



Activity patterns and torpor in two free-ranging carnivorous marsupials in arid Australia in relation to precipitation, reproduction, and ground cover

GERHARD KÖRTNER,* ALEXANDER RIEK, CHRIS R. PAVEY, AND FRITZ GEISER

Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Trevenna Rd., Armidale, New South Wales 2351, Australia (GK, AR, FG)

Department of Animal Sciences, University of Göttingen, Albrecht-Thaer-Weg 3, 37075 Göttingen, Germany (AR)

Biodiversity Conservation, Department of Natural Resources, Environment and the Arts, P.O. Box 2130, Alice Springs, Northern Territory 0871, Australia (GK, CRP)

CSIRO Land and Water, P.O. Box 2111, Alice Springs, Northern Territory 0871, Australia (CRP)

* Correspondent: gkoertne@une.edu.au

It is generally assumed that in unpredictable environments, the use of daily torpor and its interaction with daily activity are largely dependent on environmental thermal conditions and resource availability. Using temperature telemetry, we compared the thermal biology and activity patterns of 2 species of mulgaras (*Dasyercus blythi* and *D. cristicauda*) at 3 sites of different habitat types in central Australia. The work compared a dry period with a wet period (resource pulse). The most obvious functional difference among populations was observed in the timing of the onset of activity, which began significantly earlier in dense unburned spinifex (on average 17.7 min before sunset) than in burned spinifex (4.6 min after sunset) or on gibber plains (21.8 min after sunset). However, although the seasonal expression of torpor differed significantly between males and females, torpor use as well as seasonal timing was similar among sites and periods despite differences in rainfall and habitat. It appears that predominantly reproductive activity governed torpor depth and duration in all measured populations and both species. Our data suggest that while the timing of activity is modulated by the amount of vegetation cover and thus protection from diurnal predators, torpor expression and winter reproduction in mulgaras are functionally linked and surprisingly more or less independent of apparent resource availability. Consequently, in mulgaras, daily torpor does not seem to be employed in response to immediate energy shortage but more likely to allow reallocation of energy and nutrients towards reproduction.

Key words: activity, climate, desert, marsupial, rain, reproduction, torpor

Deserts are characterized by low, unpredictable resource availability and extreme temperature fluctuations. The arid zone of northern Australia (north of 27° south) has among the most unpredictable rainfall of anywhere across the globe (Van Etten 2009). This unpredictability results in cycles of resource availability driven by pulses in primary productivity that follow large rain events. While terrestrial small mammals can avoid temperature extremes in underground burrows (Merritt 2010), their intrinsic high energy turnover associated with endothermy remains problematic in a resource-poor environment. This is especially challenging if food is ephemeral and cannot be hoarded as is the case for insectivorous species. In the Australian arid zone, the mammalian insectivore niche is occupied by

marsupials of the family Dasyuridae—a diverse group of very small- to medium-sized mammals (< 250 g body mass [BM]). Many members of this group, including some of the larger species, use daily torpor (Cooper and Withers 2010; Geiser and Körtner 2010), a controlled reduction of body temperature (T_b), metabolic rate, and water loss (Ruf and Geiser 2015). Daily torpor is a highly efficient energy balancing mechanism and while it is often employed on a daily basis, torpor use and activity are inversely correlated (Ruf et al. 1991). Furthermore, because of continued foraging, energy stores in the form of body fat or food caches are not essential and therefore daily torpor, unlike classical hibernation, can be employed flexibly in response to the prevailing environmental conditions. Daily torpor is therefore

ideally suited to overcome short-term weather-related food shortage as well as interannual variations in resource availability provided that a minimum of food remains accessible. Not surprisingly, daily heterotherms are commonly found in areas with unpredictable climates, such as deserts including those in northern Australia (Lovegrove 2000).

Under laboratory conditions, food restriction and low ambient temperatures (T_a) increase torpor use in most daily heterotherms (Ruf et al. 1991; Song et al. 1995), but long-term field studies investigating how under natural conditions the expression of daily torpor changes with habitat, food availability, and/or between years are scant. In 2010/2011, most of Australia including the arid zone received exceptionally high rainfall (Wardle et al. 2013). Rivers started to flow and flood, ephemeral inland lakes filled, and generally the desert flora and fauna boomed. Our study on desert dasyurids was conducted during such a resource pulse. We chose the brush-tailed mulgara (*Dasyercus blythi*, ~70 g), because baseline torpor data were available from both the laboratory (Schmidt-Nielsen and Newsome 1962; Kennedy and MacFarlane 1971; Geiser and Masters 1994) and an extensive field study conducted in a year with average rainfall (Körtner et al. 2007, 2008; Pavey et al. 2009). Under these average conditions, torpor use in *D. blythi* was extensive and interestingly, torpor use and reproduction appeared to be closely linked and in this as in many other mammalian species, these 2 processes were not mutually exclusive (McAllan and Geiser 2014). As such, male *D. blythi* entered torpor predominantly after the mating season and females during mating and gestation until parturition. The rainfall-related resource flush therefore provided an opportunity to investigate in the field whether torpor use is modified by resource availability or is a conservatively expressed seasonal phenomenon.

The chosen study area at Andado Station is unusual because it is also inhabited by a 2nd closely related species, the crest-tailed mulgara (*D. cristicauda*), that occupies a different habitat type (Pavey et al. 2012). *D. cristicauda* weighs about 100 g and therefore ranks among the largest extant desert dasyurids (Woolley 2005). Both species are relatively rare, but occur over wide, patchy geographical ranges (Woolley 2005). Any ecological and physiological differences between the 2 sister species have yet to be established. The aims of the study were therefore 3-fold: 1) to assess the effect of a resource boom on the foraging and thermal biology of mulgaras, 2) to examine how thermoregulatory costs and foraging are balanced in a habitat with different ground cover and predator exposure, and 3) to compare the ecophysiology of the 2 congeners.

MATERIALS AND METHODS

Study sites.—The study was conducted during the Australian winter in 2010 (23 May–26 July) on 2 sites at the western edge of the Simpson Desert. The 1st site occupied by *D. cristicauda* was located on sparsely vegetated sand ridges (dunes) close to the Old Andado homestead (25°23'S, 135°26'E). Canegrass (*Zygochloa paradoxa*) was found on the dune crests and numerous short-lived forbs/subshrubs in the understory. Shrub cover was sparse (< 5%).

The 2nd site, approximately 21 km away on Andado Station (25°28'S, 135°15'E), comprised gibber plains (ironstone pebbles) and these were occupied by *D. blythi*. The habitat was characterized by a dominance of tussock grasses (on average exceeding 10% cover), particularly species that are associated with medium- to coarse-textured soils. Shrubs were present in low abundance ($\leq 5\%$) and were less than 1 m in height. The specific site chosen featured a relative high cover of surface sand (average of 23% cover) including numerous raised mounds = sand islands.

For comparison with an alternate habitat (sand plain with both dense and patch-burned spinifex, *Triodia basedowii*, cover) also used by *D. blythi*, we included data collected in 2006 from a study conducted at Uluru–Kata Tjuta National Park (henceforward Uluru; 25°20'S, 131°02'E) following the same measuring protocol. The Uluru sand plain site was characterized by a dominance of mature spinifex hummock grassland. In recently burnt areas, spinifex cover was sparse and the abundance of the shrub, *Rulingia lexyphylla*, was high. For a more detailed description of this alternate site, see Körtner et al. (2007).

Climate.—At both Andado sites, ambient temperature (T_a) and relative humidity (RH) were recorded continuously throughout the study with a miniature data logger at 30-min intervals in the shade of a tree trunk at a height of approximately 1.5 m above ground level (iButton, Hydrochron, temperature resolution 0.0625°C, humidity resolution 0.04%; Maxim Integrated Products, Sunnyvale, California). Additionally, surface (T_{surf}) and soil (T_{soil}) temperatures were measured with Thermochrons (temperature resolution 0.5°C; Maxim Integrated Products) buried at depths of 0, 5, 10, 20 and 40 cm below the ground. Rainfall data were obtained from Andado Station located approximately 5 km north of the gibber site.

