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Opportunistic hibernation by a free-ranging marsupial

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Abstract

Knowledge about the thermal biology of heterothermic marsupials in their native habitats is scarce. We aimed to examine torpor patterns in the free-ranging western pygmy-possum (*Cercartetus concinnus*), a small marsupial found in cool temperate and semi-arid habitat in southern Australia and known to express aseasonal hibernation in captivity. Temperature telemetry revealed that during two consecutive winters four out of seven animals in a habitat with Mediterranean climate used both short (<24 h in duration) and prolonged (>24 h) torpor bouts (duration 6.4 ± 5.4 h and 89.7 ± 45.9 h, respectively). Torpor patterns were highly flexible among individuals, but low ambient temperatures facilitated torpor. Maximum torpor bout duration was 186.0 h and the minimum body temperature measured was 4.1°C. Individuals using short bouts entered torpor before sunrise at the end of the active phase, whereas those using prolonged torpor entered in the early evening after sunset. Rewarming from torpor usually occurred shortly after midday, when daily ambient temperature increased. We present the first quantitative data on a marsupial species expressing opportunistic hibernation during winter in the wild, and show that torpor use in *C. concinnus* is strongly influenced by small-scale microclimatic conditions.

Introduction

Hibernation has long been recognized as a highly successful approach by small mammals to conserve energy during unfavourable environmental conditions. It is characterized by a sequence of prolonged torpor bouts (torpor bouts >24 h in duration), where, over a wide range of ambient temperatures (T_a), they can reduce metabolic rates to <1% of resting values and lower body temperature (T_b) to ~T_a (Lyman, 1982; Wang, 1989). Seasonal hibernation is most prevalent and frequently studied in small placental mammals such as rodents and bats inhabiting high northern latitudes. In winter, these environments undergo a pronounced decrease in food resources and T_a (Wang, 1978). However, seasonal hibernation is also known to occur in the southern hemisphere. For example, it is employed by *Cheirogaleus* and *Microcebus* spp. lemurs and lesser hedgehog tenrecs *Echinops telfairi* during the dry season in the tropics of Madagascar (Dausmann *et al*., 2005; Lovegrove & Génin, 2008; Kobbe & Dausmann, 2009; Schmid & Ganzhorn, 2009), the South African woodland dormouse *Graphiurus murinus* (McKechnie & Mzilikazi, 2011), and a South American armadillo *Zaedyus pichiy* (Superina & Boily, 2007). In Australia, the two known seasonal hibernators are the monotreme short-beaked echidna (*Tachyglossus aculeatus*) (Nicol & Andersen, 2002), and the marsupial mountain pygmy-possum (*Burramys parvus*) (Körtner & Geiser, 1998).

Nevertheless, several field studies conducted in the southern hemisphere have revealed that in a number of species hibernation can be irregular and differ from the ‘classical’ seasonal model. For example, the hibernation patterns of Australian tree-roosting bats that inhabit milder yet less predictable environments, where some food is available during the winter, are more variable than those of obligate seasonal hibernators (Turbill & Geiser, 2008; Stawski, Turbill & Geiser, 2009). Similar torpor use is seen for Egyptian free-tailed bats (*Tadarida aegyptiaca*), and Hottentot golden moles (*Amblysomus hottentottus longiceps*) (Scantlebury *et al*., 2008; Cory Toussaint, McKechnie & van der Merwe, 2010) of South Africa. Additionally, Malagasy mouse lemurs and tenrecs show a range of torpor strategies among conspecifics within a hibernation season (Lovegrove & Génin, 2008; Kobbe & Dausmann, 2009; Schmid & Ganzhorn, 2009; Kobbe, Ganzhorn & Dausmann, 2011). These species usually employ torpor opportunistically in direct response to prevailing poor environmental conditions, with considerable flexibility in torpor bout duration both within and among individuals.

Similar patterns can be found among Australian marsupials. The alpine *B. parvus* might be the only known marsupial seasonal hibernator, but it is not the only Australian marsupial species capable of prolonged torpor. Three other pygmy-possums of the genus *Cercartetus* (*C. concinnus*, *C. lepidus* and *C. nanus*), as well as the feathertail glider (*Acrobates pygmaeus*), which inhabit more temperate environments, readily enter prolonged torpor in captivity throughout the year, usually in response to low T_a and/or food withdrawal (Geiser, 1987; Jones & Geiser, 1992; Song, Körtner & Geiser, 1997). However, torpor patterns can differ between captive and free-ranging individuals (Geiser *et al*., 2000). Apart from some incidental accounts of *C. concinnus* and *C. nanus* being found torpid when trapped in the wild (Tulloch, 2001; Bladon, Dickman & Hume, 2002; B. Cadzow, pers. comm.), the only published accounts on torpor use in free-ranging *C. concinnus* are based on very limited data (Geiser & Körtner, 2004; Morrant & Petit, 2011). This paucity of information is impeding our appreciation of the different patterns of torpor and activity expressed by marsupial hibernators in their native habitats.

