Heat tolerance of short-beaked echidnas
(Tachyglossus aculeatus) in the field

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Abstract

(1) Echidnas occur throughout the hot arid zone of Australia yet laboratory studies have concluded that they are ill equipped physiologically to manage T_a higher than 35°C. (2) Consequently, it is generally assumed that echidnas must rely on behavioural thermoregulation, being nocturnal in hot weather and seeking less extreme microclimates during the day. (3) By monitoring T_b of echidnas in the field and relating these to T_a within their day t i m e shelters in Western Queensland during summer, this study showed that echidnas are able to tolerate T_a of 35-40°C in hollow logs for u p to 10 h. (4) Further, as T_b remains < T_a in these situations, echidnas may have physiological mechanisms for dealing with the heat after all.

Keywords: Echidna; Heat tolerance; Thermoregulation; Body temperature; *Tachyglossus aculeatus*

1. Introduction

Echidnas (*Tachyglossus aculeatus*) occur throughout Australia, a range which includes some of the hottest environments on earth,) where shaded air temperatures >37.8°C have been recorded on 160 consecutive days (Linacre and Hobbs, 1977). Yet echidnas are reputed to be inadequate thermoregulators in the heat. "Thus", wrote Griffiths (1978) "when exposed to high ambient temperatures echidnas can do very little about it, speaking in a physiological sense..." Robinson (1954) (cited in Griffiths, 1968) showed experimentally that above ambient temperatures of 35°C thermoregulation by echidnas deteriorated and that body temperatures of 38°C were fatal. Schmidt-Nielsen et al. (1966) showed that echidnas exhibited increased thermal conductance in relatively hot conditions, but this was insufficient to prevent body temperatures rising. In other laboratory studies Augee and Grant (1974) found no evidence of increased peripheral circulation, of increased metabolic rate, of sweating or of panting in echidnas exposed to ambient temperatures of 40°C. Later, Augee (1976) again found no evidence of sweating or panting in echidnas exposed to 40°C. He did find evidence of some increased metabolic rate, but echidnas failed to defend their body temperatures and one died after reaching 40°C.

Given their apparently inadequate physiological mechanisms it would be expected that echidnas place great reliance on behavioural mechanisms for thermoregulation and this is clearly the case. Activity is restricted to shaded air temperatures of <32°C at Kangaroo Island off the South Australian coast (Augee et al., 1975), in the wheatbelt of Western Australia (Abensperg-Traun and De Boer, 1992) and to < 33°C in semi-arid South West Queensland (Brice et al., submitted) so that in hot weather echidnas become wholly nocturnal (Abensperg-Traun and De Boer, 1992). During summer in South West Queensland, where temperatures reach 40°C and remain above 33°C until after dark, echidnas are active only between 2100 h and dawn (Brice et al., submitted). They spend the rest of the day in caves; burrows or logs. Echidnas elsewhere also apparently avoid hot conditions during the day by seeking shelter in similar sites (Griffiths, 1978; Augee, 1978; Abensperg-Traun, 1991; Grigg et al 1992).

Air temperatures within caves and burrows are less extreme than outside (Wilkinson et al., 1998). Caves used by echidnas at Mileura (Western Australia) were up to 12°C cooler than the maxima outside (Davies cited by Griffiths, 1968). Even so caves can be quite warm. In January the caves at Mileura had air temperatures of 32°C (Davies cited by Griffiths, 1968) equal to modal body temperatures of echidnas found elsewhere (Grigg et al., 1984, ~1992). Other sites may also be warm. Woodland logs were found to be 5°C warmer than heath burrows in summer near Kellerberrin in Western Australia (Abensperg-Traun, 1991)

No data are available on the thermal effects of microclimates on echidnas in hot conditions. In this study, body temperatures of echidnas occupying various types of shelter during hot days were recorded and related to air temperatures within these shelters to test the hypothesis that echidnas survive in hot climates by seeking relatively cool microclimates.