Trapping and temperature measurements.—Both species of mulgara were captured using box aluminum traps (type A; Elliott Scientific Equipment, Upwey, Australia; 750–7,750 trap nights per site) baited with either a mix of peanut butter and rolled oats and/or tinned sardines and set along undulating transects spaced about 5–10 m apart. For insulation, polyester fiber (Dacron) was added to each trap. Most traps were set close to or under vegetation to reduce direct sun exposure. The species of all mammals caught was determined and for mulgaras sex, reproductive status and BM was recorded upon capture.

To measure daily T_b fluctuations and activity patterns, temperature-sensitive radio transmitters (~3 g, < 5% of BM; Sirtrack, Havelock, New Zealand; calibrated to the nearest 0.1°C, sterilized) were implanted intraperitoneally under general oxygen/isoflurane anesthesia following (Rojas et al. 2010). After surgery, animals were held for the following night and day before they were released at the site of capture in the evening. Captive animals were kept in a plastic box (30×20×20 cm) with a perforated lid in a darkened room. The box contained a layer of sand and shelter material. Animals had ad libitum access to kangaroo mince and water. One female *D. cristicauda* that carried pouch young when captured precluding transmitter implantation was excluded from the study.

After release, implanted individuals were radiotracked daily with handheld radioantennas (3-element, Yagi) and receivers (IC-R10, Icom Inc., Osaka, Japan) to their burrows shortly after sunrise. The burrows were marked and the location recorded with a handheld GPS (Garmin, 400T, Oregon). For each animal, a mobile data-logging system measuring the interval between 2 transmitter pulses every 10 min was placed close to the burrow (Körtner and Geiser 1998). Log-transformed interval data were converted to T_b values using a 2nd order polynomial equation based on the original calibration of the transmitter. Torpor was defined as a drop in T_b below 30°C for 30 min or longer. This temperature threshold is commonly used in torpor research and importantly facilitates comparisons with published data on desert dasyurids including mulgaras. Due to the relatively small reception range of the data loggers, each activity period outside the burrow was defined by a break in continuous T_b records.

Mulgaras were tracked until the end of the study; however 1 *D. blythi* female died of unknown causes after 22 tracking days and the transmitters of 2 males stopped transmitting after 25 and 32 tracking days, respectively, most likely as a result of battery exhaustion. At the gibber site, access was interrupted on 13 July when flooding prevented access by vehicle for the remainder of the study period. However, we were able to retrieve the data loggers on 22 July. This provided additional data for 1 male and 2 female *D. blythi* that were included in the analyses. Monitoring animals in the sand ridges continued until 26 July until impending heavy rain forced us to terminate the study altogether.

The distance between successive burrow locations, determined by handheld GPS, as well as the maximum distance between any of the location records for an individual was calculated. Due to the relatively small number of location fixes per animal, home range analysis was restricted to the nonstatistical Minimum Convex Polygons (MCP) method (Hooge and Eichenlaub 1997).

Experimentation followed the guidelines of the American Society of Mammalogists (Gannon and Sikes 2007). The study was conducted under permits from the Parks and Wildlife Commission of the Northern Territory, Department of Natural Resources, Environment, the Arts and Sport (37305) and license from the University of New England Ethics Committee (AEC10/025).

Statistical analysis.—Data were analyzed using SAS version 9.2 (SAS Institute, Cary, NC) and R (R version 3.0.1, The R Foundation for Statistical Computing—R Development Core Team 2013). For repeated measure analyses, we used mixed effects modeling with individuals treated as random factors. A negative binomial distribution was assumed for count and frequency data. For models with multiple factors/variables, simplified models derived by a stepwise removal of interaction terms were compared with the original model. The final model selection was then based on Akaike information criterion (AIC).

Data were divided into males and females and additionally into males before frequent torpor use and males with frequent torpor use. Based on the Uluru study, this transition appears

to be linked to the end of the mating season. Data from the 2006 Uluru study (Körtner et al. 2007, 2008) on *D. blythi* were compared with data from the present study in order to detect possible differences or similarities between the 2 study sites/years that differed not only in habitat (i.e., gibber at Andado and spinifex plains at Uluru) but also in rainfall patterns (see below). Generally, these differences were assessed by using “study site” as a factor, because statistically rainfall and habitat differences could not be separated. However, a part of the Uluru site had been burned shortly before the study commenced and for the test addressing the timing of activity this change in habitat difference was included as a factor (i.e., burned versus unburned spinifex).

RESULTS

Climate data and soil temperatures.—At Andado, slight but significant differences in T_a were observed between the sand ridge and gibber site. On average, the daily maximum T_a was $2.9 \pm 2.6^\circ\text{C}$ higher ($t_{52} = 8.0$, $P < 0.001$) above the gibber plain ($24.5 \pm 5.1^\circ\text{C}$) than among the sand ridges ($21.6 \pm 3.6^\circ\text{C}$). Differences in the daily T_a minima (gibber: $7.1 \pm 3.0^\circ\text{C}$; sand ridges: $6.7 \pm 3.0^\circ\text{C}$; $t_{52} = 2.5$, $P = 0.17$) and daily average (gibber: $13.9 \pm 2.2^\circ\text{C}$; sand ridges: $13.2 \pm 2.10^\circ\text{C}$; $t_{52} = 7.7$, $P < 0.001$) were less pronounced.

Subzero temperatures occurred only once and then only at the gibber site. While the temperatures measured some years earlier at Uluru were overall similar to those at Andado, cold nights with frost were more common (Fig. 1).

Due to solar radiation, T_{surf} at Andado reached higher values ($26.6 \pm 0.8^\circ\text{C}$, range 11.0 – 39.0°C) than T_a , whereas daily averages and minima were similar. Average T_{soil} at 5, 10, 20, and 40 cm below ground were $14.4 \pm 0.3^\circ\text{C}$, $15.8 \pm 0.2^\circ\text{C}$, $16.5 \pm 0.2^\circ\text{C}$, and $18.7 \pm 0.2^\circ\text{C}$, respectively. As expected, daily amplitudes of T_{soil} decreased and were progressively delayed with increasing soil depth from $9.6 \pm 0.5^\circ\text{C}$ at 5 cm to almost stable conditions with $0.8 \pm 0.1^\circ\text{C}$ at 40 cm below ground.

Air temperature and RH are linked and therefore the RH minima and maxima also differed between the 2 habitats. The daily RH minimum, which usually occurs during the hottest part of the day, was $35 \pm 13.8\%$ at the gibber site, on average 6.7% lower than on sand ridges ($t_{55} = 8.87$, $P < 0.001$). The daily RH maximum over gibber was $88.4 \pm 10.8\%$ also 5.7% lower than in the sand ridge habitat ($t_{55} = 10.78$, $P < 0.001$).

Our study at Andado followed months with already higher than average rainfall including a pulse of high rainfall that had left several large lakes in some of the valleys (Nano and Pavey 2013; Pavey and Nano 2013). This prestudy rainfall was followed by more flooding rain during July (see Nano and Pavey 2013 for a complete description of the rainfall pattern in 2010–2011). The highest rainfall occurred on July 13 (55.4 mm) blocking the access to the Gibber study site (Fig. 1). However, while large tracts of the area became inundated the study plots themselves remained above the water line. A single rainfall event of 45 mm (Körtner et al. 2008) had also been recorded at Uluru, but this rain fell on dry ground and infiltration of water into the sand was rapid.

