29 Ecological physiology of a small arid zone marsupial in relation to its thermal environment

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Abstract

The vast arid interior of Australia is home to a surprising diversity of insectivorous marsupials (Dasyuridae). The ability to enter daily torpor in a resource-poor environment possibly contributed to the success of this group. However, most of our knowledge about the energetics of dasyurids is based on laboratory work with field data being extremely scarce. Here we present a summary of one of the first field studies using radio-telemetry on the winter thermobiology of a dasyurid living in the sandy deserts of Australia. The study organism, the nocturnal Brush-tailed Mulgara (*Dasycercus blythi*), evaded daytime temperature peaks by burrowing. However, during night-time activity mulgaras were exposed to temperatures as low as -2.9°C. The activity phase was therefore centred around dusk and was usually shorter than the scotophase. Furthermore, mulgaras entered torpor frequently and, because they often used shallow burrows, they were able to reduce body temperatures (T_b) below the average soil temperatures of 16°C. Maximal torpor bout length was 12.8 ± 6.4 hr and minimum T_b 18.5 ± 6.1°C (n = 8). Females employed torpor throughout most of pregnancy but torpor was apparently incompatible with early lactation. Torpor in males was shorter and less frequent during the early winter mating season than during late winter.

Introduction

Desert environments are characterised by temperature extremes and low food availability. Nevertheless, although the high metabolic rate of small mammals requires a high food intake, the diversity of small mammals in the Australian arid zone is high (Dickman 2003). Insectivorous marsupials of the family Dasyuridae contribute significantly to this species diversity, but usually occur at relatively low densities (Dickman *et al*. 2001). In comparison to most small mammals, dasyurids have a low basal metabolic rate, slow juvenile development and a low reproductive output (Dawson & Hulbert 1970). In mammals these energy-conserving character

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traits are often associated with arid environments (Lovegrove 2003; Withers *et al.* 2006). Furthermore, the widespread ability to enter energy-saving torpor might have contributed to the evolutionary success of dasyurids in arid environments. However, information on torpor use is based mainly on laboratory studies (Geiser 2003) because of the logistical difficulties posed by the generally low density of dasyurids in their natural habitat, their presumably shifting home ranges, and the inaccessibility of much of arid Australia (Dickman *et al.* 1995). Consequently, in dasyurids the ecological significance of torpor and even the environmental conditions encountered by these animals are largely unknown.

Here we present the first detailed data on the thermobiology and activity patterns of the Brush-tailed Mulgara (*Dasycercus blythi* syn. *cristicauda*) in relation to the thermal properties of its environment. Mulgaras have a patchy distribution on sandy plains dominated by spinifex hummocks (*Triodia* sp.), a landform that covers vast areas of central Australia. Mulgaras inhabit burrows either dug by themselves or other animals and, unlike many other dasyurids, are sedentary although home ranges are large (Körtner *et al.* 2007; Masters 2003; Menkhorst & Knight 2001).

Methods

The study was conducted during the Austral winter (June–August 2006) in Uluṟu–Kata Tjuṯa National Park, Northern Territory (25° 20' S 131° 02' E). The study area comprised a mosaic of mature and recently burned spinifex (Körtner *et al.* 2007) on a sandy plain interspersed with low sand dunes.

The thermal properties of the habitat were measured to the nearest 0.5°C every 20–40 min using a number of small temperature loggers (iButtons, Maxim Integrated Products, Sunnyvale, CA, USA). Temperature profiles were recorded in the shade at a height of ~1.5 m (T_{air}), on the ground in the shade of a spinifex hummock (T_{spin}), on the unshaded surface (T_{surf}), and underground at four different depths (T_{soil}, 17 cm, 27 cm, 37 cm and 57 cm). To describe the temperature envelope available to the animals, an average daily temperature trace was calculated for each logger location. For each 30-min time interval the maximum and minimum temperature from all combined traces was then calculated to describe the range of ambient temperatures (T_a) available at any given time of day.

Nine mulgaras (6 males, 3 females), trapped in box aluminium traps, were implanted with temperature-sensitive radio-transmitters (2.4–3.9 g, < 5% of body mass, Sirtrack, Havelock, New Zealand). Surgery was performed under general oxygen/Isoflurane anaesthesia. Transmitters were wax-coated and calibrated to the nearest 0.1°C against a mercury thermometer traceable to a national standard. After surgery, animals were held overnight and provided with food *ad libitum* before they were released at the site of capture the following evening. If animals were re-trapped at the end of the study, transmitters were removed with the exception of one female with pouch young.