2. Materials and methods

The study was conducted at Idalia National Park, a mosaic of bendee *(Acacia catenulata)* and mulga *(Acacia aneurq)* woodland-dominated mesas overlooking Mountain Yapunyah *(Eucalyptus thozetiana),* coowara box *(Eucalyptus cambageana)* and poplar box *(Eucalyptus populnea)* woodlands and brigalow *(Acacia harpophylla)* regrowth shrublands 113 km WSW of Blackall in the semiarid zone (BSfh; Gentilli, 1986) of Western Queensland.

Eight echidnas were located within 7 km of the ranger station (latitude 24°53'04"S, longitude 144°46'23"E) between 8 August and 2 September 1994 and data were collected from 15 December 1994 to 24 February 1995: Calibrated temperature sensitive radio-transmitters (Sirtrack) coated with a smooth layer of inert wax were inserted into the abdominal cavities of these echidnas (two males and six females between 2.60 and 3.97 kg) via a midline laparotomy as described by Grigg et al. (1989). The echidnas were marked with colour plastic tubing as described by Brattstrom (1973) and returned to their respective capture sites.

Echidnas in various day-time shelter sites were located (at about dawn) using a (Telonics TR-2) receiver and a hand-held (Telonics RA-2K) directional antenna. Once located, an automatic recording system consisting of a scanner/receiver (Telonies-T51) attached to a timer and tape recorder as described by Grigg et al. (1989) was placed nearby, and body temperatures of echidnas (T_b) measured as pulse intervals were recorded every hour until echidnas left the shelter during the subsequent night. Echidnas active overnight were hand tracked from a distance and T_bs were recorded as part of a wider study reported elsewhere (Brice et al., submitted) until they occupied a (usually different) shelter the next day. A datalogger (Data Electronics Data Taker DTI00) was used to record hourly air temperatures within various identified shelters (T_a) using probes (Monolithic Celsius Sensor LM35) suspended in free space close to echidnas' locations. These probes were placed after the site had been vacated for logistical reasons as well as to minimise stress for the echidna. As echidnas rarely occupied the same shelters on consecutive days, shelters were monitored only when vacant despite unsuccessful attempts to place probes in anticipation of use by echidnas. Consequently, predicted T_a within the shelter was derived for days where echidnas were present by correlating the measured T_a within the shelter with air temperatures recorded concurrently in a nearby Stevenson Screen (T_{ss}).

Maximum-minimum mercury thermometers placed as close as possible to echidna locations were also used to monitor shelter sites. Again these were placed after the sites had been vacated and predicted T_a derived by correlating maximum and minimum temperatures to maxima and minima recorded in the Stevenson Screen. The Stevenson Screen was situated close to the park HQ and was monitored by an automatic weather station (Monitor Sensors GL:-32) which recorded a variety of hourly and daily parameters including air temperatures.

4. Results

Between 15 December, 1944 and 24 February, 1995 T_b data for a total of 72 echidna days were collected, where days refer specifically to periods of daylight hours. On 41 of these 72 echidna days, the locations of the echidna were identified positively. These consisted of burrows on 11 occasions, caves on 13 occasions and logs on 16 occasions. On one occasion, an echidna (IB1) was half buried in exposed soil. In some instances, burrows, caves and logs were reused by echidnas, so the total number of sites identified was somewhat < 41. Typically, T_b of echidnas in caves declined or remained relatively unchanged during their time in the shelters (Fig. 1a). In burrows, T_b remained relatively stable or rose slightly after an initial small decline (Fig. 1b). In logs, T_b typically declined to a mid-morning minimum before rising to an evening maximum (Figs. 1c and d).

T_b of sheltering echidnas appeared to be independent of climatic conditions. There was no consistent relationship between either minimum or the maximum T_b of echidnas in these sites and the maximum T_{ss}. The range of T_b of "inactive" or "sheltering" echidnas was taken to be the difference between the maximum and the minimum T_b of echidnas during the same day while in the burrows, caves or logs. Echidnas for which more than a single day of data was available showed no consistent evidence of their resting range being related to T_{ss}.