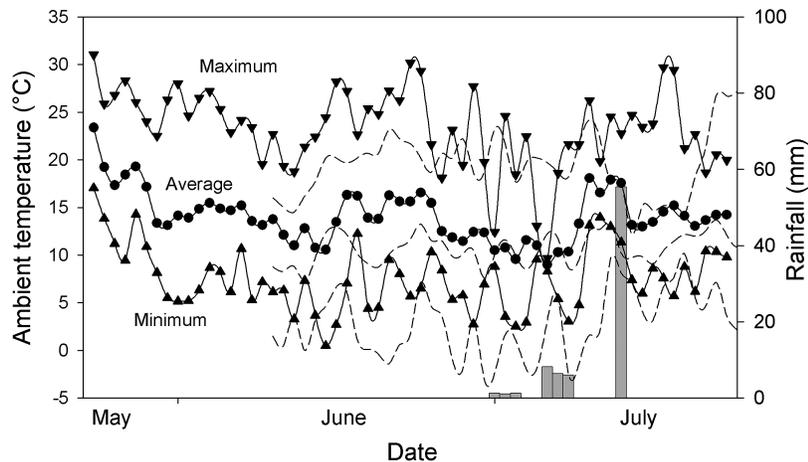


Fig. 1.—Average daily mean (circle), maximum (upper triangle) and minimum (lower triangle) ambient temperature at Andado in 2010 (solid lines) and Uluru in 2006 (dashed lines, no symbols). The bar graph depicts the rainfall at Andado during the study period.

Capture success and mammalian prey assemblage.

Trapping success and mammal assemblage differed considerably between the 3 sites at Andado and Uluru. At Andado, *D. blythi* (5 males, 3 females) were trapped exclusively at the gibber site, whereas *D. cristicauda* (1 male, 2 females) occurred on sand ridges only. The Uluru site, which comprised a sand plain with spinifex hummocks, yielded only *D. blythi* (8 males, 4 females). While trap success for dasyurids was overall low, for *D. blythi*, it was noticeably higher at both Uluru (0.6%) and Andado (2%) than *D. cristicauda* at Andado (0.05%) (Fig. 2). Furthermore, the Uluru site featured a diverse assemblage of small mammals including 3 dasyurid marsupials as well as 4 rodent species (Fig. 2). The sand ridges at Andado were inhabited by a similarly diverse mammal community but the species composition differed. In this case, the most dominant species, the long-haired rat (*Rattus villosissimus*) as well as the plains mouse (*Pseudomys australis*) are both irruptive species that occur in dune fields at high abundance erratically and only after substantial rainfall (Pavey et al. 2014). In contrast, trapping on the gibber plains at Andado revealed only *D. blythi* and a single house mouse (*Mus musculus*), although the kultarr (*Antechinomys laniger*) and sandy inland mouse (*Pseudomys hermannsburgensis*) are also known to occur in the area (C. R. Pavey, CSIRO Land and Water, pers. comm.).

Body mass.—Both at Andado as well as Uluru, BM of *D. blythi* differed between sexes ($F_{3,13} = 15.6$, $P < 0.01$) and in this respect, there was no significant difference between the 2 study locations ($F_{3,13} = 0.24$, $P = 0.63$, analysis of variance [ANOVA] BM versus Sex and Site). Specifically, at Andado, male BM averaged 83.8 ± 4.4 g (range 73.3–95.1 g; $n = 5$) and 62.0 ± 4.3 g (range 54.6–69.4 g; $n = 3$) for females. The low sample size for *D. cristicauda* precluded any statistical analyses, but sexual size dimorphism appeared to apply also to this species as the male (148.6 g) was about twice as heavy as the female (79.4 g). Furthermore, both of these individuals were heavier than any *D. blythi* of the corresponding sex.

Burrow use and activity range.—At Andado as well as Uluru (Körtner et al. 2007), *D. blythi* changed burrows regularly (Andado: 12.9 ± 5.1 ; Uluru: 9.4 ± 3.9 burrows/individual) with a

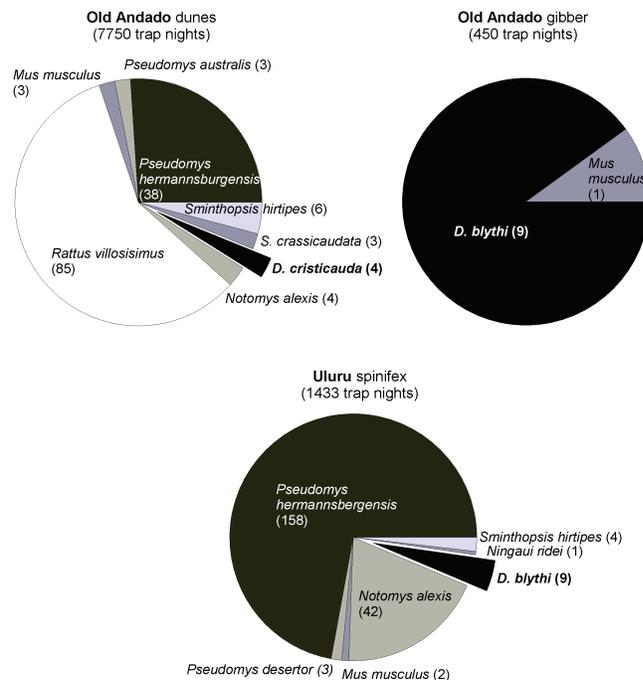


Fig. 2.—Small mammals caught during the trapping efforts at the 2 Andado sites in 2010 and at Uluru in 2006.

maximum of 22 burrows recorded for the male with the longest tracking history at Andado. On the gibber plains at Andado, burrows were almost exclusively situated on shallow sand mounds that facilitated the accumulation of a thin layer of topsoil and therefore low shrubby vegetation. Consecutively used burrows were as far as 830 m apart, but the distance between these burrows and therefore the net distance traveled overnight differed significantly between sexes ($P = 0.032$) and there was also a trend for a site difference ($P = 0.052$, General Linear Model for a negative binomial distribution [glm.nd] on counts for 100 m distance categories; based on an AIC reduction from 224 to 220, the interaction terms Distance:Sex:Site and Sex:Site were removed from the final model). It appeared that males (Andado: 294.7 ± 72.1 m, $n = 5$; Uluru: 234.9 ± 91.0 m, $n = 6$) traveled on

average further than females (Andado: 158.7 ± 55.8 m, $n = 3$; Uluru: 107.0 ± 10.8 m, $n = 3$) but for both sexes, perhaps these distances were larger at Andado than Uluru.

Consequently, both at Andado and Uluru, the area of activity of *D. blythi* differed significantly between the sexes ($F_{1,13} = 4.78$, $P = 0.048$), without any discernable habitat/site effect ($F_{1,13} = 2.19$, $P = 0.16$; ANOVA MCP versus Sex and Site). Across both habitat types, males ($n = 10$) occupied an area of 25.9 ± 7.1 ha (Andado: 26.3 ± 6.5 ha, $n = 5$; Uluru: 25.5 ± 8.4 ha, $n = 5$), whereas female MCPs ($n = 6$) were with 17.5 ± 8.9 ha (Andado: 24.1 ± 6.8 ha, $n = 3$; Uluru: 10.8 ± 4.0 ha, $n = 3$) on average smaller. The shape of the MCPs expressed here as the maximum distance between location records for an individual, however, appeared to differ between the sites ($F_{1,14} = 4.25$, $P = 0.01$) but not sexes ($F_{1,14} = 8.82$, $P = 0.06$; ANOVA Maximum Distance versus Sex and Site). At Andado, the maximum distance was 953 ± 165 m versus 726 ± 189 m at Uluru. Hence on the gibber plains of Andado, the area of activity, despite similar size, appeared to be more stretched in 1 dimension.

