

# Thermal biology, torpor use and activity patterns of a small diurnal marsupial from a tropical desert: sexual differences

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**Abstract** Many small desert dasyurids employ torpor almost daily during winter, because cold nights and low food availability impose high energetic costs. However, in Western Australia the arid zone extends into tropical, coastal regions, where winter temperature conditions are far less severe. We studied the thermal biology and activity patterns of free-ranging kaluta ( $\sim 27$  g), a dasyurid restricted to these tropical spinifex deserts, during the Austral winter (June–July) and in addition quantified activity patterns in captivity. Unlike most dasyurids, wild and captive kalutas were almost exclusively diurnal and retreated into underground burrows during the night. Despite being active during the warmer part of the day, kalutas entered torpor daily. However, torpor patterns differed remarkably between males and females. While females spent most of the night torpid at body temperatures ( $T_b$ ) as low as  $21^\circ\text{C}$ , close to soil temperature, males entered multiple short and shallow bouts ( $T_b > 25^\circ\text{C}$ ) during the night. Males also maintained higher  $T_b$ s during the early morning when active, occupied larger home ranges and covered greater distances while foraging than females. Hence, males appear to expend more energy than the similar-sized females both while foraging and during the rest phase. We propose that physiological as well as behavioural preparations for the September mating season that culminate in a complete male die-off might already impose energetic costs on males during winter.

**Keywords** Torpor · Marsupial · Desert · Tropics

## Introduction

Aridity is chiefly caused by low rainfall, high evaporation rates or a combination of both. Because precipitation can be low even in cool environments, deserts can be found in all climate zones with varying thermal conditions. Generally, however, the lack of vegetation, moisture and cloud cover in desert regions result in extreme daily and annual temperature fluctuations. These in addition to low water and food availability constitute challenges for desert animals. Peak daytime temperatures can be avoided by most small mammals because they are usually nocturnal and shelter in underground burrows. In contrast, a nocturnal lifestyle offers no protection against the cold winter nights that are also common in many desert regions even in the hot deserts of central Australia (Australian Bureau of Meteorology). Here for a diverse group of small insectivorous dasyurid marsupials (Dickman 2003) cold winter nights pose a dual energetic challenge of increased thermoregulatory costs (MacMillen and Nelson 1969) combined with temperature-related reduced prey availability (Holm and Edney 1973). Many of these small desert dasyurids meet the challenge by employing daily torpor frequently to minimise energy and water requirements (Geiser and Pavrey 2007; Körtner et al. 2008; Warnecke et al. 2008; Körtner and Geiser 2009).

However, not all Australian deserts are characterised by cold winter nights. For example, cool ocean currents along the west coast of the continent promote little precipitation and therefore arid conditions extend far northwards into the tropics. Here the annual temperature fluctuations are somewhat ameliorated by the proximity of the ocean and

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the low latitude further elevates winter temperatures (Australian Bureau of Meteorology). Considering such environmental conditions, small mammals living in these areas should be less energetically stressed than their central Australian counterparts.

We tested whether the frequent use of torpor by dasyurid marsupials in arid central Australia is a direct consequence of the cold winter temperatures or perhaps a general feature of this group of animals to combat the relatively low food availability in arid environments. Our study animal was the kaluta (*Dasykaluta rosamondae*) a small insectivorous dasyurid marsupial endemic to the tropical deserts of north-western Australia (Menkhurst and Knight 2001). Using radio-telemetry we investigated activity pattern and the thermal biology of this little-studied species in the wild and also examined daily activity patterns in captivity. Furthermore, several dasyurid marsupials are sexually dimorphic in body size and torpor use (Geiser 1988) and life history can differ substantially between the sexes (Tyndale-Biscoe and Renfree 1987). Spring reproduction of kalutas, for example, entails a complete male die-off following mating (Woolley 1991). We therefore also investigated gender-related differences in activity and torpor patterns.

## Methods

### Free-ranging kalutas

Little red kalutas (*D. rosamondae*, 7 males, 4 females) were studied near Port Hedland, northwestern Western Australia ( $20^{\circ}24'S$ ,  $118^{\circ}32'E$ ) between 1 June and 22 July 2008. The relatively flat landscape is dominated by sandy soils covered with spinifex (*Triodia* spp.), a spiky grass that forms dense hummocks that are <50 cm high. Kalutas were captured in box aluminium traps ( $33 \times 9 \times 9$  cm; Type A; Elliott Scientific Equipment, Upwey, Australia) baited with a mixture of peanut butter and oats. To prevent ants attacking animals in traps, Antex (David Gray & Co., O'Connor, Australia) containing 2 g/kg Bifenthrin was sprinkled sparingly around each trap.