There was no pattern between either minimum or maximum T_b and the type of shelter. However, the range of T_b for sheltering echidnas was consistently greater when echidnas used logs than when they used either caves or burrows (Table 1: IB7 and IB8 were not known to utilise logs during summer). An ANCOVA with the maximum $T_{\&}$ recorded as a covariate (to allow for the different weather of different days) found that shelter type was a significant ($p<0.001$, df=3) factor in determining the range of T_b. The range in those that used logs was greater than those that used' all other shelter types (pooled: see below) by a factor of about 2:5. There was no significant interaction between shelter and individual echidnas ($p = 0.1$, df=1).
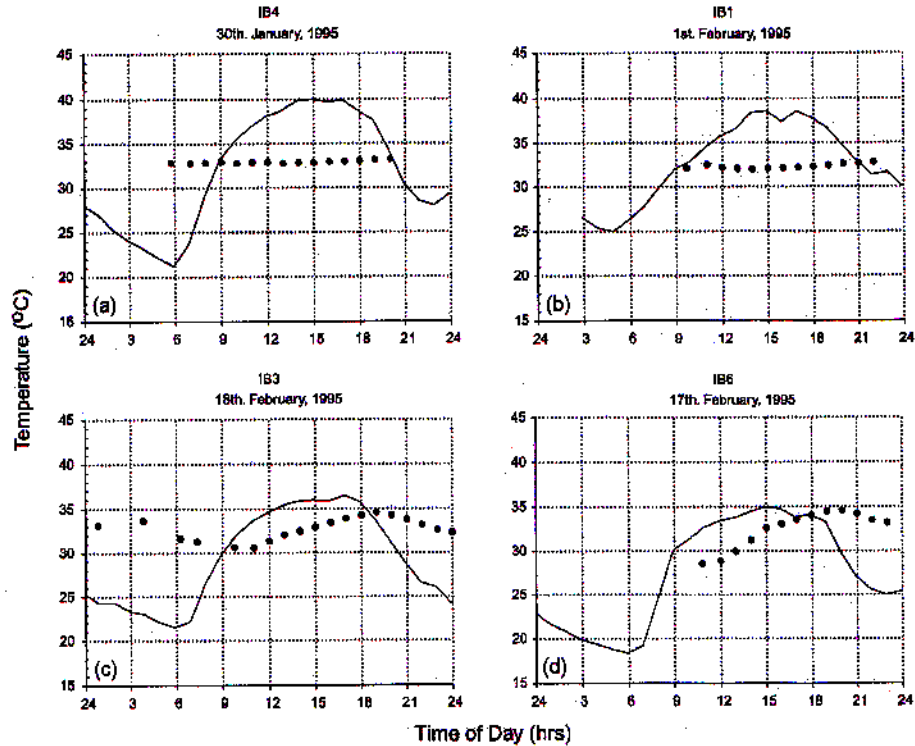
Fig. 1. Examples of T_b (points) of echidnas in a cave (a), in a burrow (b) and in logs ((c) and (d)) on days when T_{ss} were as shown by the solid lines.

Table 1. Mean ranges (and standard deviation) of body temperatures of sheltering echidnas known to be in burrows, caves (pooled: see Fig. 3) or logs

Ech	Burrows or Caves			Logs		
	mean	s.d.	*n*	mean	s.d.	*n*
IB I	0.8	-	1	4.2	0.707	2
IB2	-	-	-	1.9	-	1
IB3	1.32	0.614	5	3.55	1.714	4
IB4	1.18	0.512	5	3.4	-	1
IB5	-	-	-	0.9	-	1
IB6	1.1	0.624	3	2.757	1.725	7
IB7	1.67	0.824	6	-	-	-
IB8	1.6	0.735	4	-	-	-