Similar to their sister species, *D. cristicauda* also moved between a number of burrows and 9 burrows were detected for the female and 5 for the male. All burrow locations were along the slopes of sand ridges and none in interdune swales. Most of these burrows appeared to be coinhabited by long-haired rats, a potential prey species, as indicated by ample tracks. Surprisingly, the areas of activity of the 2 *D. cristicauda* (female 7.4 ha, male 1.4 ha) were smaller than any of the *D. blythi* monitored at both Andado and Uluru. Since the female *D. cristicauda*'s MCP stretched along the eastern face of a dune, the maximum dimension of the MCP approximated those of female *D. blythi*. As the male *D. cristicauda*'s area of activity was exceptionally small, so was its largest dimension.

Timing of activity.—Both species were largely nocturnal, but commenced activity around sunset before complete darkness and when temperature conditions were still warm. In *D. blythi* (Fig. 3), onset of activity was modulated by the vegetation

cover afforded by the habitat at the study sites ($F_{2,420} = 37.65$, $P < 0.001$; mixed effects model with individuals treated as a random factor). On average, *D. blythi* commenced activity earliest in the dense unburned spinifex at Uluru (17.7 ± 43.5 min before sunset, $n = 9$, $N = 205$), at intermediate times in burned spinifex at Uluru (4.6 ± 41.3 min after sunset, $n = 8$, $N = 47$), and latest on gibber at Andado (21.8 ± 40.2 min after sunset, $n = 8$, $N = 190$). The 2 *D. cristicauda* on sparsely vegetated dune slopes also emerged relatively late at 29.4 ± 45.2 min after sunset ($n = 2$, $N = 74$).

For male *D. blythi*, the total duration of activity per day was about twice as long during the mating season (9.02 ± 2.95 h/day, $n = 6$) than after the mating season (4.21 ± 1.50 h/day, $n = 5$) and also in comparison to females throughout the study (5.38 ± 1.61 h/day, $n = 6$; $F_{2,14} = 7.63$, $P = 0.006$, ANOVA [lm] between Females, Males before and Males after the transition followed by a Tukey's post hoc test). The inclusion of "site" as a factor rendered the model not significant ($F_{5,11} = 2.80$, $P = 0.072$) and therefore the length of daily activity was indistinguishable between Andado and Uluru. The activity period of the female *D. cristicauda* (5.81 ± 2.06 h/day, $N = 39$) resembled closely that of the female *D. blythi*. In contrast, activity in the male *D. cristicauda* was very short and averaged only 1.62 ± 1.25 h/day ($N = 16$).

Body temperature during activity, rest, and torpor.—At Andado, the 8 *D. blythi* (5 males and 3 females) were radio-tracked for a total of 224 animal days—the *D. cristicauda* male for 22 days and the female for 58 days. At Uluru, 6 male and 3 female *D. blythi* were tracked over a total of 277 animal days. While nighttime T_b readings were sporadic for most *D. blythi* on most days because individuals moved outside the reception range of the loggers, data on active phase T_b of the 2 *D. cristicauda* were more extensive, either because of the short distance movement and short activity for the male or the female's "predictable" movement between 2 main burrows that could be covered by 2 loggers (Fig. 4).

Even when torpor was excluded, both species showed pronounced fluctuations of T_b over the day with higher values during the nocturnal activity phase than during daytime (Figs. 4 and 5). When *D. blythi* were active but still close to the monitored burrow (i.e., in the reception range of the logger), T_b ranged between 37.1°C and 39.6°C ($n = 7$, $N = 124$) (Fig. 5B). In *D. cristicauda*, at times, T_b exceeded 40°C during activity (Fig. 5A). These slightly higher values could be the result of the more complete set of night records for these 2 individuals. During rest, T_b generally fell below 35°C in both species (Fig. 6). In the female *D. cristicauda*, daily T_b fluctuations abated from the beginning of June as rest-phase T_b was upregulated (Fig. 4).

Furthermore, with the exception of 1 male *D. blythi* for which only 5 days of data were available, all individuals of both species entered daily torpor. For both species, the dual peaks of the frequency distribution for minimal daily T_b indicate a clear distinction between normothermic rest and torpor (Fig. 6). The torpor peak T_b approximated 20°C , close to the stable soil temperature at depths below 40 cm. However, as

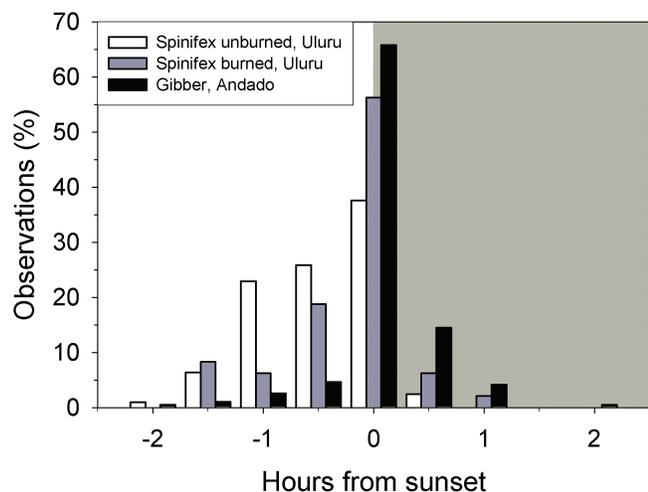


Fig. 3.—Onset of activity in relation to sunset in *Dasycercus blythi* in 3 different habitat types.

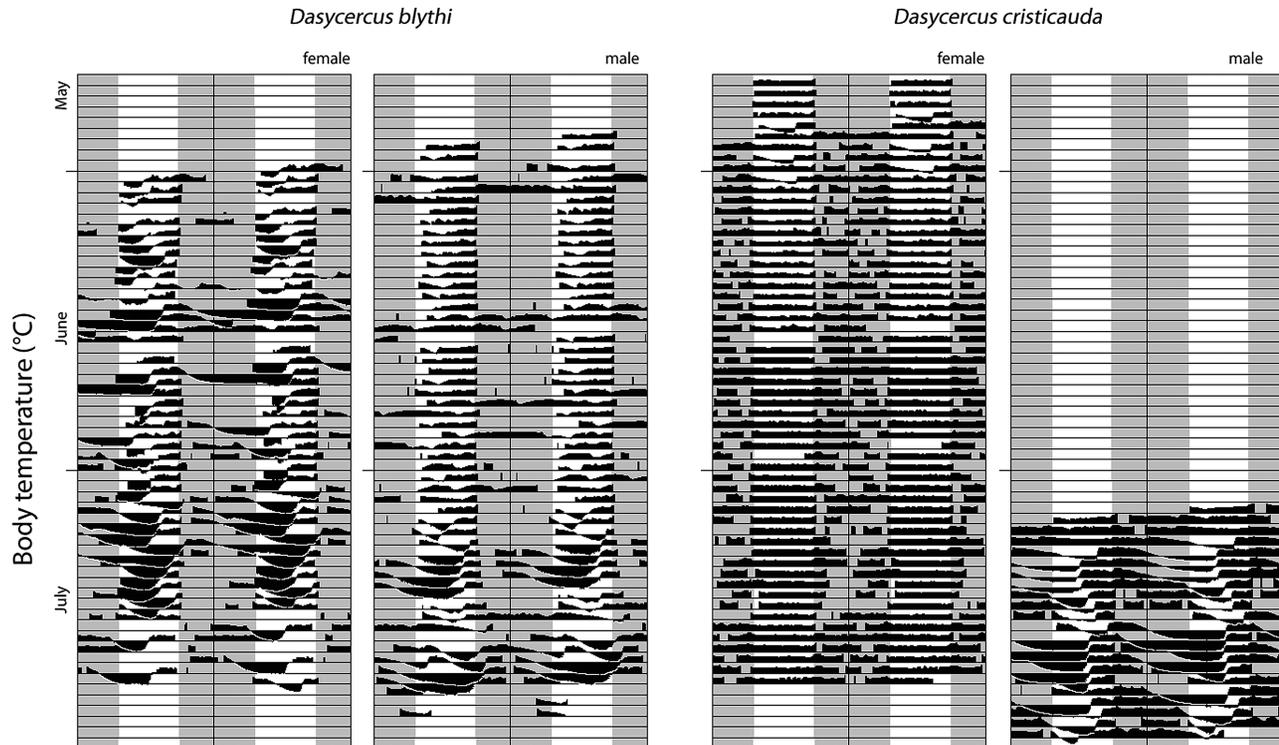


Fig. 4.—Double plots of the body temperature (T_b) traces for 2 *Dasymercus blythi* and 2 *D. cristicauda*. Each row depicts 2 days (midnight to midnight) with the 2nd day being repeated in the following row. The scale for each row is 30–42°C. Torpor bouts with T_b below 30°C are therefore represented as negative values. Shading indicates the scotophase.