To measure  $T_b$  and movement patterns, temperature-calibrated transmitters (Sirtrack, ~2 g, 7% of body mass) were implanted intraperitoneally under oxygen/Isoflurane anesthesia (for details see Körtner and Geiser 2009). The temperature sensitive transmitters had been previously calibrated in a water bath against a precision mercury thermometer to the nearest  $0.1^{\circ}\text{C}$ . Animals were tracked daily to their nest site in the evening and the location was determined using a handheld GPS (Garmin 12x and eTrex, Garmin Inc., Olathe, KS, USA). A mobile receiver data logger (Körtner and Geiser 2000) was placed close to the

burrow recording the interval between transmitter pulses every 10 min. Data were downloaded to a PC every few days and  $T_{bs}$  were calculated from the pulse interval data based on the original calibration.

Torpor entry and arousal were defined by  $T_b$  falling below and rising above  $30^{\circ}\text{C}$ , respectively, and torpor bout length was calculated from the time that  $T_b$  remained below  $30^{\circ}\text{C}$  (Körtner and Geiser 2000, 2009). As the exact temperature conditions in the burrows was unknown, cooling rates were calculated only for long torpor bouts during which  $T_b$  had reached a stable plateau following the procedure described by Nicol and Andersen (2007). 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  $30^{\circ}\text{C}$ ). In addition, the maximal arousal rate was defined as the maximal temperature increase over a 10 min interval (i.e. between two logger readings).

The activity period of kalutas was inferred from the absence or presence of records from the logger traces. In addition, movement and home range size was determined by radio-tracking kalutas during their activity phase. Animals were tracked to their location and grid coordinates were logged on a handheld GPS.

To assess whether movements were restricted to a temporal stable home range (stable over the time of the study) a “Site Fidelity Test” with the software package Animal Movement V2 (Hooge and Eichenlaub 1997) was performed for each individual. In this test 50 minimum convex polygons (MCPs) were calculated based on the original distance between sequential locations, but with randomised direction, and compared with the original MCP for the tested individual (see below).

Home range size was primarily calculated as MCP (Animal Movement V2; Hooge and Eichenlaub 1997) because the uniformity of the landscape at the study site and the even scattering of location records facilitated this geometrical method. In addition and to allow future comparisons with literature data, Kernel home range (90% and 50 isopleths) was calculated with the same software package using the default settings for an ad hoc calculation of a smoothing parameter via least square cross validation. The effect of sample size on MCPs was assessed by plotting home range size against number of location records, using stepwise removal of a random number of records from each animal's data set. Data were processed with the “MCP Sample size Bootstrap” procedure in Animal Movement V2 (Hooge and Eichenlaub 1997). Curves for our data tended to flatten between 40 and 60 locations for home range estimates.

Overlap between home ranges of two neighbouring individuals was analysed by intersecting the two home range polygons (100% MCP) and calculating percentage

overlap. Because this percentage is a function of home range size and therefore generally differs between the two members of the pair analysed, the following index was used including the home range size of both individuals (Körtner et al. 2007):

$$[(\text{area}_{\alpha\beta}/\text{home range}_\alpha) \times (\text{area}_{\alpha\beta}/\text{home range}_\beta)]^{0.5}$$

where  $\text{area}_{\alpha\beta}$  is the overlapping area and  $\text{home range}_\alpha$  and  $\text{home range}_\beta$  are the home ranges of individual  $\alpha$  and  $\beta$ , respectively.

Ambient temperature was measured at various locations throughout the study area with miniature data loggers at 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). Measurements included air temperature ( $T_{\text{air}}$ ) and humidity that were measured in the shade ~1 m above ground (in a clump of stunted trees with an additional cardboard screen), surface temperature ( $T_{\text{surf}}$ , i-Button was slightly covered with sand) that was recorded at two locations, temperature within spinifex hummocks at two locations and soil temperature ( $T_{\text{soil}}$ ) at 5, 10, 20 and 40 cm depth at two sites. Rainfall data were obtained from the Australian Bureau of Meteorology for Port Hedland's airport situated approximately 15 km from the study site.

#### Activity in captive animals

Five kalutas (4 males, 1 female) that were originally trapped in 2007 approximately 5 km north of the field study site and at the time of the measurements were about 2 years old. Animals were transferred to Armidale and housed in plastic cages ( $L \times W \times H$ : 50 × 35 × 20 cm) with sawdust bedding and cardboard boxes for shelter. They were fed daily between 14:00 and 16:00 with a mix of soaked cat food pellets and canned pet food supplemented with mealworms and vitamins, but remained undisturbed during the remainder of the day. Kalutas were maintained at room temperature (~19°C) at a photoperiod of LD 12:12 and later 14:10 to assess photoperiodic effects. Activity patterns inside their cages were measured with passive infrared sensors (Körtner and Geiser 1995). Activity counts were summed over 15-min periods and stored on a custom-made data logger and transferred to a PC every few days. Daily activity traces were averaged for each individual over an 11-day period and these were then averaged for all five kalutas.