Two burrows were monitored with the data-taker for about 12 and 10 days, respectively, and two logs for about 7 and 6 days, respectively. Additionally, two further burrows, three caves and two other logs were monitored with mercury maximum-minimum thermometers for 4, 11, 10, 4, 5, 11 and 6 days, respectively. Echidnas did not use any sites while they were being monitored by either probes or thermometers; so T_as at the time, when shelters were occupied had to be derived indirectly. As days varied in temperature, the data taken from the microenvironments was correlated to data taken concurrently (or in the case of maximum-minimum thermometers, to the maximum and minimum of the same day) from the Stevenson screen (Fig. 2). In this way, T_as of the shelters when they had been occupied were able to be predicted.
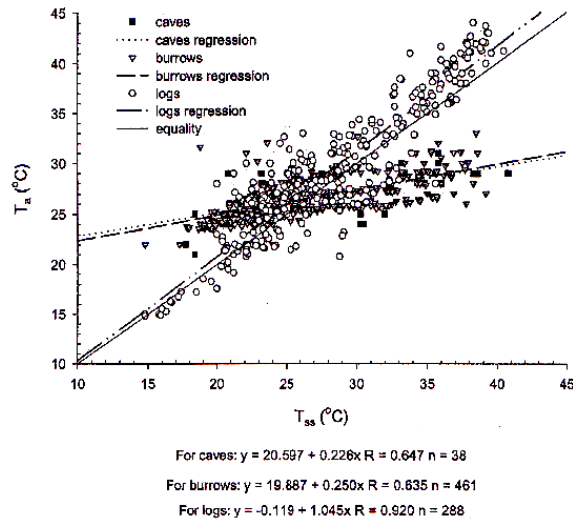
Fig. 2. Correlation of measured T_a with concurrent T_{ss} for caves, burrows and logs used by echidnas together with regression lines.

For caves: $y = 20.597 + 0.226x$ $R = 0.647$ $n = 38$

For burrows: $y = 19.887 + 0.250x$ $R = 0.635$ $n = 461$

For logs: $y = -0.119 + 1.045x$ $R = 0.920$ $n = 288$

When utilising either caves or burrows, T_b always remained above the predicted T_a within those sites (Fig. 3a). Consequently, these environments represented heat sinks for the echidnas. However, in logs, T_b was sometimes below, sometimes above T_a within the logs they were using (Fig. 3b). That is, for at least some of the time, echidnas were maintaining body temperatures below ambient in spite of their environments representing heat sources.
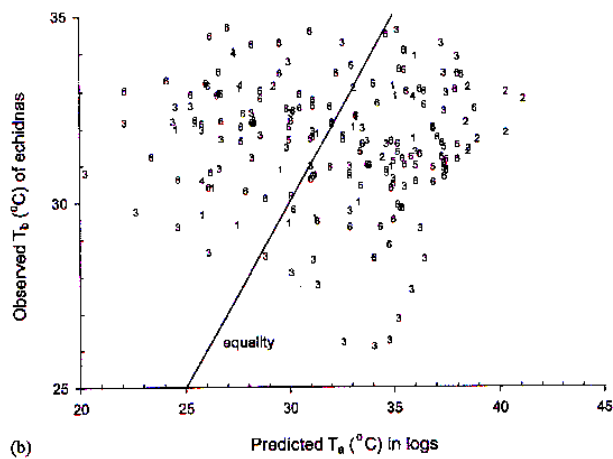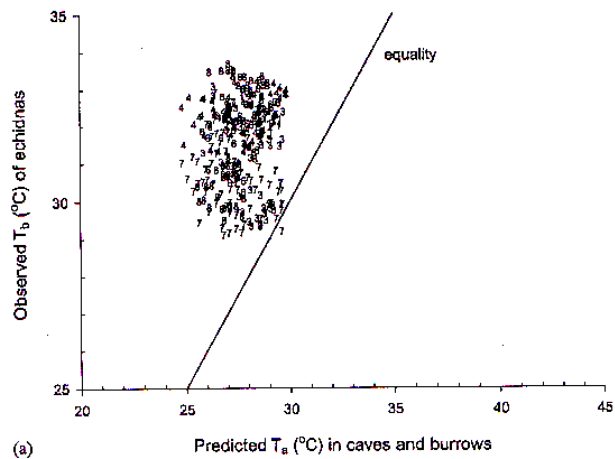

Fig. 3. T_b of echidnas while known to be sheltering in caves and burrows (a) and logs (b) against predicted T_a of those sites (numbers refer to individual echidnas).