many torpor T_b s fell below deep soil temperature, occasionally animals must have occupied shallow burrows that were subjected to nightly cooling. Consequently, torpor T_b fell as low as 12.3°C at Andado and 10.8°C at Uluru where T_a fluctuations were more extreme (see above). For *D. cristicauda*, it appeared that T_b during torpor did not fall below deep soil temperature and the absolute minimum was 18.4°C.

Minimum T_b during torpor decreased with increasing bout duration, with no significant difference between male and female *D. blythi* (Fig. 7). For torpor bouts longer than 1 h, this relationship appeared to be governed by Newton's law of cooling as indicated by the linearization after log transformation (Fig. 7B). In contrast, animals appeared to have continued with some thermoregulation during shorter torpor bouts. Minimal T_b during torpor for the slightly larger *D. cristicauda* overlapped with those from its sister species, but values were generally situated at the upper end of the range.

Animals usually entered torpor during the 2nd one-half of the night and aroused late morning when T_a increased to its daily peak (Fig. 4). As for Uluru (Körtner et al. 2008), at Andado, T_a had a marginal but significant effect on torpor entry and arousal of *D. blythi*. On average animals entered torpor earlier on cold nights (torpor entry [h after sunset] = $-2.0 * T_a$ minimum [°C] + 0.31; $R^2_{\text{adj}} = 0.06$; $P = 0.01$) and aroused earlier on warm days (arousal [h after sunrise] = $9.13 * T_a$ maximum [°C] - 0.11; $R^2_{\text{adj}} = 0.05$; $P < 0.005$).

Sexes and species differed substantially in the use of torpor. Throughout the Andado study, female *D. blythi* regularly entered long and deep torpor bouts of up to 18.9 h (Fig. 8).

Some of the days without torpor appeared to be related to mating as on 4 of these occasions, a female and 1 of the radiotagged males were found together in the same burrow for up to 2 days without leaving (Fig. 5B). In contrast, male *D. blythi* went through a pronounced transition from few shallow torpor bouts (mating) to frequent deep torpor at the end of June (postmating) (Andado range: 29 June–3 July; Figs. 4 and 8). After the mating period (the transition), male and female torpor patterns in *D. blythi* became statistically indistinguishable. Furthermore, time of male transition at the end of mating (Uluru range: 30 June–16 July) as well as all variables of torpor were indistinguishable in *D. blythi* at Andado and Uluru (Fig. 8, 1-way ANOVAs and *quasibinomial glm* for torpor frequency data followed by Tukey's post hoc tests, as "Site" was not significant in any model, it was removed). However, at Uluru, 1 female was observed to relinquish torpor and to elevate and stabilize its T_b in mid-August at about the time of giving birth. While the Andado study could not proceed long enough to allow for similar observations in the *D. blythi* there, stable T_b patterns similar to Uluru were seen in the female *D. cristicauda*, but in this case much earlier in the season. While in this individual torpor had always been infrequent and shallow even at the end of May, torpor ceased all together at the beginning of June and rest-phase T_b started to increase shortly after (Figs. 4 and 5A). While this individual could not be retrapped to confirm reproduction, another female *D. cristicauda* with 8 pouch young, each about 1 cm long, was trapped on the 22 June, indicating a 1.5–2 months earlier onset of reproduction in this species than in *D. blythi*. Fitting this interpretation of earlier onset of

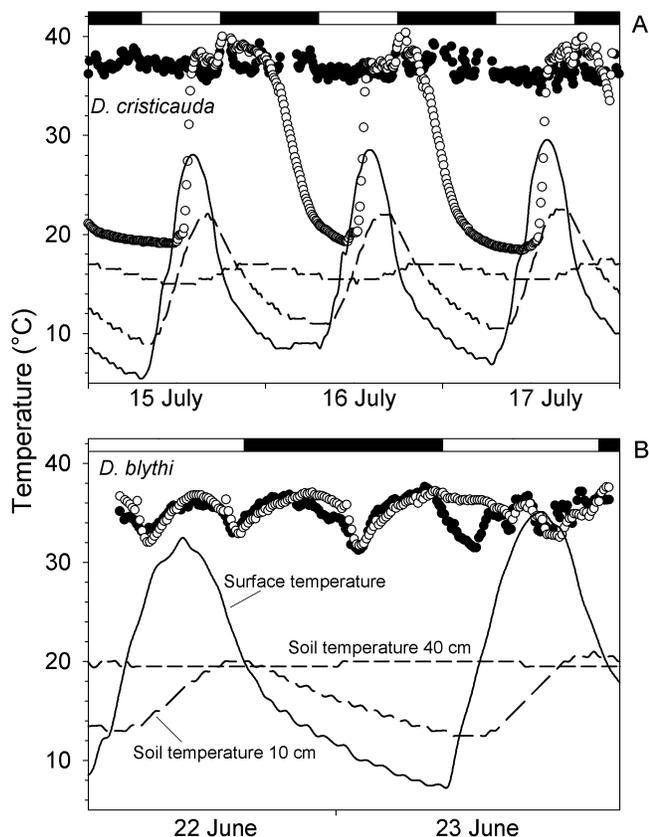


Fig. 5.—Example of the body temperature pattern of a male (open circles) and female (closed circles) A) *Dasyercus cristicauda* and B) a pair of *D. blythi*. Surface temperature as well as soil temperature at a depth of 10 and 40 cm are also depicted. The dark bars indicate the scotophase. In the case of the 2 *D. blythi*, both animals resided in the same burrow, synchronized their body temperature, and neither entered torpor nor left the burrow at night.

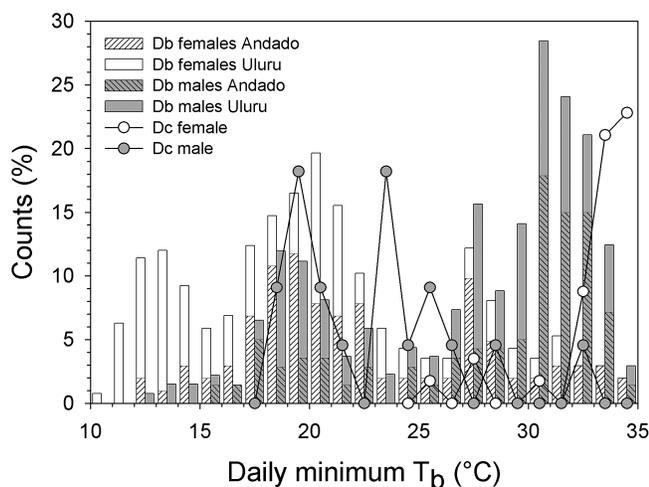


Fig. 6.—Frequency distribution of minimum daily body temperature values for 2 species of mulgaras, *Dasyercus blythi* (Db) and *D. cristicauda* (Dc).

reproduction, the male *D. cristicauda* trapped on the 30 June showed regular deep torpor, similar to male *D. blythi* after the mating season (Figs. 4, 5, and 8).