#### Statistics

Data sets were compared using Student's  $t$  tests and ANOVAs. Significance was assumed at a 5% level. Data

are presented as the mean ± 1 SD (mean of the mean of individuals); “ $n$ ” denotes the number of individuals and “ $N$ ” the number of measurements.

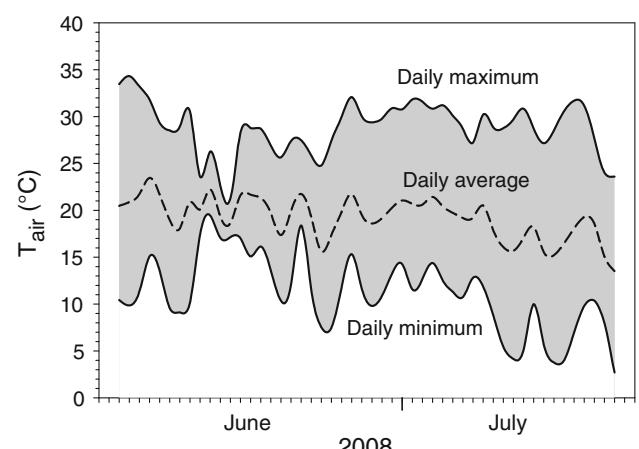
## Results

### Ambient temperature and rainfall

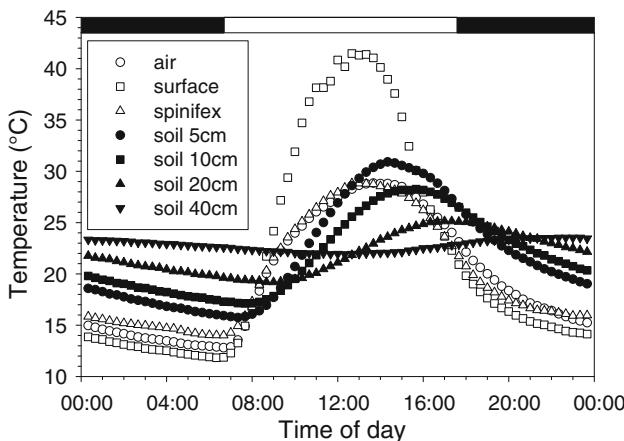
Although the study was conducted during the winter dry season, rain fell on five consecutive days (10–14 June) totalling 35 mm. Over the study period the average daily maximum  $T_{\text{air}}$  (shade, 1 m above ground) was  $28.8 \pm 2.8^\circ\text{C}$  and the average minimum  $11.2 \pm 4.0^\circ\text{C}$  (Fig. 1). Apart from the rainy period weather was predominantly sunny and  $T_{\text{air}}$  fluctuated by on average 19°C over 24 h. Temperatures within spinifex hummocks followed  $T_{\text{air}}$  closely (Fig. 2). In contrast, the amplitude of surface temperature ( $T_{\text{surf}}$ ) exceeded that of  $T_{\text{air}}$  considerably and on sunny days reached 40°C. Underground daily temperature fluctuations were progressively buffered and delayed with increasing depth. At 40 cm, the greatest depth measured,  $T_{\text{soil}}$  was about 23°C with just discernable daily temperature variations.

### Body mass and activity of wild kalutas

The body mass of trapped kalutas was on average  $26.9 \pm 3.0$  g and did not differ between males ( $n = 9$ ) and females ( $n = 4$ ) ( $T_3 = 0.87$ ,  $P = 0.447$ ). Kalutas (7 males, 4 females) were tracked for an average of  $19.8 \pm 11.6$  (range 2–40) days and the end of the measurements were determined by predation ( $n = 2$ ), transmitter failure ( $n = 4$ , confirmed by recapture) or the end of the study ( $n = 5$ ). Radio-tracking resulted in  $85.2 \pm 54.3$  (range



**Fig. 1** Daily average, minimum and maximum air temperature over the study period at the study site close to Port Hedland, Western Australia



**Fig. 2** Average temperature profiles for air temperature ( $T_{\text{air}}$ ), surface temperature ( $T_{\text{surf}}$ ), temperature within spinifex hummocks and underground ( $T_{\text{soil}}$ ) at various depths