5. Discussion

This study demonstrated that echidnas use caves, burrows and logs during the day in summer. Whereas caves and burrows are cooler inside than outside during hot weather, logs are not, with T_a regularly reaching 40°C (Fig. 2). Thus, while caves and burrows represent heat sinks for echidnas, logs represent heat sources for these animals which are reputed to lack cooling mechanisms (Griffiths, 1978) and their T_bs rise during the afternoon accordingly (Fig. 1). Given that echidnas had occupied logs on days when ambient temperatures exceeded 35°C and given the belief that echidnas die from heat stress at these temperatures (Robinson, 1954 cited in Griffiths, 1968; Augee and Grant, 1974; Augee, 1976), it was surprising to find that:

(a) echidnas regularly used such logs without suffering any apparent ill effects, and
(b) they did so even though there were always numerous caves or burrows known to be suitable (from previous or subsequent use) close to these logs; that is the echidnas appeared to use logs despite the heat.

This prompted a closer look at the shaded air temperature regime for 41 days corresponding to the known uses of various shelter types. Caves and burrows were used on 25 occasions when maximum T_{ss} varied from 30°C to 41°C (Fig. 4a). Logs were used on 16 occasions with maxima from 30°C to 40°C. Thus, maximum T_{ss} did not seem to influence the type of shelter used by echidnas. However, as echidnas were nocturnal they were selecting their day time shelters at dawn (Brice et al., submitted), a time of the day largely coinciding with minimum T_{ss} (Linacre and Hobbs, 1977) rather than maximum T_{ss}. So echidnas were actually choosing their shelter sites when the ambient temperatures were at their lowest. Looking at the minimum T_{ss} for the days when shelter sites were identified (Fig. 4b) it can clearly be seen that echidnas only chose logs on one occasion when the ambient temperature was > 22°C; and that was on a day when the temperature was 22.5°C. It seems that during the summer at Idalia, echidnas were avoiding logs except on the coolest of mornings and this reinforces the view that behavioural thermoregulation is of prime importance. Nevertheless, on some relatively cool mornings (<22°C) temperatures later reached the high 30s and some echidnas found themselves in hot logs anyway. In terms of the investigation into their heat tolerance, that these echidnas survived these regular events without apparent ill effects is of interest.
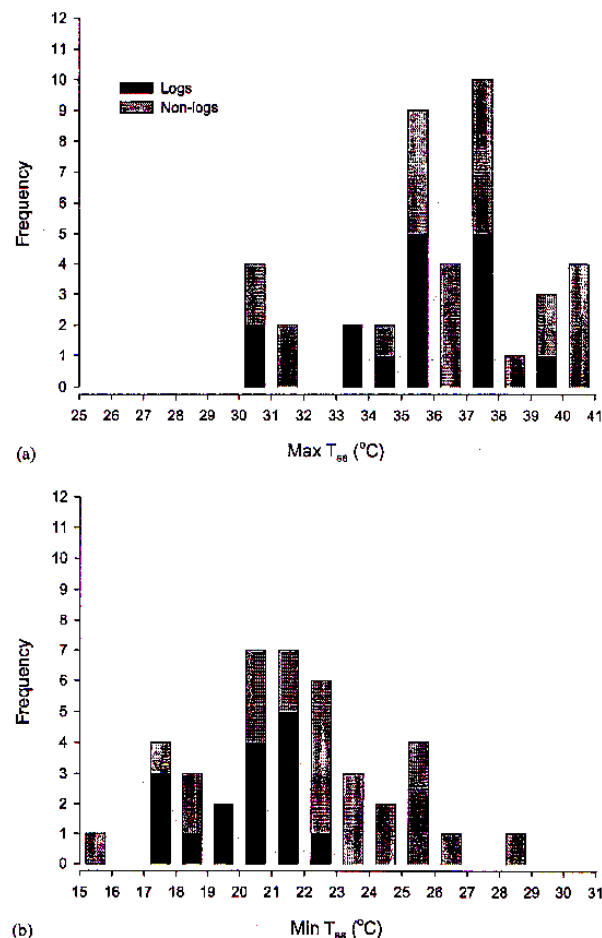