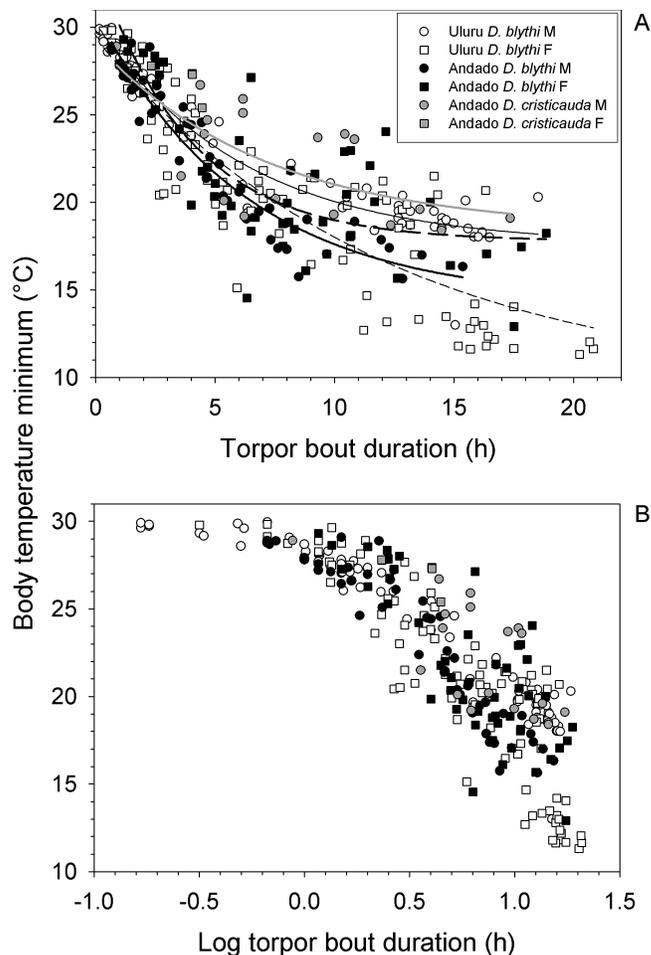


Fig. 7.—Relationship between torpor bout duration and minimum body temperature during torpor for 2 species of mulgaras at 2 study sites, i.e., Andado and Uluru, Australia (see text for details). Circles and solid regression lines refer to males, while squares and dashed lines to females. Thin lines stand for the Uluru data set.

DISCUSSION

Our data on the 2 mulgara species, both of which are endemic to the Australian arid zone, show that the frequent expression of daily torpor in either sex is neither effected by rainfall nor habitat and therefore probably not a response to resource availability. These results seem to contradict the traditional view of daily torpor as an emergency response to breach energetic bottlenecks. However, while under laboratory conditions, food withdrawal, especially in conjunction with low T_a s, triggers or enhances torpor in most daily heterotherms (Song and Geiser 1997), in an ecological context, the proximate link between food availability and torpor has been surprisingly difficult to prove (Vuarin and Henry 2014). In fact, only for a small number of species, mainly those which enter torpor only irregularly, is the direct link between torpor and environmental conditions compelling (Körtner and Geiser 2000; Doucette et al. 2012; Nowack et al. 2015; Stawski et al. 2015). Mulgaras clearly do not fit this pattern. At 2 geographical locations that occur in separate desert systems and that differ in habitat and mammalian prey assemblages and which were investigated over 2 study

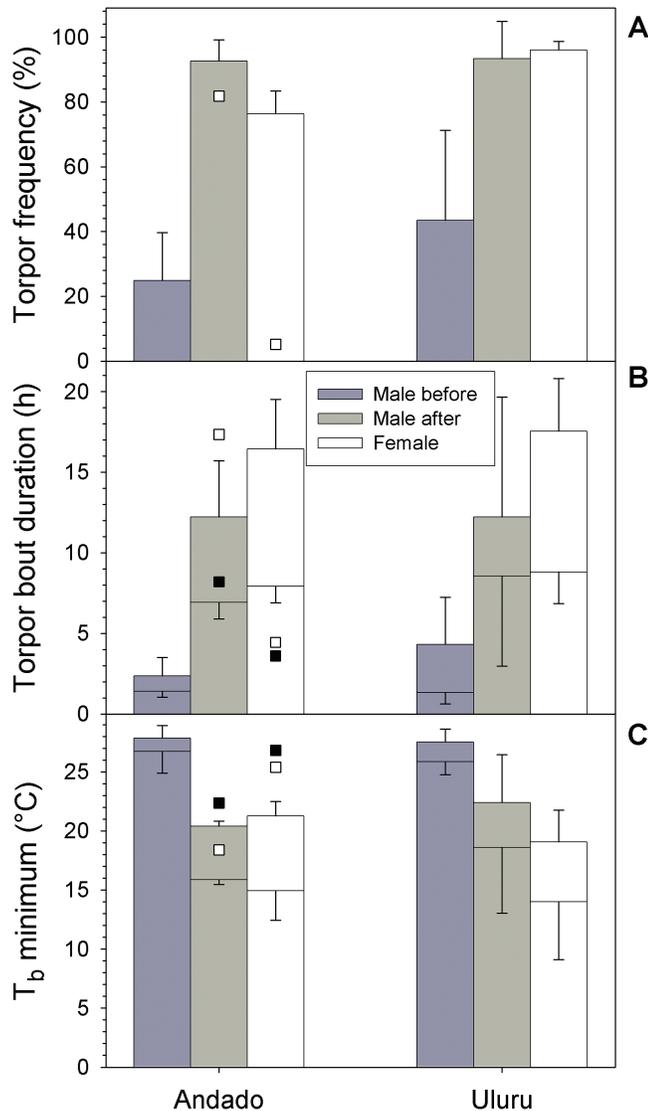


Fig. 8.—A) Torpor frequency, B) torpor bout duration, and C) minimum body temperature during torpor in *Dasymercus blythi* (bars) and *D. cristicauda* (squares) at Andado and Uluru. For (B) and (C), the bars show both the mean of the mean of the parameters as well as the mean of the most extreme values for each individual. The male data set was split into “before” and “after,” referring to an obvious transition in torpor use, probably related to the end of the mating season (see main text for details).

periods with very different rainfall records, torpor expression during winter was generally high, regular, and predictable. Furthermore, the periods with and without torpor, which for *D. blythi* were observed consistently at the same time of the year during the 2 studies, did not correspond between the sexes, because periods without torpor occurred only when reproduction was apparently incompatible with torpor (i.e., mating for males and parturition and lactation for females). As a consequence, the prevailing climatic conditions merely modulated torpor bout length and depth. In part, this variation resulted from the relatively shallow burrows used by *D. blythi*, but not necessarily *D. cristicauda*, which only moderately insulated their inhabitants from the temperature fluctuations outside.

As torpor reduces energy expenditure, daily torpor and activity are intrinsically linked (Ruf et al. 1991). Accordingly, the time spent active was significantly shorter in mulgaras that used torpor highlighting the energetic significance of daily torpor. However, a shortened activity phase has not only energetic implications but also reduces predator exposure (Bieber and Ruf 2009), which is especially important for animals that occupy habitats that offer little cover. For example, at Uluru, 3 *D. blythi* were killed by introduced cats and foxes all in areas where spinifex had been burned (Körtner et al. 2007). Raptors also constitute a potential threat to small mammals in these habitats, whereas predatory reptiles are less active during winter. As such, *D. blythi* adjusted the onset of activity according to the cover and hence the protection the vegetation was providing from visually hunting predators. Shading and consequently an earlier decrease in light level around dusk could have been mediating factors. At Uluru, spinifex (*Triodia* spp.) was one of the most dominant habitat features and this spiky grass can form such impenetrable hummocks that the related kaluta (*Dasykaluta rosamondae*) is able to forage during the day in winter (Körtner et al. 2010). While mulgaras remained nocturnal, the main activity occurred early in the night sometimes commencing before sunset when winter T_a s are still moderate. Fire can obliterate the highly flammable spinifex hummocks and consequently in a postfire landscape *D. blythi* emerged later. While this delay in emergence time presumably ameliorates the predation risk from diurnal predators, nocturnal predators remain a threat that can increase postfire (McCarthy and Masters 2005; Körtner et al. 2007). For example, feral cats are known to move into recently burnt habitat because there they can forage more effectively (McGregor et al. 2014). Gibber plains may be equivalent to recently burnt spinifex in terms of the lack of vegetation and exposure to visually hunting predators, because again *D. blythi* emerged late from their burrows in this habitat.

