

Activity and torpor in two sympatric Australian desert marsupials

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Abstract

Many biological variables related to energy turnover including torpor, the most efficient energy-saving mechanism available to mammals, scale with body size, but the implications for animals living in their natural environment remain largely unknown. We used radio-telemetry to obtain the first data on the activity patterns and torpor use of two sympatric, free-ranging dasyurid marsupials, the stripe-faced dunnart *Sminthopsis macroura* (16.6 ± 1.5 g) and the more than six-times larger kowari *Dasyuroides byrnei* (109.4 ± 16.4 g), during winter in arid Queensland, Australia. Eight dunnarts and six kowaries were surgically implanted with temperature-sensitive radio-transmitters and monitored for 14–59 days. Both species commenced activity shortly after sunset, but while kowaries remained active through most of the night, dunnarts usually returned to their burrows before midnight. In dunnarts, short activity was associated with the frequent use of daily torpor (99.1% of observation days). Torpor often commenced at night, with body temperature (T_b) decreasing to a minimum of 11.3°C , and torpor lasted up to 26 h. In contrast, only 50% of the kowaries entered torpor and torpor was brief (maximum 4 h), shallow (minimum T_b 25.3°C) and restricted to the daytime rest-phase. Our study suggests that in winter, the smaller dunnarts can remain active only during the warmer first half of the night and energy-saving torpor becomes part of their daily routine. In contrast, it appears that the larger kowaries are less affected by cold winter nights and can maintain high night-time activity levels and commence reproduction already in winter. Hence, they enter torpor only occasionally and only during the rest phase.

Introduction

Generally, in animals, energy turnover and metabolic rate scale with body mass. In addition, in endothermic species that maintain body temperatures (T_b) above ambient (T_a), such as mammals and birds, heat loss and therefore thermoregulatory costs are also affected by body size. Smaller animals with limited body energy stores and a larger surface to volume ratio lose heat faster than larger species and therefore are burdened with not only higher basal metabolic rates (BMR) but also higher energy demands for thermoregulation. Although as a consequence the energy turnover and food requirements of endotherms are by an order of magnitude higher than that of similar-sized ectotherms (Else & Hulbert, 1981), the functional advantages of a constant high T_b irrespective of T_a are obvious nevertheless, as it allowed endotherms to colonize cold habitats and to remain active during the nadir of the annual and/or the daily T_a cycle.

While this also applies to many desert environments with often frigid winter nights, the high energy turnover and hence food intake can hardly be seen as a favourable trait in a generally resource-poor environment. Despite this

apparent energetic burden, the diversity of mammals in deserts can be high. In Australia, a range of insectivorous marsupials of the Family Dasyuridae (Dickman, 2003) have managed to reduce energy demands sufficiently to survive in these seemingly inhospitable areas (Körtner, Pavey & Geiser, 2007). One energy-saving mechanism is the lower BMR of desert mammals in comparison with their mesic counterparts (Lovegrove, 2003; Withers, Cooper & Larcombe, 2006). Furthermore, many small desert mammals can achieve far greater energy savings by entering daily torpor, a temporary controlled reduction of T_b and metabolic rate (Godfrey, 1968; Geiser, 2004). While laboratory data suggest that many functional variables such as minimum T_b , torpor bout length as well as metabolic rate of daily heterotherms scale with body mass (Geiser & Ruf, 1995), the implications for free-ranging animals in their natural environment remain to be tested. To date, only a few small- to medium-sized marsupials (7–80 g) have been studied in the wild in some detail (Geiser, Goodship & Pavey, 2002; Körtner, Pavey & Geiser, 2008; Warnecke, Turner & Geiser, 2008; Körtner & Geiser, 2009; Warnecke & Geiser, 2009). While all of these species use daily torpor regularly, it does

appear that torpor might be less frequent for the larger species presumably because of better insulation and earlier commencement of reproduction. However, the observed differences might also be a result of the vastly different habitats in which these studies were conducted.

To gain a better understanding of how body size affects the energetics of wild dasyurid marsupials, we simultaneously monitored the activity and torpor patterns of two different-sized species via radio-telemetry at the same site. Both insectivorous/carnivorous species occur on the vast gibber and Mitchell grass plains of central Australia. The kowari *Dasyuroides byrnei* (~110 g) represents the upper size range of desert dasyurids. In contrast, the stripe-faced dunnart *Sminthopsis macroura* (17 g) is close to the smallest body size that can be monitored with currently available radio-transmitters.

Methods

The study was conducted in Astrebla Downs National Park, south-western Queensland (24°10'S, 140°34'E, ~120 m a.s.l.), during the Austral winter (June–August 2007). Annual rainfall measured at the two closest weather stations is on average 223 mm (Boullia, Bedourie ~150 km from study site, Australian Bureau of Meteorology). Plains of cracking clay soils supporting ephemeral Mitchell grass (*Astrebla* spp.) are interspersed with gibber (ironstone pebbles), a substrate that is virtually devoid of vegetation. During the time of the study, above-ground vegetation was restricted to some of the larger drainage lines and most of the Mitchell grass plains were reduced to bare ground. Strong winds prevailed on most days.

Nine established pitfall lines were used to trap dunnarts. Each line consisted of six vertically buried storm-water pipes (depth 60 cm, diameter 15 cm) spaced at 4–5 m that were linked with a fine wire-mesh drift fence. The distance between pitfall lines was at least 1 km. In addition, up to 36 box aluminium traps (Type A; Elliott Scientific Equipment, Upwey, Vic., Australia) baited with peanut butter and rolled oats were set along some of the vehicle tracks at locations where kowari tracks were seen regularly.