Every morning, mulgaras were radio-tracked to their burrow and the location was recorded with a handheld GPS. A data logger unit was placed near the burrow to record the interval between transmitter pulses every 10 min. Logged data were later downloaded to a PC and converted to T_b using the original transmitter calibration (Körtner & Geiser 1998). Up to two loggers per animal were employed at different burrows, improving the chances of recording the end of the activity phase and the timing of torpor entry. Because of the relatively small reception range of the data loggers, the activity phase could be inferred from the absence of data from the logger trace. Torpor was defined by a T_b threshold of 30°C (Körtner & Geiser 2000). Rate of rewarming during arousal was averaged over the time period from the start of the arousal process to when a maximum had been reached (usually above 30°C). In addition the maximal arousal rate was defined as the maximal temperature difference over a 10-min interval (i.e. between two logger readings). The rate of cooling during torpor entry was calculated for the relatively small number of long torpor bouts, during which a stable minimal T_b plateau had been reached. Following the model of Newton's law of cooling, the differential between T_b and the final T_b equilibrium was log-transformed, whereby the slope of the resulting regression gives the cooling constant (Nicol & Andersen 2007).

Data are presented as means ± 1SD, whereby the average for a group of animals was calculated using the means for each individual; n refers to the number of animals and N to the number of measurements. Radio tracking locations were analysed for home range size (100% Minimal Convex Polygon, MCP) using the Animal Movement extension (V2, Hooge & Eichenlaub 1997) for Arcview. Regression analyses were performed in SigmaPlot 7.0 (SPSS Inc.) and all other statistical procedures in Minitab (Minitab Inc.).

Results

During most days of the study, cloud cover was minimal and hence daily fluctuations in T_a were pronounced. Averaged over the time of the study (10 June–18 August) T_{air} fluctuated by 18.0 ± 5.5°C (average T_{air} 11.7 ± 2.1°C) over the day and subzero T_{air}s were common in the early morning (absolute minimum: -2.9°C, maximum: 30.2°C). Daily variation in T_{spin} (amplitude: 22.1 ± 6.1°C, average: 11.5 ± 2.1°C) was slightly higher, whereas the most extreme daily variation was for T_{surf} (amplitude: 33.4 ± 8.6°C, average: 12.8 ± 2.3°C). Daily temperature fluctuations experienced underground were progressively attenuated with increasing depth and at 57 cm approached the logger resolution of 0.5°C. The buffering properties of soil also delayed the extremes of the daily temperature cycle by up to 14 hr at the maximal depth measured. In contrast, average daily T_{soil} was similar at all depths measured (15.8 ± 0.4°C, n = 4) and higher than averages for above-ground temperatures.

Twelve mulgaras were trapped and of these 9 were radio-tracked for between 6 to 55 days. Short monitoring periods were attributed to early transmitter failure in one case and several predation events (for details see Körtner *et al.* 2007). Male mulgaras were on average heavier than females (males: 85 ± 12.7 g, n = 8; females: 57.4 ± 3.9 g, n = 4; $T_9 = 5.6$, $p < 0.001$). All mulgaras monitored inhabited overlapping home ranges with male home ranges (25.5 ± 8.4 ha) being significantly larger than those of females (10.8 ± 4.0 ha; $T_5 = 3.33$, $p = 0.21$). Within the home range the study animals used on average 9.4 ± 3.9 burrows and frequently moved between them.

Activity usually commenced around sunset after above-ground temperatures had subsided substantially (Figure 1a). The end of the activity phase could occur anytime during the night ranging from shortly after sunset to sunrise; the coldest time of the day above ground (Figure 1a). Occasionally, animals were observed to interrupt activity by a period of rest in one of their burrows before commencing another bout of activity later at night. On 6 out of 277 observation nights, a mulgara remained in its burrow throughout the night.

Torpor in mulgaras was shorter than 24 hr, with a maximum duration of 20.8 hr. Maximum torpor bout length of individuals did not differ between males and females and was on average 12.8 ± 6.4 hr (n = 8; $T_5 = 2.24$, $p = 0.075$). Occasionally two torpor bouts per day were observed. Torpor commenced either during the night, often shortly after sunset, or during daylight prior to mid-day (Figure 1b). On average, torpor entry occurred somewhat earlier on cold nights (torpor entry [hr from sunset] = 0.28 T_{air}min[°C] - 3.72, $R^2 = 0.03$, $p = 0.02$). Timing of arousal was more uniform and most arousals coincided with the steep rise in T_a above ground and at shallow underground depths (Figure 1b). Arousals tended to occur slightly earlier on hot days (time of arousal [hr to sunrise] = -0.07 T_{surf}max[°C] + 7.8, $R^2 = 0.086$, $p < 0.001$) and on the nine occasions when torpor extended to dusk overcast conditions prevailed.