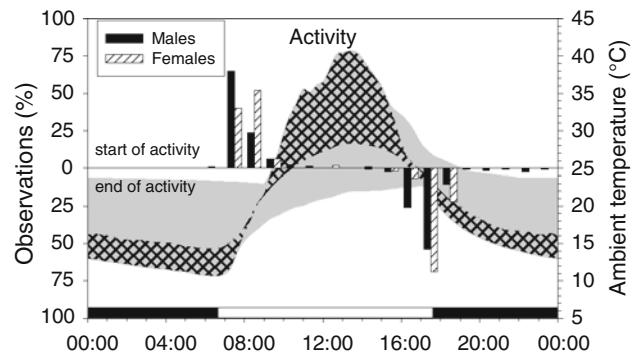
12–187) location records per individual including burrow locations and daytime tracking during the active phase.

Individual kalutas used up to six burrows during the monitoring period. Two of these burrows were excavated and in one instance the entrance was found more than 2 m away from the nest chamber with a maze of tunnels in between. The nest chamber was situated 33 cm under ground and was lined sparsely with dried grass. The other burrow constituted a simple 80 cm long tunnel with a grass-lined nest chamber 35 cm deep. It remains unclear whether the burrows had been constructed by the kalutas themselves or by some of the rodents found in the same area. Individual burrows were used for up to 16 consecutive days.

Kalutas were almost entirely diurnal. The inference of activity from the presence and absence from burrows was supported by the patterns of  $T_b$  (see below). Excluding the rainy period in June, activity commenced on average  $84.7 \pm 33.2$  min ( $n = 10, N = 167$ ) after sunrise and animals usually returned to their burrows  $1.06 \pm 36.1$  min ( $n = 10, N = 157$ ) before sunset (Fig. 3). However, occasionally animals moved between nest locations during the early night. These general activity patterns changed only during the rainfall period in June when the activity patterns became disrupted and activity onset was often delayed.

Most foraging took place within spinifex hummocks and the bare ground between hummocks was covered at high speed. Overall, foraging patterns appeared to differ between the sexes. When the distance between subsequent locations recorded <60 min apart were compared, males had travelled significantly further  $1.93 \pm 0.58$  m/min than females  $1.22 \pm 0.29$  m/min ( $T_8 = 2.7, P = 0.027$ ).

Sequential location records suggested site fidelity for all individuals ( $P < 0.02$ ), with the exception of the single female that was killed by a predator shortly after release. The MCP home range of males (MCP:  $3.1 \pm 1.0$  ha,



**Fig. 3** Activity timing of male and female kalutas. Positive bars indicate the onset and negative bars the end of the activity period. The envelope of ambient temperatures available to animals (see Fig. 2) over time is shown as greyed area. Temperatures available above ground are represented by the hatched area. Black horizontal bars indicate the dark phase (sunset to sunrise)

Kernel 90%:  $1.3 \pm 0.5$  ha, Kernel 50%:  $0.2 \pm 0.1$  ha,  $n = 7$ ) was significantly larger than that of females (MCP:  $1.0 \pm 0.4$  ha, Kernel 90%:  $1.1 \pm 0.6$  ha, Kernel 50%:  $0.2 \pm 0.1$  ha,  $n = 4$ ;  $T_8 = 4.96, P = 0.001$ ), although there was no discernable difference in habitat structure. In fact, home ranges (MCP) of individuals of either sex overlapped substantially by an average of  $24.9 \pm 17.5\%$ . We recorded overlap between three male–male pairs, two female–female pairs and eight male–female pairs without apparent differences in overlap. Despite the overlap between home range, burrow sharing was observed only once in two males.