The western pygmy-possum (*C. concinnus*) (henceforth 'pygmy-possum') is a small (8–20 g), cryptic marsupial of the family Burramyidae, which inhabits mallee heath and dry sclerophyll forest with semi-arid and Mediterranean climates (i.e. hot dry summers and cool wet winters). It is nocturnal and arboreal by habit, and feeds mainly on a diet of nectar, pollen and invertebrates (Menkhorst & Knight, 2001; Carthew, Cadzow & Foulkes, 2008). Nest sites include tree hollows, leaf litter, tree canopies and disused burrows of other terrestrial species (Misso, 1997; Kemp & Carthew, 2004; Pestell & Petit, 2007; Morrant & Petit, 2011). To date, the only quantitative studies examining this species' torpor physiology have been derived from captive individuals (Wakefield, 1970; Geiser, 1987). Based on these studies, and those examining related species (Geiser, 1987, 1993), we expected torpor use in free-ranging pygmy-possums to be closely related to changes in T_a. Specifically, we hypothesized that individuals would remain in prolonged torpor if T_a stayed cold for extended periods, and use short torpor bouts (<24 h in duration) on days that were comparatively warmer. Therefore, we monitored T_b during winter to examine the temporal organization of torpor use in response to environmental conditions, and to see whether and to what extent pygmy-possums express hibernation in the wild.

Methods

The study was conducted in an open mallee heathland in Newland Head Conservation Park in south-east South Australia (35°36'S., 138°31'E.) in winter of 2008 (22 May to 1 June) and 2009 (8 July to 23 August). Seven pygmy-possums (14.0 ± 3.2 g; two males in 2008, two females and three males in 2009) were wild-caught using 20-L bucket pitfall traps without drift fences. Animals were transported to a field laboratory where they were housed in individual plastic cages (38 × 26 × 23 cm) under natural photoperiod for less than 3 days. Food (pureed fruit and a nectar substitute consisting of high protein baby cereal, honey and vitamins) and water were freely available.

We measured T_b using temperature-sensitive FM radio transmitters (1.0–1.4 g BD-2TH; Holohil Systems Ltd, Carp, ON, Canada), which were within the mass range recommended for small terrestrial mammals (Rojas, Körtner & Geiser, 2010). Transmitters were implanted into the intraperitoneal cavity of pygmy-possums under inhalation anaesthesia of isoflurane in oxygen (4% induction, 1–3% maintenance). The midline incision in the abdominal cavity was sutured closed using Coated Vicryl (2.0 metric, Ethicon Inc., Sommerville, NJ, USA) for the muscle layer and Chromic Gut (2.0 metric, Ethicon Inc.) for the skin. After the procedure a local anaesthetic (Ban Itch; Apex Laboratories, Sommerby, NSW, Australia) and a spray bandage (Leuko; BSN Medical, Clayton, Vic, Australia) were applied. Animals were warmed after surgery and were given a honey-flavoured oral analgesic (Metacam; Boehringer Ingelheim, North Ryde, NSW, Australia) after regaining consciousness. Prior to implantation, transmitters were coated with an inert wax and calibrated to the nearest 0.1°C in a water bath from 3–40°C at ~7°C increments using a mercury thermometer traceable to the national standard. Animals were allowed to recover for ~48 h before release at sunset at the point of capture, where they were given an additional spray bandage application. No individuals were recaptured after release.

Pygmy-possums were located daily using radio receivers (Telonics TR-4 and Icom IC-R10) and Yagi antennas (AY/C, Titley Scientific, Lawnton, QLD, Australia). The T_b of individual animals at their nest sites was measured remotely at 10-min intervals using mobile receiver/loggers (for details, see Körtner & Geiser, 1998), which also provided information on times that pygmy-possums departed from and arrived at a nest site. Because of the short transmitter detection range (<20 m), the receiver/loggers required relocating if an animal changed its nesting spot, and as a result, not all torpor entries were recorded. Data were downloaded every 2–5 days. Additionally, manual T_b readings were taken using a receiver and a stopwatch several times each day. Absolute T_b values for one individual whose transmitter's thermal characteristics apparently drifted after 25 days were excluded from analyses.