For 23 of the longer torpor bouts (i.e. those that reached an equilibrium T_b minimum) the fall of T_b followed Newton's law of cooling and T_b data were linearised by log transformation (Figure 2a). For these the cooling constant was on average 0.438 ± 0.057 hr^{-1} (n = 4, N = 23). However, in most torpor cases cooling deviated from the law of cooling (Figure 2b), most likely because T_a changed during the cooling phase (see below). Arousal was usually fast and the maximal rate of rewarming during arousal was 0.24 ± 0.09°C min^{-1} (n = 8, N = 212). From start to finish, the average arousal rate was 0.12 ± 0.04°C min^{-1} (n = 8, N = 211).

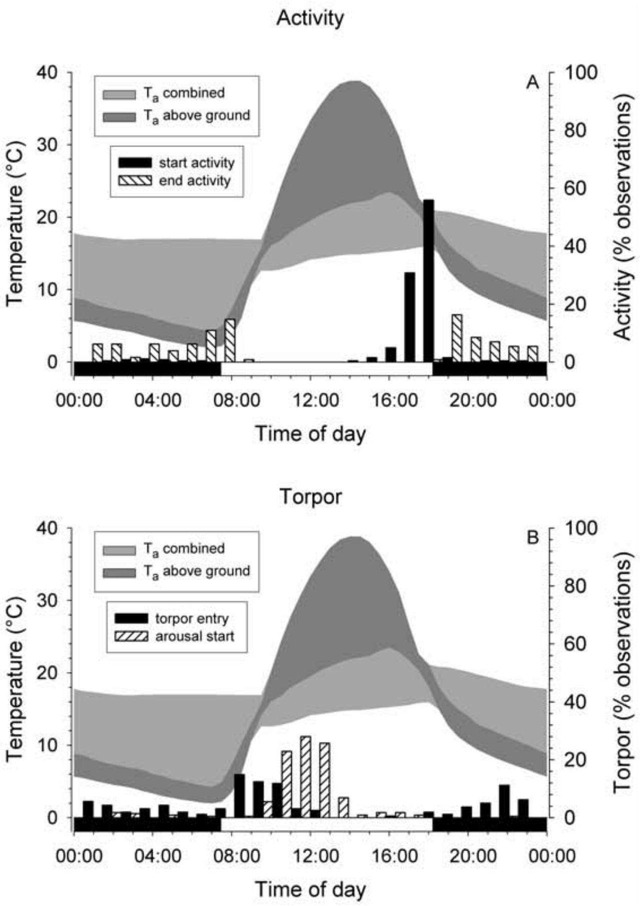

Figure 1.

Start and end of the daily activity phase in relation to an average daily T_a cycle (A). Timing of torpor entry and arousal (B). Horizontal dark bars at the bottom of the graph represent the scotophase.

Minimum T_b during torpor was mostly reached during the first half of the photophase shortly before arousal commenced (Figures 3, 4). On most occasions T_b remained above the average T_{soil} of 15.8°C. However, during a considerable number of torpor bouts T_b fell well below this threshold, indicating that animals resided in burrows shallow enough to be affected by daily fluctuations in T_a. This is also illustrated in Figure 4 where the two females (F1, F2), which reached T_bs below average T_{soil}, exhibit continuous cooling and also initial slow, possibly passive rewarming. On average, the absolute minimum T_b reached by individuals did not differ between males and females ($T_4 = 1.96$, $p = 0.12$) and was 18.5 ± 6.1°C ($n = 8$). The lowest T_b observed was 10.8°C in a female.

Female mulgaras without pouch young, but including a pregnant individual, entered torpor almost daily (95.8 ± 2.5% of days, $n = 3$, $N = 134$). In contrast, towards the end of the study one female with pouch young maintained a stable high T_b throughout the day from about the time of parturition onwards. Torpor patterns in males were more complex, but torpor frequency appeared to increase over the course of the study. In the four males monitored during June and early July for more than one week, torpor was observed on 50.8 ± 25.9% of days ($N = 79$) and torpor bouts were generally brief. In contrast, in the two males monitored beyond mid-July, torpor frequency increased to 100% of days ($N = 44$) and torpor increased both in length and depth.