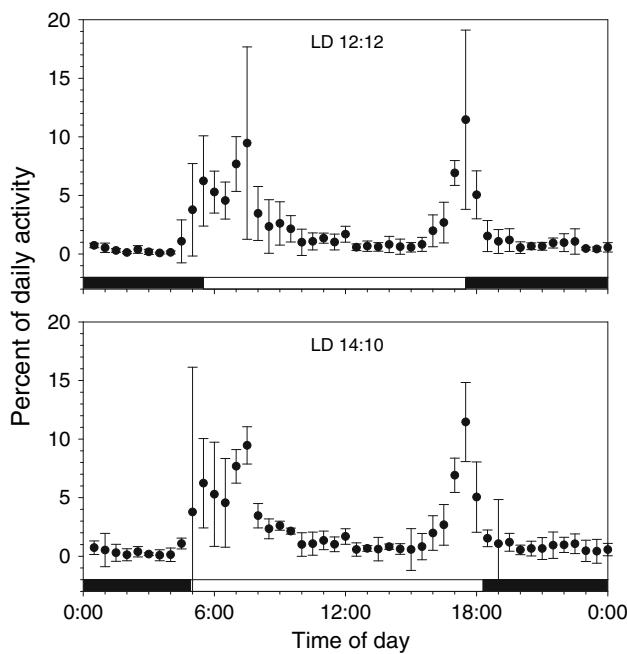
#### Activity in captive animals

Similar to wild kalutas, captive individuals exhibited predominantly diurnal activity (i.e. activity commenced after lights on and terminated with lights off) (Fig. 4). However, most activity occurred in the early morning and late afternoon with less activity during the middle of the day. Animals were fed daily between 14:00 and 16:00 and feeding activity would have contributed to the afternoon activity bout. However, even then maximum activity was observed 1–2 h after feeding. Hence it is unlikely that afternoon activity occurred only in response to food provision.

Although patterns of daily activity were similar for the kalutas measured, total daily activity scores varied substantially between individuals. It was lowest in the female, but because only one female was measured a statistical comparison between sexes was not possible.

#### Body temperature and torpor

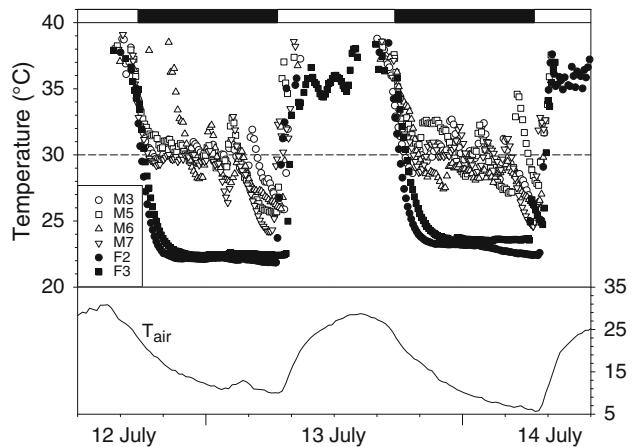
Body temperature in free-ranging kalutas was significantly influenced by the daily activity cycle ( $F_{1,16} = 703.3$ ,



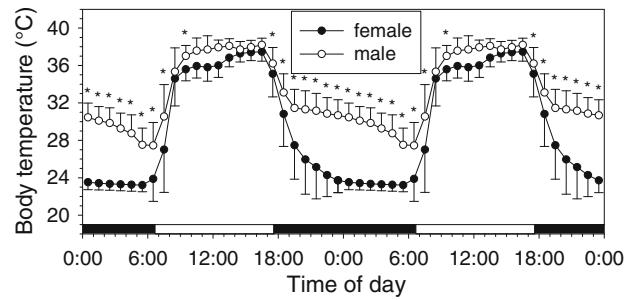
**Fig. 4** Average activity patterns of kalutas (4 males, 1 female) in the laboratory subjected to a photoperiod of LD 12:12 and 14:10. Animals were kept at room temperature ( $\sim 19^{\circ}\text{C}$ ). Activity scores are expressed as percentage of total daily activity

$P < 0.001$ ) and by gender ( $F_{1,16} = 114.0$ ,  $P < 0.001$ ). There was also a significant interaction between these two factors ( $F_{1,16} = 40.6$ ,  $P < 0.001$ ). In both sexes  $T_b$  was significantly higher during the active phase (mean of the mean male:  $37.2 \pm 0.52^{\circ}\text{C}$ ,  $n = 7$ ; female:  $35.8 \pm 0.73^{\circ}\text{C}$ ,  $n = 3$ ) than during the rest phase (male:  $30.7 \pm 0.90$ ,  $n = 7$ ; female:  $25.1 \pm 0.27$ ,  $n = 3$ ;  $P < 0.001$ ; Figs. 5, 6). Furthermore, males maintained higher  $T_b$ s than females during active ( $T_{16} = 3.04$ , adj  $P = 0.035$  Tukey–Kramer) as well as rest phase ( $T_{16} = 12.04$ , adj  $P < 0.001$  Tukey–Kramer). When all  $T_b$  measurements were separated into 1-h intervals (Fig. 6), it appeared that males maintained a higher  $T_b$  than females throughout the rest phase and also during the early morning after activity had commenced. During the afternoon male and female  $T_b$ s matched closely (Figs. 5, 6).