Torpor bout entry was calculated as the time that T_b dropped below 32.1°C ($T_{b\text{-onset}}$) after Willis (2007): $T_{b\text{-onset}} = (0.041)*BM + (0.040)*T_{nest} + 31.083$, where BM is mean body mass (14.0 g), and T_{nest} is mean ambient nest site temperature measured at the time when normothermic T_b began to fall constantly before a torpor bout (10.6°C). The end of a torpor bout was defined as the time when T_b during rewarming increased to above 32.1°C. Any animal that was found with its T_b below this threshold was deemed to be torpid on that day. We use the terms 'short torpor' to describe a torpor bout <24 h in duration, 'prolonged torpor' for torpor bouts >24 h in duration, and 'hibernation' for a series of two or more prolonged torpor bouts, interrupted by rewarming to normothermia, but without activity.

The T_a was recorded to the nearest 0.5°C using data loggers (DS 1921G Thermochron iButtons, Dallas Semiconductor, Dallas, TX, USA) placed 1 m above ground in the shade within the study site (T_a; mean of $n = 16$ in 2008, $n = 11$ in 2009), as well as in positions analogous to the pygmy-possums' nesting sites in 2009 (T_{nest}; $n = 5$; e.g. in leaf litter beneath an adjacent tree of the same species).

Statistical analyses were conducted using *statistiXL* v1.8 and Statistical Package for the Social Sciences (SPSS Inc., Chicago, IL, USA) SigmaPlot v8.0. Differences among means (means of means for each individual) were evaluated using one-way analysis of variance (minimum T_b during torpor and effect of time on torpor use), paired *t*-tests (T_{nest} and T_a comparisons) and unpaired *t*-tests (T_b at start of active rewarming and T_a at torpor entry and rewarming times). An exponential decay function was used to examine the effect of minimum T_b during a torpor bout (independent variable) on torpor bout duration. The timing of torpor entry and rewarming was tested for non-random distribution using a Rayleigh's test (providing an *r*-value for significance), after which a Watson–Williams test was used to compare times among these variables (Zar, 1999). To improve the accuracy of the torpor entry time estimates derived from the Rayleigh's test, one outlying entry time value was omitted for each mean because it was >10 h later than the average for short bouts and >7 h later for prolonged bouts. The inclusion of these two outliers did not render the analyses insignificant ($P < 0.001$ for both, Rayleigh's test). Data are presented as mean ± 1 standard deviation; *n* denotes the number of individuals, *N* the number of measurements.

Results

Ambient conditions

The average daily minimum and maximum T_as during the 2008 tracking period were 7.4 ± 2.0°C (range 0.5–14.0°C) and 17.0 ± 4.0°C (11.0–31.5°C), respectively, and 6.6 ± 1.2°C (-2.5–16°C) and 15.2 ± 1.4°C (10–24°C) for 2009. Neither average minimum ($t_{24} = 1.31$, $P = 0.201$) nor maximum T_a ($t_{20} = 1.66$, $P = 0.113$) differed between years.

Individuals were almost always found nesting under leaf litter, usually at the base of dead *Banksia ornata* trees. T_{nest} (measured in 2009 only) was buffered to some extent from daily T_a fluctuations: the average minimum T_{nest} was 8.2 ± 2.1°C (1.0–11.5°C) and maximum was 13.2 ± 2.1°C (7.5–24.0°C). The mean daily variation for T_{nest} was 5.2 ± 2.1°C ($n = 5$, $N = 140$), which was significantly less than 8.6 ± 2.8°C for T_a ($n = 11$, $N = 462$; $t_{39} = 6.12$, $P < 0.001$, Fig. 1). In 2008, sunrise occurred at 07:13 h ± 2 min, sunset at 17:13 h ± 2 min; in 2009, at 07:10 h ± 12 min and 17:32 h ± 10 min. Day length ranged from 9.9–10.1 h in 2008 and 9.9–11.0 h in 2009.

Activity

Pygmy-possums were strictly nocturnal. Active animals left their nesting sites to forage ~2 h after sunset (19:15 h ± 68 min; $n = 7$, $N = 67$) and returned ~1.5 h before sunrise (05:33 h ± 115 min; $n = 5$, $N = 34$).