Core T_b was measured in eight dunnarts (6M:2F) and six kowaries (4M:2F) that were implanted intraperitoneally with disinfected temperature-sensitive radio-transmitters (1.9–3.7 g; Sirtrack, Havelock, New Zealand) under general oxygen/isoflurane anaesthesia. The heavier transmitters contained a larger loop antenna (increased range) and a higher capacity battery and were used for the kowaries. Before implantation, all transmitters were coated with inert wax and then calibrated over a temperature range of 9–40 °C to the nearest 0.1 °C against a mercury thermometer traceable to a national standard. The surgical incision was closed using Chromic Gut (2.0 metric, Ethicon Inc., Sommerville, NJ, USA) for the muscle layer and also for the skin in dunnarts. For kowaries, coated Vicryl (3.0 metric, Ethicon Inc.) was used for the skin. Afterwards, a topical anaesthetic (Ban Itch, Apex Laboratories Pty Ltd, Sommerby, NSW, Australia) and Leuko Spray Bandage [BSN medical (Aust) Pty Ltd, Clayton, Vic., Australia] was applied. After

surgery, animals were given liquid Children's Panadol (Ermington, NSW, Australia), and were held for the following night and day while being provided with kangaroo mince *ad libitum* supplemented with freshly caught locusts.

Two separate field trips were conducted (1–30 June 2007 and 11 July–15 August 2007). Tagged individuals were radio-tracked to their burrows daily in the early morning. Burrow locations were marked and recorded with a handheld GPS (Garmin Inc., Olathe, KS, USA). A mobile data logging system measuring the interval between two transmitter pulses every 10 min was placed close to the burrow of each animal (Körtner & Geiser, 1998). Data were downloaded to a laptop computer after several days. Interval data were log-transformed and then converted to T_b values using a second-order polynomial equation based on the calibration of the transmitter. Activity outside the burrow was inferred from the absence of interval data from the logger trace. Torpor entry and arousal were defined by T_b declining below and rising above 30 °C, respectively, and torpor bout length was calculated from the time that T_b remained below 30 °C (Körtner & Geiser, 2000). Alternative statistical methods to determine the torpor threshold were not explored because the recording technique did not allow continued sampling of T_b over 24 h. The rate of rewarming during arousal was averaged over the time period from the start of the arousal process to when a maximum T_b had been reached (usually above 30 °C). In addition, the maximal arousal rate was defined as the maximal temperature increase over a 10-min interval (i.e. between two logger readings).

Ambient temperature profiles were measured using miniature data loggers at 30- or 40-min intervals (Thermochron and Hydrochron with 0.5 and 0.06 °C temperature resolution, respectively, humidity 0.04% Hydrochron only; i-Buttons, Maxim Integrated Products, Sunnyvale, CA, USA) at various locations throughout the study area. Air temperature (T_{air}) and relative humidity (RH) were measured in the shade ~1 m above ground, clay surface temperature (T_{surf}) was recorded at two locations and soil temperature (T_{soil}) at 5, 10, 20 and 40 cm depths at two sites in June/July and another two sites in July/August. In addition, the temperature and humidity in two relatively large soil cracks were measured at a depth of approximately 30 cm (T_{crack}).

The effect of T_{air} on activity and torpor was assessed using linear mixed-effects models accounting for the repeated measures design (R 2.10.1, R Development Core Team, 2009). All other statistical tests were conducted in MINITAB V13.1 (Minitab Inc., State College, PA, USA). Significance was assumed at a 5% level. Data are presented as the mean of the mean of individuals ± 1 SD and 'n' denotes the number of individuals and 'N' the number of measurements.

Results

Weather, T_a , thermal diffusivity of soil and humidity

Fine weather prevailed through most of the study. Nevertheless, a slight drizzle occurred on 17–18 June, but the

overall precipitation remained <1 mm. The T_{air} started to increase from the second half of July and hence the daily average T_{air} was somewhat lower during the first survey (12.2 ± 2.2 °C) than during the second one (15.9 ± 4.1 °C). Daily fluctuations in T_{air} were pronounced (18.6 ± 4.0 °C), but those in T_{surf} were 35.3 ± 7.9 °C, twice as high (Fig. 1). The average T_{soil} was 15.2 ± 3.7 °C. The amplitude of temperature fluctuations of the two measured soil cracks (7.5 ± 3.7 and 4.7 ± 2.4 °C, respectively) was, as expected, buffered by the surrounding soil, but the daily average was 14.2 ± 0.1 °C ($n = 2$), similar to that of T_{air} . The daily average T_{soil} was 18.9 ± 0.9 °C ($n = 4$) for all depths. Hence, the average daily T_{soil} s were above those of T_{air} , T_{surf} and also T_{crack} . In addition, the insulation of the soil attenuated daily fluctuations at the soil surface by more than 70 and 90% at depths of 10 and 20 cm, respectively (Fig. 1).