Torpor was observed on 165 out of 166 observation days (99%). Only one male did not enter torpor during the first night after his release following transmitter implantation. Although both sexes used torpor extensively, torpor patterns differed substantially (Fig. 5). Females usually entered torpor shortly after having returned to their burrow in the evening,  $T_b$  fell to  $\sim 24^{\circ}\text{C}$ , close to average  $T_{\text{soil}}$ , and was maintained at this low level until morning arousal. In contrast, males regulated their  $T_b$  around  $30^{\circ}\text{C}$  through most of the night, but showed frequent cooling and rewarming episodes that culminated into usually one sometimes several short torpor bouts before final arousal in

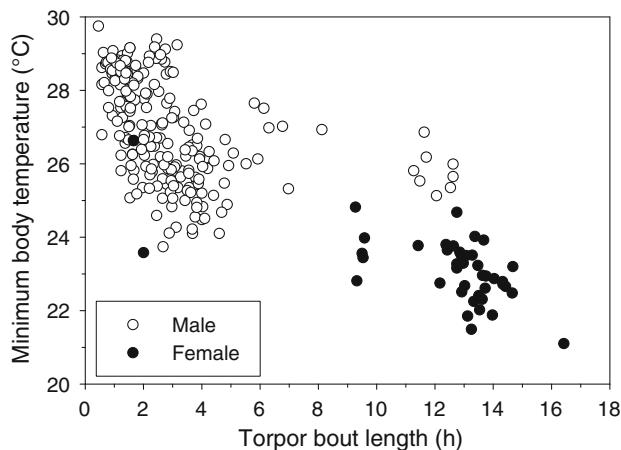


**Fig. 5** Body temperature traces of four male (open symbols) and two female kalutas (closed symbols) over two consecutive days. The bottom panel depicts  $T_{\text{air}}$  over the same time period. Black horizontal bars indicate the dark phase



**Fig. 6** Average (mean of the means for individuals)  $T_b$  of male ( $n = 7$ ) and female kalutas ( $n = 3$ ). Original data were divided into 30 min bins. Significant differences between the sexes are indicated with asterisks. Black horizontal bars indicate the dark phase. To show the patterns more clearly, data are repeated over 2 days

the morning (Fig. 5). Consequently most torpor bouts in males were shorter than 6 h (mean of the mean:  $2.68 \pm 0.63$  h,  $n = 7$ ) whereas female torpor lasted, with the exception of two short bouts, 9–16.4 h (mean of the mean  $12.33 \pm 0.31$  h,  $n = 3$ ;  $T_7 = 32.5$ ,  $P < 0.001$ ) (Fig. 7). Even when multiple torpor bouts were summed up over the entire rest phase males ( $5.49 \pm 1.29$  h,  $n = 7$ ) spent significantly less time torpid than females ( $13.59 \pm 1.27$  h,  $n = 3$ ;  $T_3 = 9.2$ ,  $P < 0.01$ ). Mainly because of their longer torpor bouts (Fig. 7), females reached significantly lower minimum  $T_b$ s during torpor ( $23.8 \pm 1.0^{\circ}\text{C}$ ,  $n = 3$ ) than males ( $27.0 \pm 0.4^{\circ}\text{C}$ ,  $n = 7$ ;  $T_2 = 5.4$ ,  $P < 0.05$ ). Accordingly, the absolute  $T_b$  minimum observed for each individual also differed between the sexes (males:  $24.5 \pm 0.5^{\circ}\text{C}$ ,  $n = 3$ ; females:  $21.4 \pm 0.4^{\circ}\text{C}$ ,  $n = 3$ ;  $T_4 = 10.0$ ,  $P = 0.001$ ). However, even during the few long torpor bouts observed in males,  $T_b$  remained above that of females (Fig. 7). In contrast,



**Fig. 7** Relationship between minimum  $T_b$  during torpor and torpor bout length in free-ranging male and female kalutas

arousal rate did not differ between the sexes and was on average  $0.20 \pm 0.05\text{ }^{\circ}\text{C}/\text{min}$  ( $T_3 = 2.1$ ,  $P = 0.129$ ) and the maximal arousal rate over 10 min was  $0.32 \pm 0.05\text{ }^{\circ}\text{C}/\text{min}$  ( $T_2 = 1.7$ ,  $P = 0.236$ ). As the exact  $T_a$  in the burrows was not known, cooling could be assessed only for 26 of the female torpor bouts when  $T_b$  had reached a plateau. The cooling constant for these bouts was  $-1.20 \pm 0.23\text{ h}^{-1}$  ( $n = 3$ ,  $N = 26$ ).