Discussion

During winter, critical high T_as for mulgaras were reached for only a few hours during sunny days and then only on the unshaded sand surface. During daytime the scope for temperature

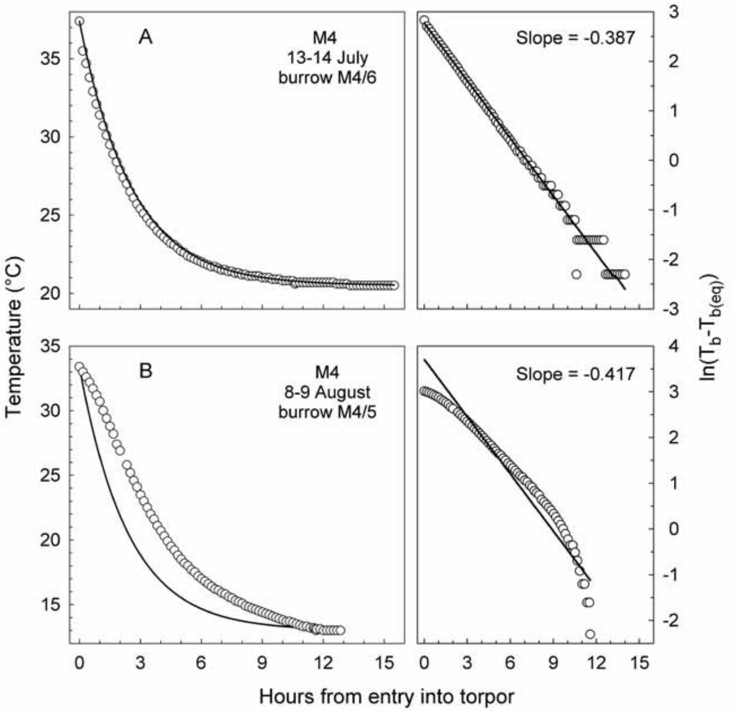

Figure 2.

Cooling during torpor entry (left panels) and log-transformed data (right panels). Circles represent the original data and the solid lines are the extrapolations based on Newton's law of cooling (for details see text). In A the fall of T_b during torpor entry conforms to Newton's law, but not in B, probably because T_a also fell during the cooling process.

selection even above ground was substantial and for mulgaras, which spend most of the daytime in burrows, the zenith of the daily T_a cycle remained unproblematic. In contrast, low T_as encountered during the night, the activity phase of mulgaras, provided a greater energetic challenge. Starting before dusk T_as fell rapidly and towards the end of the cooling phase at dawn, sub-zero T_as were regularly observed above ground. The range of T_as available above ground at night was also much narrower than during daytime. Because thermoregulatory costs increase progressively with the intensifying cold, it is not surprising that the activity phase was often terminated long before sunrise (Figure 5) and sometimes was omitted altogether. Occasionally, mulgaras commenced activity before sunset, presumably because the locally dense spinifex hummocks provided sufficient protection from diurnal avian predators.

The use of burrows alleviates costs for thermoregulation, but winter T_{soil}s were still well below thermoneutral, which is about 30°C for mulgaras (MacMillen & Nelson 1969). Furthermore, in the sandy soil stable temperature conditions were reached only at depths greater than about 60 cm. Therefore, animals residing in shallow burrows would still be affected by the extreme daily T_a cycle. Surprisingly, cooling profiles and low T_bs during torpor suggested that such shallow burrows were often used by mulgaras. Whether use of shallow burrows simply reflects burrow availability or selection is unknown, but it could well be that mulgaras gain energetic

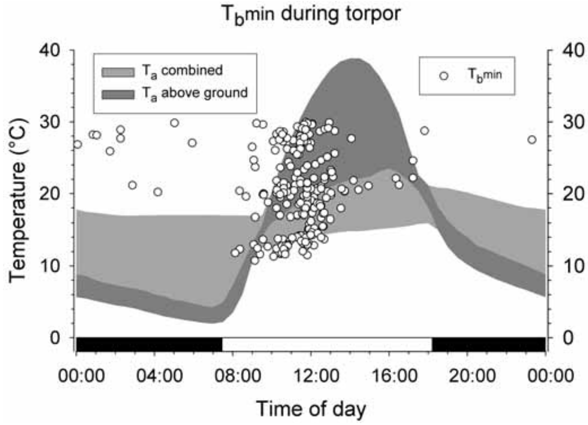

Figure 3.