Being partly a function of T_{air} , daily fluctuations in RH of air were also pronounced and fluctuated on average between $64.6 \pm 15.7\%$ during the cool nights and $24.3 \pm 8.5\%$ on warm days (1 June–15 August). These daily variations were reduced to an amplitude of $9.8 \pm 0.8\%$ ($n = 2$) in the two soil cracks measured. However, apart from this mainly temperature-related effect, the soil cracks did not appear to retain moisture as the average daily RH was the same in air ($43.2 \pm 11.2\%$) and soil cracks (43.5 ± 5.5 and $43.8 \pm 6.8\%$, respectively).

Body mass

Male (16.6 ± 1.7 g, $n = 7$) and female (16.6 ± 1.2 g, $n = 2$) stripe-faced dunnarts were of a similar size ($T_2 = 0.01$, $P = 1.0$), and the average body mass of captured adults was 16.6 ± 1.5 g ($n = 9$). Kowaries were substantially larger and males (117.6 ± 11.6 g, $n = 6$) were on average heavier than females (93.2 ± 10.3 g, $n = 4$, $T_7 = 3.5$, $P = 0.01$).

The relative transmitter mass ranged from 11% for the dunnarts to 3% for male kowaries.

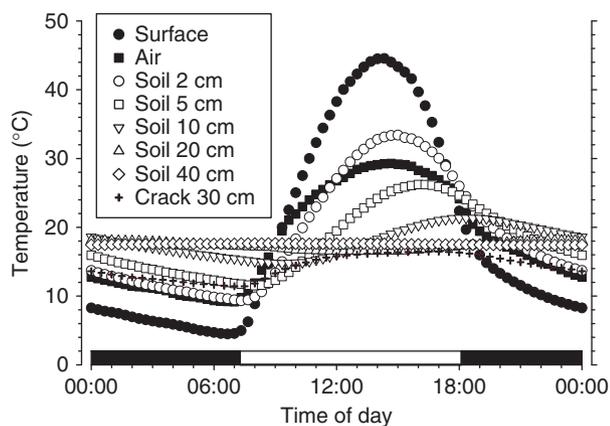


Figure 1 Average temperature profiles for air temperature (measured in the shade), surface temperature, soil temperature at various depth and temperature in soil cracks. Profiles for the two cracks measured were similar and an average of the two sites is illustrated. The dark bars at the bottom of the graph depict the scotophase.

Activity

Both species were strictly nocturnal and started their activity shortly after sunset (Fig. 2). The final T_b measurement before animals ventured out of range of the data logger, presumably to forage, was similar for both species (dunnart: 37.6 ± 0.6 °C, $n = 8$; kowari: 37.4 ± 0.5 °C, $n = 6$). The end of the activity phase was considerably more variable and differed among species and sexes. Activity in dunnarts was usually much shorter than the scotophase and they were active predominantly during the first, warmer part of the night. Moreover, dunnarts remained inactive on 26 out of 209 observation nights and one female remained inactive for 5 consecutive nights. On average, female dunnarts returned to their burrows first (10.1 ± 0.7 h before sunrise, $n = 2$), significantly earlier than males (7.3 ± 1.5 h before sunrise, $n = 6$, $T_4 = 3.44$, $P = 0.026$). Kowaries remained active considerably longer than dunnarts ($T_{11} = 7.6$, $P < 0.001$). Similar to dunnarts, female kowaries terminated activity earlier (3.4 ± 0.4 h before sunrise, $n = 2$) than males, which remained active until dawn (1.5 ± 0.5 h before sunrise, $n = 4$, $T_2 = 5.2$, $P = 0.036$).

Furthermore, the timing of the end of the activity period for male dunnarts and kowaries was influenced by the minimum T_a of the night (Fig. 3). Male dunnarts returned to their burrows earlier on cold nights [end of activity (hours

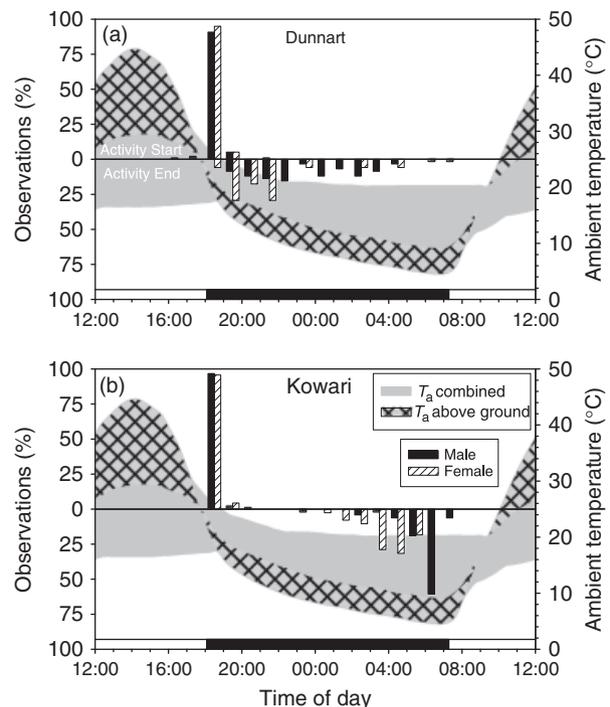


Figure 2 Timing of activity in male and female dunnarts (a) and kowaries (b). Observation scores for the start of the activity period are shown as positive bars and the end of the activity period as negative bars. The temperature envelope available to animals (range of temperatures in the environment as shown in Fig. 1) is depicted as a greyed area. The temperature profile above ground is hatched. The scotophase is represented as a dark bar at the bottom of the plots.

to sunrise) = $-0.53 T_{\text{air minimum}} (^{\circ}\text{C}) + 10.97$, $P < 0.001$], whereas the activity phase of females remained short irrespective of night T_{air} ($P = 0.167$). Similar patterns were observed for male [end of activity (hours to sunrise) = $-0.10 T_{\text{air minimum}} (^{\circ}\text{C}) + 2.07$, $P = 0.05$] and female kowaries [end of activity (hours to sunrise) = $-0.14 T_{\text{air minimum}} (^{\circ}\text{C}) + 4.46$, $P = 0.007$] but females returned to their burrows significantly earlier (intercept: $F_{1,79} = 118.6$, $P < 0.001$; slope: $F_{1,79} = 0.2$, $P = 0.63$).