Protection from predators and temperature extremes are essential for small mammals and hence availability and distance between burrows are critical habitat features. While smaller dasyurids regularly occupy burrows created by other small vertebrates and invertebrates (Haythornthwaite and Dickman 2006), the options for larger animals are more limited. Furthermore, on gibber plains, only the sparse sand mounds allow burrow construction and therefore the area of activity was more longitudinally stretched than in the more homogenous spinifex. However, there appears to be a limit to the distance mulgaras will travel between cover. The distance between consecutive burrows was similar for Uluru and Andado and, in fact, a higher than average density of sand islands is a determining factor for the presence of *D. blythi* on gibber habitat (Pavey et al. 2012). The restrictions of burrow availability might also explain why mulgaras are more sedentary than most of the smaller arid zone dasyurids (Gibson and Cole 1992; Masters 1998), which exhibit shifting home ranges and long distance movements (Read 1984; Dickman et al. 1995; Letnic 2002). In contrast, mulgara populations might fluctuate in size but persist for many years and some of the established burrow systems can become elaborate (Woolley 1990; Gibson and Cole 1992;

Masters 1998, 2003). In this respect, it is interesting to note that at Andado, none of the habitat patches that were inhabited by the mulgaras became inundated even after the final heavy rain that terminated the study. Perhaps in the longer term flood-prone areas are unsuitable for mulgara populations.

The prey spectrum also sets mulgaras apart from most other desert dasyurids. Both species are capable of taking a wide size range and taxonomic diversity of prey ranging from small to large invertebrates through to reptiles, birds, and mammals up to the size of themselves (Ewer 1969; Chen et al. 1998; Pavey et al. 2009). Larger prey items offer more reward and the proportion of mammalian prey in the diet is known to modulate torpor use in *D. blythi* (Pavey et al. 2009). It therefore could have been expected that the pronounced site differences in the small mammal assemblage/abundance could have affected the energetics of mulgaras. For example, the mammal diversity and abundance at the Andado gibber site was relatively low by comparison with both the sand ridges inhabited by *D. cristicauda* at Andado and the sand plains at Uluru (Fig. 2). The irruption of long-haired rats, a known prey species of mulgaras (Chen et al. 1998), had reached the sand dunes during the 2010 study, but they did not arrive at the gibber habitat until the following summer; at least 4 months after the completion of our research (C. R. Pavey, CSIRO Land and Water, pers. comm.). The activity in the male *D. cristicauda* was certainly shorter and the extent of his movements much smaller than in any other individual monitored. Furthermore, considering the earlier onset of reproduction in *D. cristicauda* in the sand ridge habitat, it is possible that a high abundance of mammalian prey shifted the seasonal timing of reproduction, but an intrinsic difference between the 2 species perhaps related to BM differences is an alternative explanation that remains to be tested. Importantly in either case, torpor use at least in the male *D. cristicauda* remained as high as in both studies on *D. blythi*. Hence, a resource flush in mammalian prey, similar to rainfall and climate, did not stop torpor use.

Mulgaras show a number of typical adaptations to a desert environment including low energy and water turnover (Schmidt-Nielsen and Newsome 1962; Kennedy and MacFarlane 1971) further enhanced by torpor as well as energetically exploiting the daily T_a cycle (Geiser et al. 2008). Otherwise, mulgaras appear to be quite unusual in their rather conservative life strategy for an unpredictable arid environment. From a trophic perspective, a rather large body size provides advantages in enabling a diversity of prey to be captured and being able to cover substantial distances over night. On the other hand, mulgaras are not large enough to have outgrown the predation risk posed by raptors and placental carnivores, restricting diel activity patterns especially in habitats where cover is sparse. Furthermore, a high BM presents energetic and reproductive challenges that appear to necessitate a consistent expression of daily torpor across habitat types and are independent from resource availability. Hence the energetic constraints of mammalian endothermy and elevated costs for reproduction might impinge on mulgaras more than on smaller dasyurids supporting the hypothesis that the life history of mulgaras is more suited to localities that feature a better than average

productivity (Masters 1998; Pavey et al. 2012) explaining the patchy distribution over a variety of habitat types.

ACKNOWLEDGMENTS

Rainfall data were kindly provided by Andado Station. We thank the Costello family and M. Sullivan for allowing us to carry out this research on Andado Station and Old Andado, respectively. Field assistance was provided by A. James, P. Nunn, P. McDonald, and J. Cole. S. Cairns helped with some of the statistical analyses. The project was funded by an ARC grant to F.G., a research scholarship from the Alexander von Humboldt Foundation to A.R., and by the Northern Territory Department of Natural Resources, Environment and the Arts and Territory NRM (to G.K. and C.P.).

LITERATURE CITED

- BIEBER, C., AND T. RUF. 2009. Summer dormancy in edible dormice (*Glis glis*) without energetic constraints. *Naturwissenschaften* 96:165–171.
- CHEN, X., C. R. DICKMAN, AND M. B. THOMPSON. 1998. Diet of the mulgara, *Dasyercus cristicauda* (Marsupialia: Dasyuridae), in the Simpson Desert, central Australia. *Wildlife Research* 25:233–242.
- COOPER, C. E., AND P. C. WITHERS. 2010. Comparative physiology of Australian quolls (*Dasyurus*; Marsupialia). *Journal of Comparative Physiology B: Biochemical Systemic and Environmental Physiology* 180:857–868.
- DICKMAN, C. R., M. PREDAVEC, AND F. J. DOWNEY. 1995. Long-range movements of small mammals in arid Australia: implications for land management. *Journal of Arid Environments* 31:441–452.
- DOUCETTE, L., R. M. BRIGHAM, C. PAVEY, AND F. GEISER. 2012. Prey availability affects daily torpor by free-ranging Australian owl-nightjars (*Aegotheles cristatus*). *Oecologia* 169:361–372.
- EWER, R. F. 1969. Some observations on the killing and eating of prey by two dasyurid marsupials: the mulgara, *Dasyercus cristicauda*, and the Tasmanian devil, *Sarcophilus harrisi*. *Zeitschrift für Tierpsychologie* 26:23–38.
- GANNON, W. L., AND R. S. SIKES. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- GEISER, F., ET AL. 2008. Torpor in marsupials: recent advances. Pp. 297–306 in *Hypometabolism in animals: hibernation, torpor and cryobiology* (B. G. Lovegrove and A. E. McKechnie, eds.). Interpak Books, Pietermaritzburg, South Africa.
- GEISER, F., AND G. KÖRTNER. 2010. Hibernation and daily torpor in Australian mammals. *Australian Zoologist* 35:204–215.
- GEISER, F., AND P. MASTERS. 1994. Torpor in relation to reproduction in the Mulgara, *Dasyercus cristicauda* (Dasyuridae: Marsupialia). *Journal of Thermal Biology* 19:33–40.
- GIBSON, D. F., AND J. R. COLE. 1992. Aspects of the ecology of the mulgara, *Dasyercus cristicauda*, (Marsupialia: Dasyuridae) in the Northern Territory. *Australian Mammalogy* 15:105–112.
- HAYTHORNTHWAITE, A. S., AND C. R. DICKMAN. 2006. Long-distance movements by a small carnivorous marsupial: how *Sminthopsis youngsoni* (Marsupialia: Dasyuridae) uses habitat in an Australian sandridge desert. *Journal of Zoology (London)* 270:543–549.
- HOOG, P. N., AND B. EICHENLAUB. 1997. Animal movement extension to ArcView. Version 1.1. Biological Science Office, United States Geological Survey, Anchorage, Alaska.