Minimum T_bs during torpor plotted against time of day. The gray areas illustrate the range of T_as available on an average day and the dark gray area those above ground only. The horizontal dark bars at the bottom of the graph represent the scotophase.

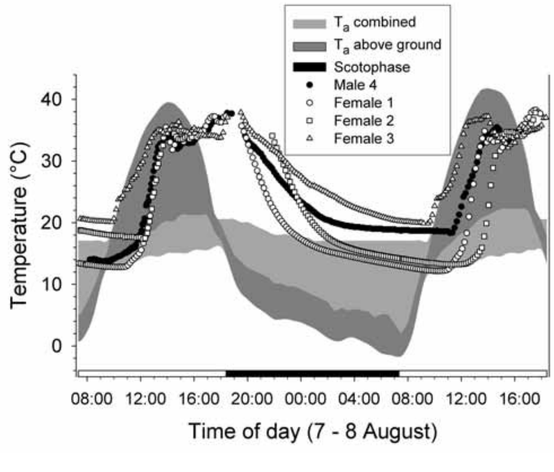

Figure 4.

T_b traces for four mulgaras from the time of sunrise on 7 August 2006 to sunset on 8 August 2006. The T_a profiles shown as grayed areas are the profiles measured on these days. The horizontal dark bar at the bottom of the graph illustrates the scotophase.

benefits from exposure to an attenuated T_a cycle in shallow burrows, provided they enter torpor. For example, a reduction of T_b below average soil temperature would have further reduced the metabolic rate of a torpid individual and morning rise in T_a at shallow depths offered them a degree of passive rewarming that was often evident as a slow increase of T_b prior to arousal (Figure 4). Hence when subjected to a T_a cycle the benefits of a lowered T_b are not necessarily offset by increased arousal costs if passive rewarming is employed (Lovegrove *et al.* 1999).

The frequency of torpor use by mulgaras in our study demonstrates that torpor was clearly part of the daily routine. However, temporal changes in torpor use were observed in both sexes (Figure 5). Non-lactating female mulgaras spend on average more than 75% of the day resting and slightly less than half of this time was spent torpid (Figure 5). However, these patterns changed and torpor use ceased around parturition, which occurred in one of the monitored females during the second week of August. In mulgaras, lactation appeared to be incompatible with torpor, confirming earlier observations in the laboratory on this and other dasyurids (Geiser *et al.* 2005; Geiser & Masters 1994). Gestation in mulgaras varies from 30–48 days (Geiser & Masters 1994; Michener 1969; Woolley 1971) and hence mating would have occurred around the beginning of July, when torpor in males was still infrequent and shallow and the activity phase was prolonged (Figure 5). Therefore, it is likely that for males reproductive effort entails noticeable energetic costs in terms of prolonged activity and thermoregulation. The temporal changes in torpor use exhibited by both sexes illustrate that daily torpor in mulgaras, despite its frequent use, is not essential in balancing energy budgets on a daily basis. Nevertheless, torpor is clearly important for minimising foraging requirements and perhaps for a seasonal re-allocation of energy resources facilitating reproduction in a resource-poor environment.

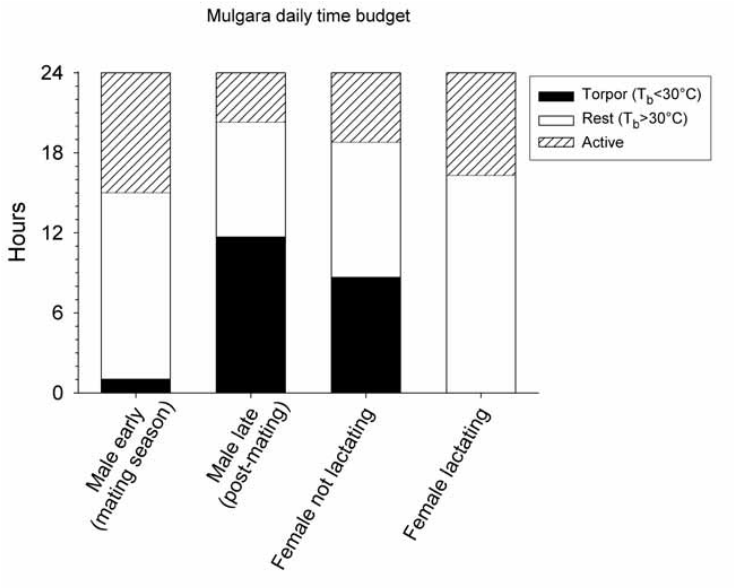

Figure 5.