For both species, the T_b at the time when animals returned to their burrows differed from the start of the activity phase. The T_b of dunnarts was on average lower at the end of the activity phase ($36.3 \pm 0.6^{\circ}\text{C}$, $n = 8$) compared with the beginning (37.6 ± 0.6 , paired t -test: $T = 4$, $P = 0.005$), whereas kowaries returned with a higher T_b (end: $38.4 \pm 0.4^{\circ}\text{C}$, beginning: 37.4 ± 0.5 , $n = 6$, paired t -test: $T = 6.5$, $P = 0.001$).

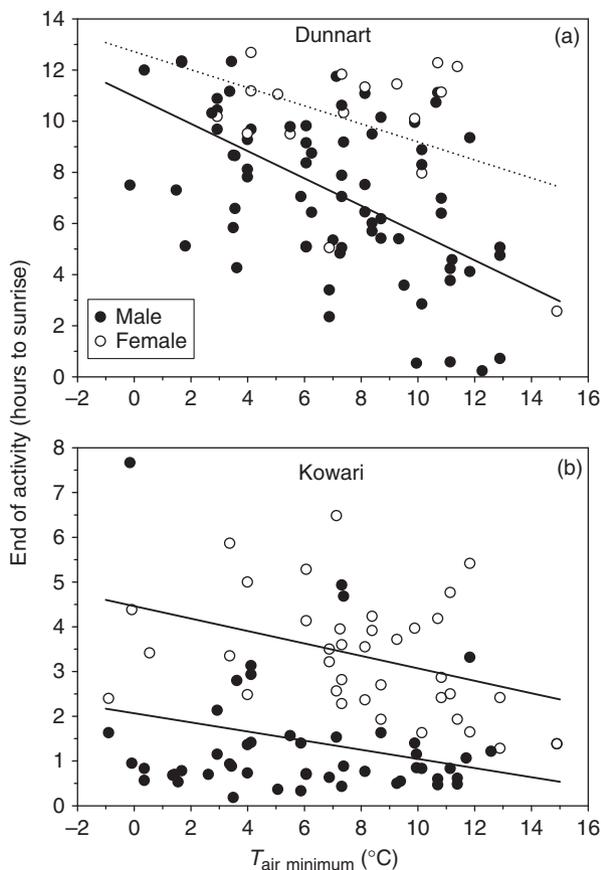


Figure 3 End of the nightly activity period (expressed as hours to sunrise) as a function of the $T_{\text{air minimum}}$ of that night in dunnarts (a) and kowaries (b). Significant relationships are shown as solid lines and non-significant regressions as dotted lines. Male dunnarts: end of activity (hours to sunrise) = $-0.53 T_{\text{air minimum}} (^{\circ}\text{C}) + 10.97$, $P < 0.001$; male kowaries: end of activity (hours to sunrise) = $-0.10 T_{\text{air minimum}} (^{\circ}\text{C}) + 2.07$, $P = 0.05$; female kowaries: end of activity (hours to sunrise) = $-0.14 T_{\text{air minimum}} (^{\circ}\text{C}) + 4.46$, $P = 0.007$.

Torpor

Daily torpor was observed in both species, but only dunnarts used torpor as part of their daily routine. Torpor frequency for dunnarts was $99.1 \pm 2.5\%$ (mean of the eight individuals), whereas only three out of the six radio-tagged kowaries (1M:2F) used torpor, and even for these three torpor frequencies were considerably lower than those for dunnarts ($37.0 \pm 18.7\%$, $n = 3$, $N = 72$; $T_2 = 5.7$, $P = 0.029$). The average for all six kowaries torpor frequency was only $18.5 \pm 23.5\%$ ($n = 6$, $N = 139$). One of the female kowaries, which had entered torpor on five of the first 8 monitoring days, maintained a stable high T_b throughout the remaining 23 days of the measurement when she was re-captured carrying six pouch young of a body length of ~ 0.7 cm. Therefore, this individual entered torpor while pregnant, but not after parturition.

Torpor was expressed predominantly during the cooler second part of the night and early morning (Fig. 4). Four of the eight dunnarts but none of the kowaries occasionally entered a second shorter torpor bout in the late afternoon with an arousal around sunset, shortly before the onset of the activity phase. These torpor bouts did not exceed 2.5 h in length, whereas the overall maximal torpor bout length for individual dunnarts was 15.9 ± 5.9 h ($n = 8$), with an absolute maximum of 25.9 h. The maximal torpor bout length observed in kowaries was only 3.9 ± 0.6 h ($n = 3$) and the absolute maximum was 4.4 h. Consequently, torpor in kowaries was much shorter than in dunnarts ($T_1 = 15.6$, $P < 0.001$) and no gender differences were apparent.