- KENNEDY, P. M., AND W. V. MACFARLANE. 1971. Oxygen consumption and water turnover of the fat-tailed marsupials *Dasyercus cristicauda* and *Sminthopsis crassicaudata*. *Comparative Biochemistry and Physiology* 40A:723–732.
- KÖRTNER, G., AND F. GEISER. 1998. Ecology of natural hibernation in the marsupial mountain pygmy-possum (*Burrhamys parvus*). *Oecologia* 113:170–178.
- KÖRTNER, G., AND F. GEISER. 2000. Torpor and activity patterns in free-ranging sugar gliders *Petaurus breviceps* (Marsupialia). *Oecologia* 123:350–357.
- KÖRTNER, G., C. R. PAVEY, AND F. GEISER. 2007. Spatial ecology of the mulgara in arid Australia: impact of fire history on home range size and burrow use. *Journal of Zoology (London)* 273:350–357.
- KÖRTNER, G., C. R. PAVEY, AND F. GEISER. 2008. Thermal biology, torpor, and activity in free-living mulgaras in arid zone Australia during the winter reproductive season. *Physiological and Biochemical Zoology* 81:442–451.
- KÖRTNER, G., A. D. ROJAS, AND F. GEISER. 2010. Thermal biology, torpor use and activity patterns of a small diurnal marsupial from a tropical desert: sexual differences. *Journal of Comparative Physiology B* 180:869–876.
- LETNIC, M. 2002. Long distance movements and the use of fire mosaics by small mammals in the Simpson Desert, central Australia. *Australian Mammalogy* 23:125–134.
- LOVEGROVE, B. 2000. Daily heterothermy in mammals: coping with unpredictable environments. Pp. 29–40 in *Life in the cold* (G. Heldmaier and M. Klingenspor, eds.). Springer, Berlin, Germany.
- MASTERS, P. 1998. The mulgara *Dasyercus cristicauda* (Marsupialia: Dasyuridae) at Uluru National Park, Northern Territory. *Australian Mammalogy* 20:403–407.
- MASTERS, P. 2003. Movement patterns and spatial organisation of the mulgara, *Dasyercus cristicauda* (Marsupialia: Dasyuridae), in central Australia. *Wildlife Research* 30:339–344.
- MCCALLAN, B. M., AND F. GEISER. 2014. Torpor during reproduction in mammals and birds: dealing with an energetic conundrum. *Integrative and Comparative Biology* 54:516–532.
- MCCARTHY, M. A., AND P. MASTERS. 2005. Profiting from prior information in Bayesian analyses of ecological data. *Journal of Applied Ecology* 42:1012–1019.
- MCGREGOR, H. W., S. LEGGE, M. E. JONES, AND C. N. JOHNSON. 2014. Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. *PLoS ONE* 9:e109097.
- MERRITT, J. F. 2010. *The biology of small mammals*. The Johns Hopkins University Press, Baltimore, Maryland.
- NANO, C. E. M., AND C. R. PAVEY. 2013. Refining the ‘pulse-reserve’ model for arid central Australia: Seasonal rainfall, soil moisture and plant productivity in sand ridge and stony plain habitats of the Simpson Desert. *Austral Ecology* 38:741–753.
- NOWACK, J., A. D. ROJAS, G. KÖRTNER, AND F. GEISER. 2015. Snoozing through the storm: torpor use during a natural disaster. *Scientific Reports* 5:11243.
- PAVEY, C. R., C. J. BURWELL, G. KÖRTNER, AND F. GEISER. 2009. Vertebrate diet decreases winter torpor use in a desert marsupial. *Naturwissenschaften* 96:679–683.
- PAVEY, C. R., J. R. COLE, P. J. McDONALD, AND C. E. M. NANO. 2014. Population dynamics and spatial ecology of a declining desert rodent, *Pseudomys australis*: the importance of refuges for persistence. *Journal of Mammalogy* 95:615–625.
- PAVEY, C. R., AND C. E. M. NANO. 2013. Changes in richness and abundance of rodents and native predators in response to extreme rainfall in arid Australia. *Austral Ecology* 38:777–785.
- PAVEY, C. R., C. E. M. NANO, S. J. B. COOPER, J. R. COLE, AND P. J. McDONALD. 2012. Habitat use, population dynamics and species identification of mulgara, *Dasyercus blythi* and *D. cristicauda*, in a zone of sympatry in central Australia. *Australian Journal of Zoology* 59:156–169.
- R Development Core Team. 2013. R: a language and environment for statistical computing. R version 3.2.0. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>. Accessed 16 April 2015.
- READ, D. G. 1984. Movements and home ranges of three sympatric dasyurids, *Sminthopsis crassicaudata*, *Planigale gilesi* and *P. tenuirostris* (Marsupialia), in semiarid western New South Wales. *Australian Wildlife Research* 11:223–234.
- ROJAS, A. D., G. KÖRTNER, AND F. GEISER. 2010. Do implanted transmitters affect maximum running speed of two small marsupials? *Journal of Mammalogy* 91:1360–1364.
- RUF, T., AND F. GEISER. 2015. Daily torpor and hibernation in birds and mammals. *Biological Reviews* 90:891–926.
- RUF, T., M. KLINGENSPOR, H. PREIS, AND G. HELDMAIER. 1991. Daily torpor in the Djungarian hamster (*Phodopus sungorus*): interaction with food intake, activity, and social behaviour. *Journal of Comparative Physiology B* 160:609–615.
- SCHMIDT-NIELSEN, K., AND A. E. NEWSOME. 1962. Water balance in the mulgara (*Dasyercus cristicauda*), a carnivorous desert marsupial. *Australian Journal of Biological Sciences* 15:683–689.
- SONG, X., AND F. GEISER. 1997. Daily torpor and energy expenditure in *Sminthopsis macroura*: interaction between food and water availability and temperature. *Physiological Zoology* 70:331–337.
- SONG, X., G. KÖRTNER, AND F. GEISER. 1995. Reduction of metabolic rate and thermoregulation during daily torpor. *Journal of Comparative Physiology B* 165:291–297.
- STAWSKI, C., G. KÖRTNER, J. NOWACK, AND F. GEISER. 2015. The importance of mammalian torpor for survival in a post-fire landscape. *Biology Letters* 11:20150134.
- VAN ETTEEN, E. J. B. 2009. Inter-annual rainfall variability of arid Australia: greater than elsewhere? *Australian Geographer* 40:109–120.
- UARIN, P., AND P.-Y. HENRY. 2014. Field evidence for a proximate role of food shortage in the regulation of hibernation and daily torpor: a review. *Journal of Comparative Physiology B* 184:683–697.
- WARDLE, G. M., C. R. PAVEY, AND C. R. DICKMAN. 2013. Greening of arid Australia: new insights from extreme years. *Austral Ecology* 38:731–740.
- WOOLLEY, P. A. 1990. Mulgaras, *Dasyercus cristicauda* (Marsupialia: Dasyuridae); their burrows, and records of attempts to collect live animals between 1966 and 1979. *Australian Mammalogy* 13:61–64.
- WOOLLEY, P. A. 2005. The species of *Dasyercus* Peters, 1875 (Marsupialia: Dasyuridae). *Memoirs of Museum Victoria* 62:213–221.

Submitted 13 December 2015. Accepted 10 June 2016.

Associate Editor was Loren D. Hayes.