## Discussion

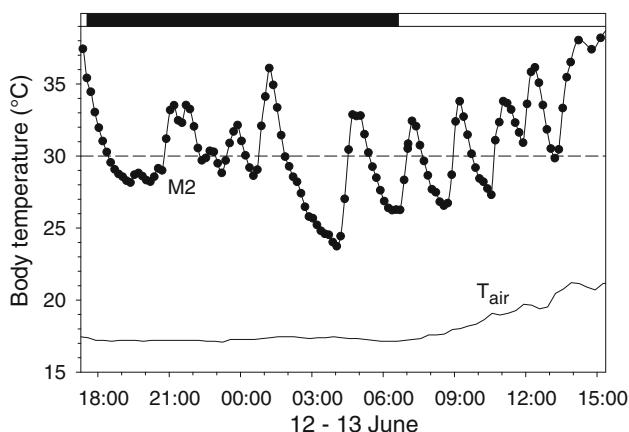
As our study site was situated in a tropical desert, winter temperature conditions including the underground temperatures were more than  $5^{\circ}\text{C}$  warmer than those reported from previous studies conducted in central Australia (Geiser and Pavey 2007; Körtner et al. 2008; Warnecke et al. 2008; Körtner and Geiser 2009). However, more importantly and rather unexpectedly, kalutas were active during the day and hence avoided the cooler nights entirely by resting in their burrows. These patterns were apparently not a direct effect of the daily cycle in  $T_{\text{air}}$ , since it persisted in kalutas even at constant room temperature of  $\sim 19^{\circ}\text{C}$  in the laboratory. Such strict diurnal activity patterns are not only unusual for dasyurid marsupials (Croft 2003), but for small mammals in general presumably because during the daytime they would be more vulnerable to visually hunting predators such as raptors (Vaughan 1986), which were also common at the study site. In the case of kalutas, it is probably the protection offered by in-penetrable and closely spaced spinifex hummocks, in which most foraging took place that allowed diurnal activity. Occasional activity bouts during the daytime have also been observed in a few other desert dasyurids that live in highly structured habitats that offer foraging

opportunities in sheltered locations such as rock crevices and soil cracks (Geiser and Pavey 2007; Warnecke and Geiser 2009). The cooler temperature conditions within spinifex hummocks would also prevent hyperthermia, which because of solar radiation, high  $T_{\text{surf}}$ s exceeding  $40^{\circ}\text{C}$ , and minimal capacity for heat storage associated with small body size presents a risk even in winter.

While the shade provided by spinifex was evidently sufficient during winters, summer temperature conditions will be more problematic. Kalutas are able to cope with higher ambient temperatures better than most other small mammals. Assisted by their low basal metabolic rate they can tolerate  $T_{\text{air}}$ s of at least  $38^{\circ}\text{C}$  (Withers and Cooper 2009), which is in fact above the average monthly  $T_{\text{air}}$  maximum (measured in the shade) during summer at the study site ( $\sim 36.5^{\circ}\text{C}$ , Port Hedland; Australian Bureau of Meteorology). At these high  $T_{\text{air}}$ s evaporative water loss is of course elevated (Withers and Cooper 2009), usually not viable in a desert environment, and there will be many days when  $T_{\text{air}}$  exceeds the monthly average.  $T_{\text{air}}$ s of up to  $49^{\circ}\text{C}$  that have been recorded at the site and with intense solar radiation operational temperatures even in spinifex hummocks could be higher again. Hence temperature conditions during summer will regularly reach lethal levels for small mammals and kalutas would have to shelter in their burrows. Therefore, during hot summer days bimodal patterns with early morning and late afternoon activity bouts similar to those observed in the laboratory are more likely.

Given the mild climatic conditions, diurnal activity patterns and low metabolic rate of kalutas (Withers and Cooper 2009; present data), in comparison to other small desert mammals the species is well placed to survive in a resource-poor desert environment. Yet during winter daily torpor remains as much a part of the daily routine as it is for central Australian dasyurids. In fact, torpor expression in kalutas is similar to some of the smallest arid zone marsupials, dunnarts (*Sminthopsis* spp.; Warnecke et al. 2008; Körtner and Geiser 2009) and planigales (*Planigale gilesi*; Warnecke and Geiser 2009) living in the more extreme central Australian deserts.