With a single exception, kowaries entered torpor after sunrise during their rest phase (2.2 ± 1.0 h after sunrise, $n = 3$). Torpor entry in dunnarts was more variable and on average occurred earlier, usually during the night (6.7 ± 3.9 h before sunrise, $n = 8$). For both sexes, the timing of torpor entry was a function of T_{air} , with entries occurring earlier on cold nights, with sex being a significant factor ($P = 0.011$) [male: time of entry (hours to sunrise) = $-0.57 T_{\text{air minimum}} (^{\circ}\text{C}) + 8.77$, $P < 0.001$; female: time of entry (hours to sunrise) = $-0.34 T_{\text{air minimum}} (^{\circ}\text{C}) + 13.99$, $P < 0.001$; Fig. 5]. The intercept differed significantly between the regressions ($F_{1,106} = 70.1$, $P < 0.001$) but not the slope ($F_{1,106} = 1.8$, $P = 0.183$). Similar gender differences and T_{air} effects were not detectable in kowaries (Fig. 5).

Arousal timing for night/morning torpor was more uniform than torpor entry and similar for both species (4.2 ± 1.0 h after sunrise for both species), with arousal usually occurring in the late morning, coinciding with the rapid increase in T_a (Fig. 4). However, in dunnarts, arousal occurred significantly earlier on warm days, while on average, females remained torpid longer (male: time of arousal (hours after sunset) = $-0.14 T_{\text{air maximum}} (^{\circ}\text{C}) + 7.38$, $P < 0.001$; female: time of arousal ([hours after sunset) = $-0.14 T_{\text{air maximum}} (^{\circ}\text{C}) + 9.06$, $P < 0.001$; Fig. 6]. The intercept of the regression lines differed significantly ($F_{1,196} = 2159$, $P < 0.001$) but not the slope ($F_{1,196} = 0$, $P = 0.98$). In contrast, arousal timing of kowaries was apparently not influenced by T_{air} (Fig. 6). Both

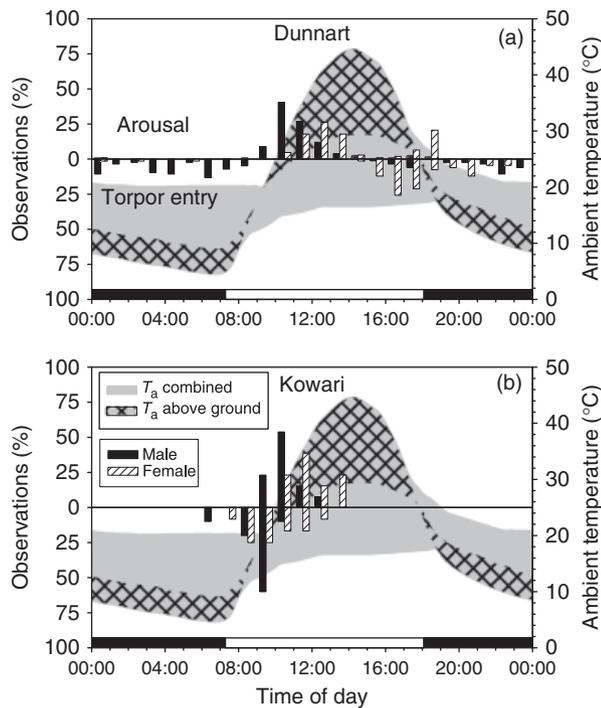


Figure 4 Timing of daily torpor in male and female dunnarts (a) and kowaries (b). Observation scores for arousals are shown as positive bars and torpor entry as negative bars. The temperature envelope available to animals (range of temperatures in the environment as shown in Fig. 1) is depicted as a greyed area. The temperature profile above ground is hatched. The scotophase is represented as a dark bar at the bottom of the plots.

normothermic kowaries and torpid dunnarts ($T_b = 19.3^\circ\text{C}$) were seen to venture to the surface in the morning.

The minimum T_b during torpor was a function of torpor bout length (Fig. 7). Reflecting the progressive cooling during torpor entry, this relationship was described for both species by a function for exponential decay [dunnart: $T_{b \text{ minimum}} (^\circ\text{C}) = 15.01 + 15.04e^{-0.21 \text{ bout length[h]}}$, $R^2 = 0.88$, $P < 0.001$; kowari: $T_{b \text{ minimum}} (^\circ\text{C}) = 25.52 + 4.79e^{-0.47 \text{ bout length[h]}}$, $R^2 = 0.84$, $P < 0.001$], whereby the first term in the equations gives the asymptotic value of the T_b minimum, the sum of the two first terms equals the initial conditions (i.e. close to the torpor threshold of 30°C) and the third exponential term describes the steepness of the curve. Although torpor in female dunnarts was longer, the T_b minimum did not differ between the sexes ($T_1 = 0.1$, $P = 0.961$) and was on average $18.6 \pm 1.6^\circ\text{C}$ ($n = 8$, $N = 232$), with individually recorded minima of $12.3 \pm 2.2^\circ\text{C}$ ($n = 8$); the lowest recorded T_b was 11.3°C . Torpid kowaries remained significantly warmer ($27.5 \pm 0.9^\circ\text{C}$, $n = 3$, $N = 25$, $T_6 = 12.2$, $P < 0.001$); individually recorded minimal values were $25.9 \pm 0.5^\circ\text{C}$ ($n = 3$) and the lowest T_b recorded was 25.4°C . However, the relatively short bouts of kowaries meant that cooling was still in progress when arousal was initiated. Hence, the T_b minima did not represent steady-state torpor.