Average daily time budgets for male and female mulgaras over winter.

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References

DAWSON, T.J. & HULBERT, A.J. 1970. Standard metabolism, body temperature, and surface areas of Australian marsupials. *American Journal of Physiology*218:1233–1238.

DICKMAN, C.R. 2003. Distributional ecology of dasyurid marsupials. Pp. 318–331in Jones, M., Dickman, C.R. & Archer, M. (eds), *Predators with pouches: the biology of carnivorous marsupials*. CSIRO Publishing, Collingwood, Australia.

DICKMAN, C.R., PREDAVEC, M. & DOWNEY, F.J. 1995. Long-range movements of small mammals in arid Australia: implications for land management. *Journal of Arid Environments* 31:441–452.

DICKMAN, C.R., HAYTHORNWAITE, A.S., MCNAUGHT, G.H., MAHON, P.S., TAMAYO, B. & LETNIC, M. 2001. Population dynamics of three species of dasyurid marsupials in arid central Australia: a 10-year study. *Wildlife Research* 28:493–506.

GEISER, F. 2003. Thermal biology and energetics of carnivorous marsupials. Pp. 238–253in Jones, M., Dickman, C.R. & Archer, M. (eds), *Predators with pouches: the biology of carnivorous marsupials*. CSIRO Publishing, Collingwood, Australia.

GEISER, F. & MASTERS, P. 1994. Torpor in relation to reproduction in the mulgara, *Dasycercus cristicauda* (Dasyuridae: Marsupialia). *Journal of Thermal Biology* 19:33–40.

GEISER, F., MCALLAN, B.M. & BRIGHAM, R.M. 2005. Daily torpor in a pregnant dunnart (*Sminthopsis macroura* Dasyuridae: Marsupialia). *Mammalian Biology* 70:117–121.

HOOGE, P.N. & EICHENLAUB, B. 1997. *Animal movement extension to Arcview*. Version 1.1. Alaska Science Center, Biological Science Office, US Geological Survey, Anchorage, AK.

KÖRTNER, G. & GEISER, F. 1998. Ecology of natural hibernation in the marsupial mountain pygmy-possum (*Burramys parvus*). *Oecologia* 113:170–178.

KÖRTNER, G. & GEISER, F. 2000. Torpor and activity patterns in free-ranging sugar gliders *Petaurus breviceps* (Marsupialia). *Oecologia* 123:350–357.

KÖRTNER, G., PAVEY, C.R. & GEISER, F. 2007. Spatial ecology of the mulgara (Marsupialia: Dasyuridae) in arid Australia: impact of fire history on home range size and burrow use. *Journal of Zoology, London* 273:350–357.

LOVEGROVE, B.G. 2003. The influence of climate on the basal metabolic rate of small mammals: a slow-fast metabolic continuum. *Journal of Comparative Physiology B* 173:87–112.

LOVEGROVE, B.G., KÖRTNER, G. & GEISER, F. 1999. The energetic cost of arousal from torpor in the marsupial *Sminthopsis macroura*: benefits of summer ambient temperature cycles. *Journal of Comparative Physiology B* 169:11–18.

MACMILLEN, R.E. & NELSON, J.E. 1969. Bioenergetics and body size in dasyurid marsupials. *American Journal of Physiology* 217:1246–1251.

MASTERS, P. 2003. Movement patterns and spatial organisation of the mulgara, *Dasycercus cristicauda* (Marsupialia: Dasyuridae) in central Australia. *Wildlife Research* 30:339–344.

MENKHORST, P. & KNIGHT, F. 2001. *A field guide to the mammals of Australia*. Oxford University Press, Melbourne, Australia.

MICHENER, G.R. 1969. Notes on the breeding and young of the crest-tailed marsupial mouse, *Dasycercus cristicauda*. *Journal of Mammalogy* 50:633–635.

NICOL, S.C. & ANDERSEN, N.A. 2007. Cooling rates and body temperature regulation of hibernating echidnas (*Tachyglossus aculeatus*). *Journal of Experimental Biology* 210:586–592.

WITHERS, P.C., COOPER, C.E. & LARCOMBE, A.N. 2006. Environmental correlates of physiological variables in marsupials. *Physiological and Biochemical Zoology* 79:437–453.

WOOLLEY, P.A. 1971. Maintenance and breeding of laboratory colonies of *Dasyuroides byrnei* and *Dasycercus cristicauda*. *International Zoological Yearbook* 11:351–354.