Fig. 4. Logs (black) as a proportion of all identified shelter sites used by echidnas on days with given maximum (a) and minimum (b) T_{ss}; $n = 41$.

Further investigation found that in the case of IB2, at least half of the echidnas were buried in copious dirt within the log and that the temperature of this dirt was substantially lower than that of the air just above it (Fig. 5). As with echidnas in the Western Australian wheatbelt (Abensperg-Traun, 1991), echidnas at Idalia seemed to be burying themselves in the cool dirt within logs. This would facilitate the conduction of heat away from the body to the substrate. However, inspection of other logs known to be used by echidnas on hot days found this not always to be the case. In several of the logs used by echidnas, < 5 mm of dirt was found and in some, almost no dirt at all. It is prima facie hard to envisage in these logs, the echidna being able to lose enough heat to the sparse coating of dirt to counteract heat gained by conduction and convection from the air within the log and by radiation from the internal surface of the log itself. Temperatures of the internal surfaces of logs were not measured during this study, so it is not possible to quantify the effect of such radiation, Clearly further study incorporating such factors is warranted. Nonetheless, echidnas did use logs with high T_a from time to time with no apparent ill effects.

Echidnas are able to spend a day in a hot log but apparently have to tolerate a rise in their body temperature while doing so. This implies that the T_bs of sheltering echidnas passively follow that of their microenvironment and that thermal inertia plays an important part in the temperature relations of echidnas. A cool body placed in a hot environment does not become hot immediately but reaches thermal equilibrium only after some time. The time taken to reach this thermal equilibrium depends upon the absorptivity of the body, its surface area, its mass and its heat capacity as well as the temperature gradients between the surface of the body and its environment. Thus, an endotherm may well be able to survive short-term (i.e., daily) exposure to temperatures that might be lethal over the longer term. It was not possible to measure T_a in logs with echidnas present. However, observations from echidnas while they were resting in logs show that, their T_bs frequently started rising around noon and reached a maximum in the evening as would be expected for bodies warming passively due to convection, conduction and radiation (Fig. 1). The extent of this rise, reflected in the range of T_b, may be affected by the available quantity of soil acting as a heat sink within the hot log. The Tb of IB2 rose $1.9^{\circ}C$ in a log with copious soil while the T_b of the similarly sized IB6 rose by more than 6°C in a log with only a sparse coating of soil. The variability of ranges of T_b (Table 1) may, therefore, be related to the variable soil depth within logs. As T_a of > 35°C was recorded in logs on several occasions far periods exceeding 4 h and up to 10 h, the hypothesis that thermal inertia alone could explain how echidnas maintain body temperatures below that of the immediate environment during the heat of the day is not a definitive answer.
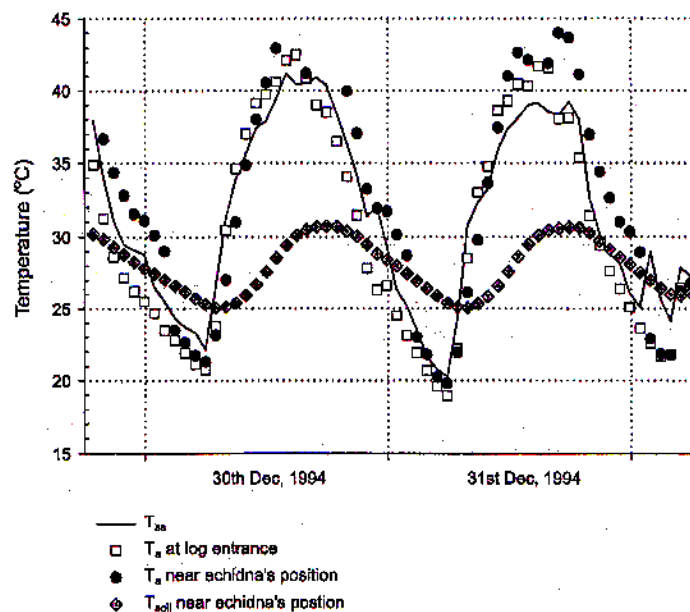