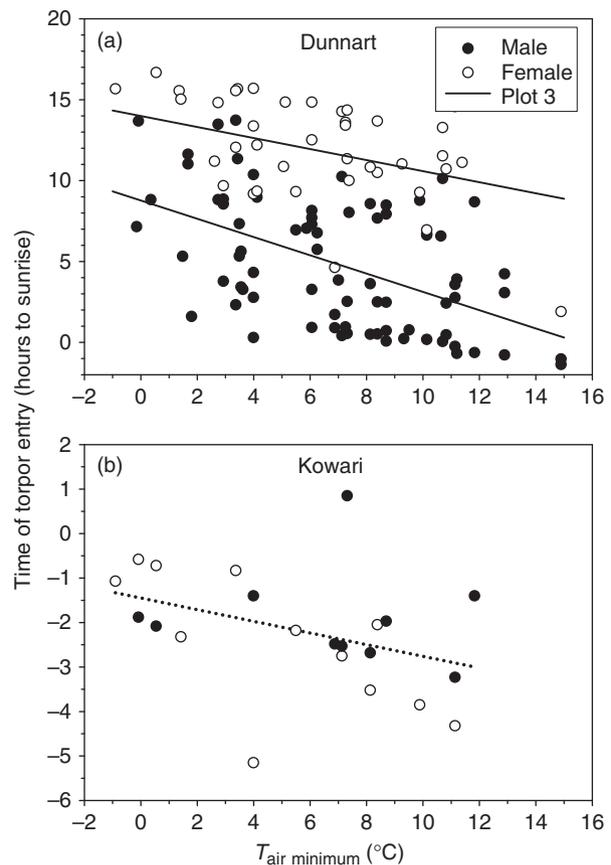


Figure 5 Time of torpor entry (expressed as hours to sunrise) as a function of the $T_{\text{air minimum}}$ in dunnarts (a) and kowaries (b). For dunnarts, the occasional second torpor bouts in the afternoon have been excluded. Significant relationships are shown as solid lines and non-significant regressions as dotted lines. Male dunnarts: time of entry (hours to sunrise) = $-0.57 T_{\text{air minimum}} (^\circ\text{C}) + 8.77$, $P < 0.001$; female dunnarts: time of entry (hours to sunrise) = $-0.34 T_{\text{air minimum}} (^\circ\text{C}) + 13.99$, $P < 0.001$.

Although there was a trend for the larger species to rewarm more slowly, differences in the average rewarming rate during arousal (dunnart: $0.15 \pm 0.03^\circ\text{C min}^{-1}$, $n = 8$; kowari: $0.11 \pm 0.03^\circ\text{C min}^{-1}$, $n = 3$; $T_4 = 1.7$, $P = 0.016$) as well as the maximal arousal rate over a 10-min interval (dunnart: $0.30 \pm 0.04^\circ\text{C min}^{-1}$, $n = 8$; kowari: $0.19 \pm 0.05^\circ\text{C min}^{-1}$, $n = 3$; $T_4 = 3.6$, $P = 0.071$) were not significant.

Discussion

Our study provides the first comparative field data for two differently sized, sympatric marsupial mammals on activity, thermal biology and torpor use, key components of an animal's energy turnover and essential criteria for survival in a resource-poor environment. Despite being exposed to the same environmental conditions, the thermoregulatory and behavioural response differed markedly between the species. Many of these differences appeared to be directly or

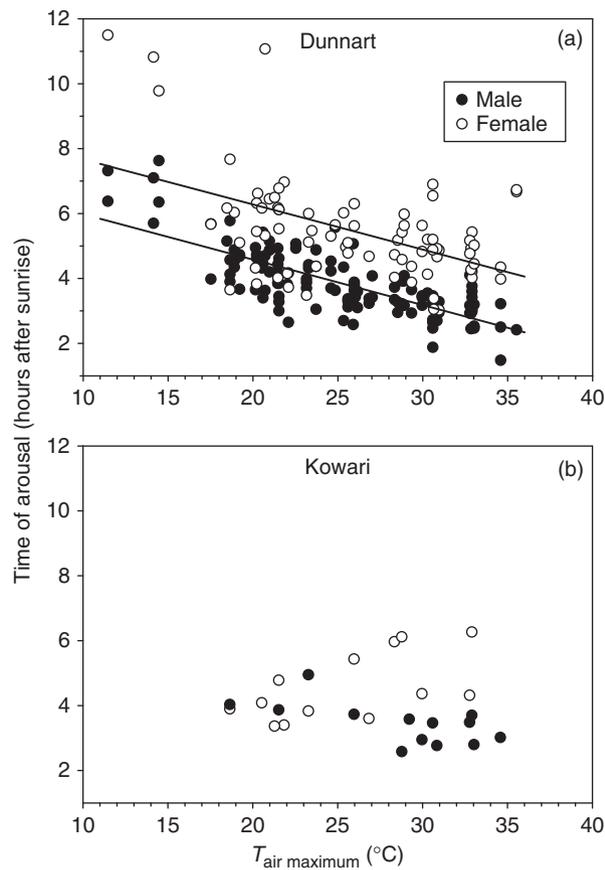


Figure 6 Time of arousal from torpor (expressed as hours after sunrise) as a function of the $T_{air\ minimum}$ in dunnarts (a) and kowaries (b). For dunnarts, the occasional second torpor bouts in the afternoon have been excluded. Significant relationships are shown as solid lines. Male dunnarts: time of arousal (hours after sunset) = $-0.14 T_{air\ maximum}$ ($^{\circ}C$) + 7.38, $P < 0.001$; female dunnarts: time of arousal (hours after sunset) = $-0.14 T_{air\ maximum}$ ($^{\circ}C$) + 9.06, $P < 0.001$.