While the mild temperature conditions did not influence torpor frequency, some effects were apparent when compared to central Australian dasyurids. The minimum  $T_b$  reached during torpor remained above  $20^{\circ}\text{C}$ , just above  $T_{\text{soil}}$  and was therefore considerably higher in the tropical kalutas than in central Australian species in which  $T_b$  approaches  $10^{\circ}\text{C}$  (Körtner et al. 2008; Warnecke et al. 2008; Körtner and Geiser 2009; Warnecke and Geiser 2009). Accordingly, the physiological limit for a reduction in  $T_b$  appears to be only  $\sim 18^{\circ}\text{C}$  (Withers and Cooper 2009), also higher than in many other desert dasyurids (Geiser and Körtner 2009). Hence it appears that the limits



**Fig. 8** Body temperature trace of a male kaluta during a rainy day. The animal remained in its burrow for most of the day and entered multiple short torpor bouts. Air temperature is represented by a solid line and the dark phase by a horizontal black bar

of torpor physiology are linked to the environmental conditions animals experience in their natural habitat. Nevertheless, despite the higher  $T_b$  during torpor and the reversed activity/rest cycle, arousal rates observed for kalutas was consistent with that observed in other free-ranging desert dasyurids, i.e. slower than in the smaller *Sminthopsis crassicaudata* (10 g, mean arousal rate  $0.27 \pm 0.01$  °C/min, Warnecke et al. 2008) and faster than in the larger *Dasyurus blythi* (75 g,  $0.12 \pm 0.04$  °C/min, Körtner et al. 2008).

There were other significant differences between the torpor patterns observed in nocturnal desert dasyurids and the diurnal kaluta. In nocturnal insectivorous species including both marsupials and placentals torpor often commences during the night after an only short activity period and terminates halfway during the rest phase at about midday often assisted by passive rewarming and occasionally basking (Turbill et al. 2003; Geiser et al 2004; Geiser and Pavey 2007; Körtner et al. 2008; Warnecke et al. 2008; Lovegrove and Génin 2008; Körtner and Geiser 2009). While arousal during the hottest time of the day reduces arousal costs (Lovegrove et al. 1999; Geiser and Drury 2003; Warnecke et al. 2008; Körtner and Geiser 2009), early torpor entry during the night curtails normal activity and therefore foraging success. In contrast, in kalutas torpor was, with the exception of rainy days (Fig. 8), always restricted to the rest phase and activity was therefore not compromised—an arrangement that maximises both foraging return as well as energy savings. Nevertheless, it appears that only female kalutas used this strategy to its full potential whereas the similar-sized males usually remained normothermic through most of the night albeit at a lowered  $T_b$ . Consequently, thermoregulatory costs would have been higher in males than in females, but

perhaps not excessively so because of low  $T_{bs}$  and the mild  $T_{soil}$  in the tropics. The lower limit of thermoneutral zone of kalutas is about 26°C (Withers and Cooper 2009), only a few degrees above average  $T_{soil}$ . This might explain why burrow sharing was observed only once in kalutas, whereas huddling can be common in some other desert dasyurids (Morton 1978; Körtner et al. 2007). Despite overlapping home ranges, kalutas remained largely solitary during winter prior to the reproductive season starting in September (Woolley 1991).

Besides higher energy expenditure during rest associated with elevated  $T_{bs}$ , the active phase is probably also more energy demanding for males than females. In males movements were more extensive, home range size was more than twice as large as that of females with likely energetic consequences (Kelt and Van Vuren 2001), and during early morning  $T_b$  was again regulated at a higher level than that of females. Although mating in kalutas commences not before September (Woolley 1991), it is possible that the gender-related differences in life history, which become most eminent during the reproductive season, impinge early on the behaviour and physiology of kalutas. The overlap of male home ranges with that of several females should maximise mating success during the single short mating season that will culminate in a complete male die-off in the wild (Woolley 1991), an unusual fate that kalutas share with some other dasyurid marsupials (Tyndale-Biscoe and Renfree 1987). In contrast, females can live more than 2 years and reproduce twice. Hence, female reproduction requires not only sustained and substantial energy transfer to offspring, but also offers the prospect of survival and a second reproductive season. For example, in the related antechinus (*Antechinus* spp.), which show similar mating and life history patterns to kalutas, females also use torpor more extensively than males (Geiser 1988). Furthermore, female mulgaras (*Dasyurus* spp.) are able to accumulate body energy stores prior to giving birth by entering torpor extensively and thus surplus energy can be later transferred to the growing offspring (Geiser and Masters 1994).

In conclusion, daily torpor is used extensively in some tropical mammals and is by no means restricted to temperate climates. A growing number of tropical species is known to be able to enter torpor, and also to employ it frequently in the wild. This includes bats (Audet and Thomas 1997; Bartels et al. 1998; Bonaccorso and McNab 1997; only laboratory data to date), primates (Dausmann 2008), Afrotheria (Lovegrove and Génin 2008) and now also dasyurids. Probably, torpor is more commonly used in warmer climates than previously thought. There is also mounting evidence that differences in life history between the sexes can result in pronounced differences in the use of energy saving mechanisms such as torpor. This

phenomenon questions the validity of single species-specific physiological values—a field that warrants further investigation.

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