooling constant is the time constant, and the average time constant was 12.9 ± 1.9 h. An exponential curve falls by $1/e$ (≈0.37) during one time constant, and three time constants represent a 95% response, providing a useful measure of the time required to equilibrate. The 95% response time for echidna cooling was 39 ± 6 h ($N=28$). Because cooling takes several days, daily torpor with a stable torpid T_b is clearly not an option for echidnas. The low rate of cooling contrasts strongly with what would be expected from an ectotherm: for an alligator of a similar mass (approx. 4 kg) the 95% cooling time in air would be about 3.25 h (Smith, 1976), demonstrating that a hibernating echidna has a very low conductance.

The cooling constant, *a*, for an animal is a function of its body mass (M_b), specific heat (*h*) and its thermal conductance (*C*) (Bakken, 1976), i.e. $a=C/hM_b$. With a body fat composition of 25–35% (Green et al., 1992), specific heat of echidna tissues would average 3.35 J g^{-1} °C^{-1}, and the average *C* during the cooling episodes would be 0.024 ± 0.003 J g^{-1} ° h^{-1} C^{-1}. Assuming a heat equivalent of oxygen of 20.1 J ml^{-1}, this can be expressed in terms of oxygen consumption as 0.013 ± 0.002 ml O$_2$ g^{-1} h^{-1} °C^{-1}, identical to the value of 0.013 ± 0.0005 measured in cold-exposed, non-hibernating Tasmanian echidnas (McNab, 1984).

Similarly, when *C* of dormice (*Glis glis*) was calculated from cooling curves, no change was found in *C* during entry into torpor and during hibernation, and daily torpor *C* was identical to the value measured in cold exposed euthermic dormice (Wilz and Heldmaier, 2000). Our results for the echidna provide no support for the suggestion (Snyder and Nestler, 1990) that entry into torpor is facilitated by changes in *C*.

The very close fit of a Newtonian cooling curve to our data (Fig. 5), supports the comment (Lasiewski and Lasiewski, 1967) for humming birds entering torpor: "*The lowering of body temperature during entry into torpor approximates a Newtonian cooling curve, suggesting that once entry into torpor is initiated, the rate of entry is determined by physical phenomena.*" Although the slope of the line, and thus the calculated *C*, will not be affected by a constant rate of heat production, it will be affected if MR varies with T_b (Bakken and Gates, 1974), but in previous laboratory experiments, we were unable to find any relationship between T_b and MR in hibernating echidnas (Nicol et al., 1992). A similar independence of MR from T_b has been observed in a variety of hibernating rodents during thermoconforming hibernation at low T_b (Buck and Barnes, 2000; Heldmaier and Elvert, 2004; Heldmaier et al., 1993; Ortmann and Heldmaier, 2000). Although some small hibernators show a temperature effect on hibernating MR, particularly at high T_b (Geiser, 2004), the linearity of the semi-log plots of the echidna cooling curves (Fig. 5) implies that there is no significant change in echidna heat production or conductance during the cooling period.

These results help us to understand how echidnas use hibernation. It has been well documented that echidnas do not hibernate to avoid periods of extreme cold or absolute food shortage (Grigg and Beard, 2000; Nicol and Andersen, 1996; Nicol and Andersen, 2002). Grigg and Beard (Grigg and Beard, 2000) have described echidnas as "*using cold as a resource*"; they use hibernation to conserve energy, although food is available, and conditions may be mild, when there is no necessity for them to be active. Early in the hibernation season when soil temperatures are high, echidnas will seek out cooler places to hibernate, but in the coldest months they prefer hibernacula where they can maintain T_b in the range 8–10°C. Thermal buffering against excessive variation in T_b may be just as important as maintaining a low T_b.

List of abbreviations

a	cooling constant
C	conductance
h	average specific heat of tissues
M_b	body mass
MR	metabolic rate
T_a	ambient temperature
T_b	body temperature
T_{ref}	reference soil temperature at 20 cm
$\dot{V}_{O_2}$	rate of oxygen consumption

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