indirectly linked to body mass, but the sexual dimorphism in activity and torpor seen in both species was not necessarily related to body size. Furthermore, it appears unlikely that the disparity in relative transmitter mass would have contributed significantly to the differences observed between species and gender, because (1) muscle strength is related to the cross section area and hence geometrically scales to body mass^{2/3} (Calder, 1996); (2) it has been shown that in dunnarts transmitter mass up to 14% does not impair running performance (Rojas, Körtner & Geiser, 2010) and even heavy radio-collars do not increase the daily energy expenditure in small rodents (Berteaux *et al.*, 1996); (3) activity and torpor expression differed between similar-sized male and female dunnarts with equal transmitter mass.

Like most small mammals, the kowaries and dunnarts were strictly nocturnal, which likely offers protection from diurnal avian predators (i.e. raptors and corvids). However, activity at night also entailed high thermoregulatory costs because T_{air} began to decline rapidly after sunset facilitated by usually cloudless skies and sparse vegetation cover.

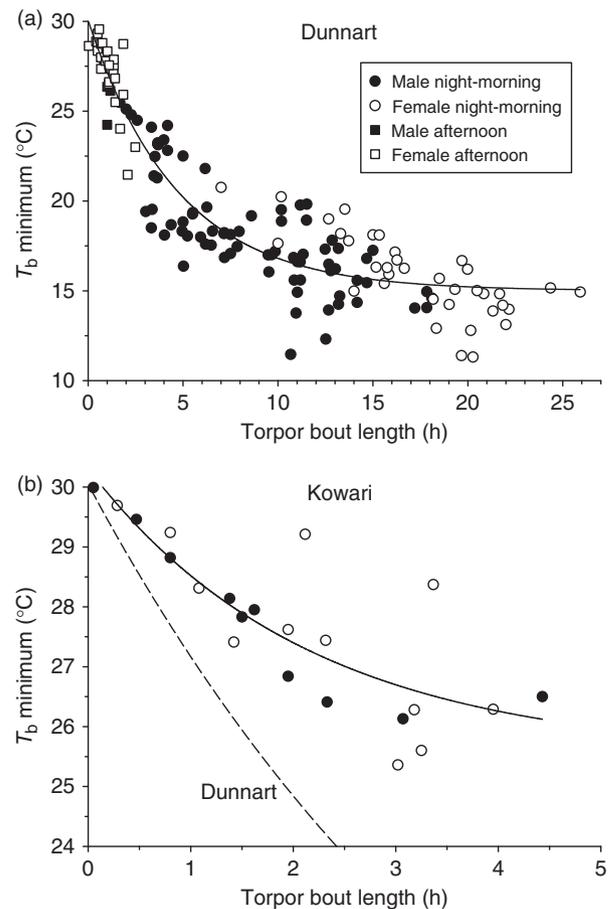


Figure 7 $T_b\ minimum$ as a function of torpor bout length in dunnarts (a) and kowaries (b). In both species, a function of exponential decay describes this relationship (dunnart: $T_b\ minimum$ ($^{\circ}C$) = $15.01 + 15.04e^{-0.21\ bout\ length[h]}$, $R^2 = 0.88$, $P < 0.001$; kowari: $T_b\ minimum$ ($^{\circ}C$) = $25.52 + 4.79e^{-0.47\ bout\ length[h]}$, $R^2 = 0.84$, $P < 0.001$). The first term of the equation gives the asymptotic minimum of cooling and the exponent describes the steepness of the curve – the speed of cooling. For comparison, the curve for dunnarts is also depicted in graph (b) as a dashed line.

Smaller species such as dunnarts lose body heat faster and are inherently more affected by temperature extremes. For example, even at a moderate $10^{\circ}C$, the resting MR of dunnarts is about $5 \times BMR$, whereas the increase in MR of the larger kowaries at the same T_a is $< 2 \times BMR$ (Geiser & Baudinette, 1987). It was probably this body size effect that enticed the dunnarts to retreat into their burrows after only a few hours of activity, whereas kowaries remained active through most of the night. Likely because T_{soil} s during winter were also below thermoneutrality, dunnarts usually entered torpor shortly after activity ceased. It is conceivable that food/insect availability also declined overnight with the decrease in T_a (e.g. Holm & Edney, 1973), making foraging uneconomical, but the much longer activity phase of kowaries seems to indicate that food in the form of invertebrates and possibly some vertebrates was still obtainable. It therefore appears likely that the short activity and early torpor

onset in dunnarts was more a direct result of increased thermoregulatory costs rather than diminished food availability.