Fig. 5. Temperature aspects of the microenvironment of a log used by IB2.

A further possible explanation lies in the echidnas' labile T_b. Echidnas undergo marked daily fluctuations in T_b and routinely enter torpor to varying degrees throughout much of their range (Grigg et al., 1989,1992; Rismiller and McKelvey, 1996; Nicol and Andersen, 2000; Beard and Grigg, 2000). Metabolic heat production is an important element in mammalian heat budgets and torpor may be a mechanism to reduce this source in am animal subject to high exogenous heat loads. Grigg et al. (1989) speculated on the extent of torpor and the possibility of aestivation in echidnas particularly in hotter parts of their range. Echidnas apparently use torpor associated with a reduced T_b at least occasionally during summer at Idalia (Brice et al., submitted) so the

possibility that echidnas can vary their metabolic rate to manage their thermal relations remains a possibility to be tested.

This study has been able to demonstrate that, in the field echidnas are able to maintain their body temperature below about 35°C despite at least some of these shelter sites having ambient air temperatures somewhat warmer for several hours. This seems to contradict the findings of those workers (e.g. Griffiths, 1968, 1978; Augee and Grant, 1974; Augee, 1976) who concluded that echidnas are unable to defend their body temperatures in conditions of heat stress. These earlier studies were not done in the field but in laboratories and at least three factors may contribute to their different findings. Firstly, animals that struggle increase their metabolic rate and, therefore, their total heat load by adding greater endogenous heat to the exogenous heat of the experiment. Parer and Hodson (1974) questioned the findings of Bentley et al. (1967) on the basis that animals were frequently observed to be struggling in the earlier study: Secondly, even inactive animals may be under stress in artificial surroundings and this stress may contribute to an increased body temperature again though increased metabolic heat production. Augee and Ealey (1968) monitored the heart rates of echidnas using probes inserted via hollow spines; which seemed not to induce as much struggling. Their reported heart rates of 116 and 70 beats/min for non-torpid (presumably resting) echidnas were much higher than the 55 and 68 beats/min measured by telemetry from resting non-torpid echidnas in. the field with similar ambient temperatures (Grigg et al., 1992; Grigg and Beard, 1996). Thirdly, the controlled environment of a laboratory is likely to be more homogeneous (especially if that environment is kept at a constant temperature) than that associated with a log in nature. The animal in an experimental situation may not have access to a cool floor or to cool dirt, whereas in a log in the field, an animal may be able to lose heat to a cool wooden substrate and can almost certainly loose heat to a loose dirt substrate.

To test the hypothesis that torpor is used to manage high heat loads, metabolic rates need to be measured directly. Metabolic rate correlates with heart rate (Fanning and Dawson, 1989; Grigg and Beard, 1996) which can be measured in the field using telemetry. By monitoring metabolic rate using heart rates of echidnas in hot field environments it may be possible to determine whether an animal reputed to be a poor thermoregulator, unable to pant or sweat, can keep its cool by staying calm.

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