The shorter activity periods of female kowaries on cold nights might have also been partly caused by the smaller body size of females. However, kowaries also commenced reproduction in winter and prolonged activity in males could have been related to mating effort as has been suggested for the closely related brush-tailed mulgara *Dasyercus blythi* (Körtner *et al.*, 2008). Furthermore, as in mulgaras, reproduction also influenced thermoregulation in females. While pregnant female kowaries entered torpor (gestation 30–36 days; Woolley, 1971; Meißner & Gansloßer, 1985), during lactation, they maintained high normothermic T_b 's throughout. In dunnarts, the activity was also shorter in females than in males, but in this species, sexes were similar sized. Reproduction might have played a role and the only case of a dunnart not entering torpor occurred in early June in a male on a night when we trapped a female close to his burrow sites. Unfortunately, however, the reproductive status of dunnarts in late winter remained unresolved because we were neither able to trap any females in August nor was it possible to infer reproduction from T_b traces. Pregnant dunnarts can enter torpor (Geiser, McAllan & Brigham, 2005) like kowaries and mulgaras, but the thermoregulatory behaviour of females with pouch young is unknown.

Underground burrows and soil cracks provide some relief from temperature extremes but, during winter, were still cold enough to require thermoregulatory heat production in either species. However, if an animal enters torpor, these cool T_a 's can become an advantage as lower T_b 's and hence lower MRs can be achieved (Song, Körtner & Geiser, 1995). In this respect, energy savings were also much greater in dunnarts than in kowaries, as torpor was not only longer but also deeper. In fact, dunnarts regularly cooled below the average T_{soil} , a feat that can either be achieved by remaining close to the surface, where daily temperature fluctuations are still pronounced, or using soil cracks that were well ventilated cooling further than the surrounding soil. In contrast, the T_b of kowaries always remained above the average T_{soil} , but torpor bouts were too short to have reached steady-state conditions. In general, these differences in the minimum T_b between the two species were consistent with allometric predictions for daily heterotherms [$T_b = 5.57 + 8.49 \log_{10}(\text{BM})$; Geiser & Ruf, 1995]. However, qualitatively dunnarts reached consistently lower T_b 's than predicted from allometry (dunnart 16.6 g: $T_{b \text{ minimum field}} 12.3 \pm 2.2^\circ\text{C}$, predicted 15.9°C ; Geiser & Ruf, 1995) or recorded in the laboratory (14.0°C ; Geiser & Baudinette, 1987), whereas kowaries maintained T_b qualitatively above the allometric prediction (kowari 109 g: $T_{b \text{ minimum field}} 27.6 \pm 1.3^\circ\text{C}$, predicted 22.8°C ; Geiser & Ruf, 1995) as well as above laboratory measurements (20.4°C , Geiser & Baudinette, 1987).

After the cool mornings, T_{surf} and T_{air} increased rapidly with the rising sun and with some delay at shallow depth T_{soil} also increased. Accordingly, in both kowaries and

dunnarts, arousal from torpor was usually completed by midday. Thus, in comparison with laboratory observations, slow warming rates might have been a result of partly passive rewarming process (Geiser & Baudinette, 1990) ameliorating arousal costs. However, significant saving by passive rewarming can be made only at very shallow depths or preferably by seeking direct exposure to solar radiation (Warnecke & Geiser, 2010). Apparently, dunnarts, similar to some other small dasyurids, were mobile enough when torpid to venture to the surface (Geiser *et al.*, 2002; Warnecke *et al.*, 2008; Körtner & Geiser, 2009) and they also aroused earlier on warm days. In contrast, in kowaries, arousal timing was not affected by T_{air} , possibly because kowaries, which most often used old bilby burrows (G. Körtner, A. Trachtenberg, F. Geiser, unpubl. data) that can be quite deep, were not exposed to daily temperature fluctuations to the same extent as dunnarts. However, it is more difficult to explain why female dunnarts remained torpid for longer than males. Either the two females ventured consistently deeper underground or their temperature threshold for triggering arousal was higher.

As kowaries and on most days also dunnarts spend the afternoon normothermic, residing at a shallow depth or on the surface has energetic advantages beyond reducing arousal costs. Unfortunately, we were only able to observe but not quantify basking in either species, because animals were cryptic and extremely wary of observers. Nevertheless, basking did occur and similar observations have been made recently in three other small desert dasyurids (Geiser *et al.*, 2002; Warnecke *et al.*, 2008; Warnecke & Geiser, 2009) and it is therefore likely to be a common behaviour for dasyurids in arid environments.

Conclusion

Despite cold nights and reduced insect availability during winter (Holm & Edney, 1973), it appears that only smaller dasyurids such as planigales, fat-tailed and stripe-faced dunnarts regularly use daily torpor as one of the most effective energy-saving mechanisms available to mammals (Warnecke *et al.*, 2008; Warnecke & Geiser, 2009; present data). All of these forage only for a relatively short period every night, spend most of the night including the early morning and some afternoons in torpor and use torpor almost every day. Medium-sized desert dasyurids such as mulgaras and fat-tailed pseudantechinus *Pseudantechinus macdonnellensis* show intermediate torpor patterns verging towards frequent and deep torpor (Geiser & Pavey, 2007; Körtner *et al.*, 2008). The largest desert dasyurids, the kowaries, appear to sustain activity through most of the cold nights, resort to short torpor only occasionally and also commence reproduction. Hence, field data obtained in winter seem to support allometric predictions from the laboratory (Geiser & Ruf, 1995). However, most likely, not only the direct effects of body size on heat loss but also the consequences it has on the rate of juvenile development, and hence the timing of reproduction, seem to shape the patterns of activity and thermal biology in desert dasyurids.

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