The average normothermic T_b was 37.5 ± 0.6°C ($n = 6$). The T_b of normothermic animals was high when they returned to nest sites after foraging, before initially cooling sharply and then increasing slowly over the course of a resting period (Fig. 2).

Torpor patterns

Pygmy-possums were found torpid on 63% of the 136 observed possum-days. The four individuals that were observed entering torpor were radio-tracked for 10–42 days, whereas the three that did not use torpor were only radio-tracked for between 2 and 11 days. The two individuals radio-tracked in 2008 did not enter torpor. The percentage of days that animals used torpor did not differ between the first and second halves of the radio-tracking period ($n = 5$; $F_{2,5} = 4.41$, $P = 0.079$).

We recorded a total of 38 individual torpor bouts ($n = 4$), 23 of which were measured in their entirety, while the records of the remaining bouts were incomplete because the pygmy-possums were located after they were already torpid. All individuals that entered torpor used both short torpor bouts (bouts <24 h in duration) and prolonged torpor bouts (>24 h in duration; Fig. 3). Interestingly, bouts were rarely synchronized and different individuals were not necessarily found to be torpid at the same time (Fig. 1). Three individuals entered series of between two and nine prolonged torpor bouts; we consider these examples of short-term hibernation. Short torpor bouts lasted for 6.4 ± 5.4 h (range 2.5–21.2 h; $n = 4$, $N = 10$), and prolonged bouts for 89.7 ± 45.9 h (range 38.5–186.0 h; $n = 4$, $N = 13$).

The nights that an animal entered torpor were significantly colder ($T_a = 8.6 \pm 1.0$°C, $n = 3$, $N = 32$) than those it remained normothermic (10.6 ± 0.6°C, $n = 3$, $N = 29$; $t_2 = 5.66$, $P = 0.030$). Similarly, on days a pygmy-possum rewarmed from prolonged torpor, T_a was significantly warmer (13.2 ± 0.7°C, $n = 4$, $N = 37$) than on days it remained torpid (11.7 ± 0.5°C, $n = 4$, $N = 45$; $t_3 = 8.06$, $P = 0.004$). Within a period of hibernation the duration of normothermic periods, after animals periodically rewarmed from torpor, was 5.5 ± 2.5 h (range 3.0–9.3 h; $n = 3$, $N = 10$). The mean T_b during these periods was 37.2 ± 0.4°C.

There was a clear bimodal distribution of T_b between normothermia and torpor ($n = 3$; Fig. 4). For T_b during torpor, the mean minimum T_b of short torpor bouts (11.1 ± 2.5°C; $n = 2$, $N = 8$) was higher than that of prolonged torpor (8.4 ± 2.3°C; $n = 3$, $N = 47$; $F_{3,51} = 4.21$, $P = 0.010$), and the absolute minimum T_b measured was 4.1°C at $T_a = 1.0$°C at 08:07 h, 33 h into a 111-h torpor bout. If an animal changed its nest site and an entire torpor bout was not recorded, minimum T_b was not used for calculations. After the initial cooling during torpor entry, the T_b of torpid animals closely followed daily T_{nest} fluctuations, which was especially pronounced for animals using prolonged torpor (see Figs 1 and 4). The mean daily minimum T_b of all torpid animals was 8.2 ± 1.4°C ($n = 3$, $N = 51$), which did not differ significantly from the mean daily minimum T_{nest} of 8.2 ± 1.8°C ($n = 3$, $N = 51$; $t_2 = 0.04$, $P = 0.971$). The minimum T_b during a torpor bout did not affect torpor bout duration ($n = 3$, $N = 16$; $R^2 = 0.227$, $F_{1,14} = 4.11$, $P = 0.067$).

On average, the T_b of torpid animals increased passively by 2.1 ± 1.7°C (range 0.1–5.8°C; $n = 3$, $N = 20$) with increasing T_{nest}, which was ~9% of the total T_b increase, before beginning active rewarming. The T_b at which active rewarming from torpor was initiated, as indicated by the steep rise of T_b above T_{nest}, was approximately the same for short (10.8 ± 2.0°C; $n = 3$, $N = 13$) and prolonged bouts (12.2 ± 0.2°C; $n = 3$, $N = 11$; $t_2 = 1.20$, $P = 0.354$). The maximum rewarming rate (calculated as the T_b difference during rewarming divided by the rewarm-

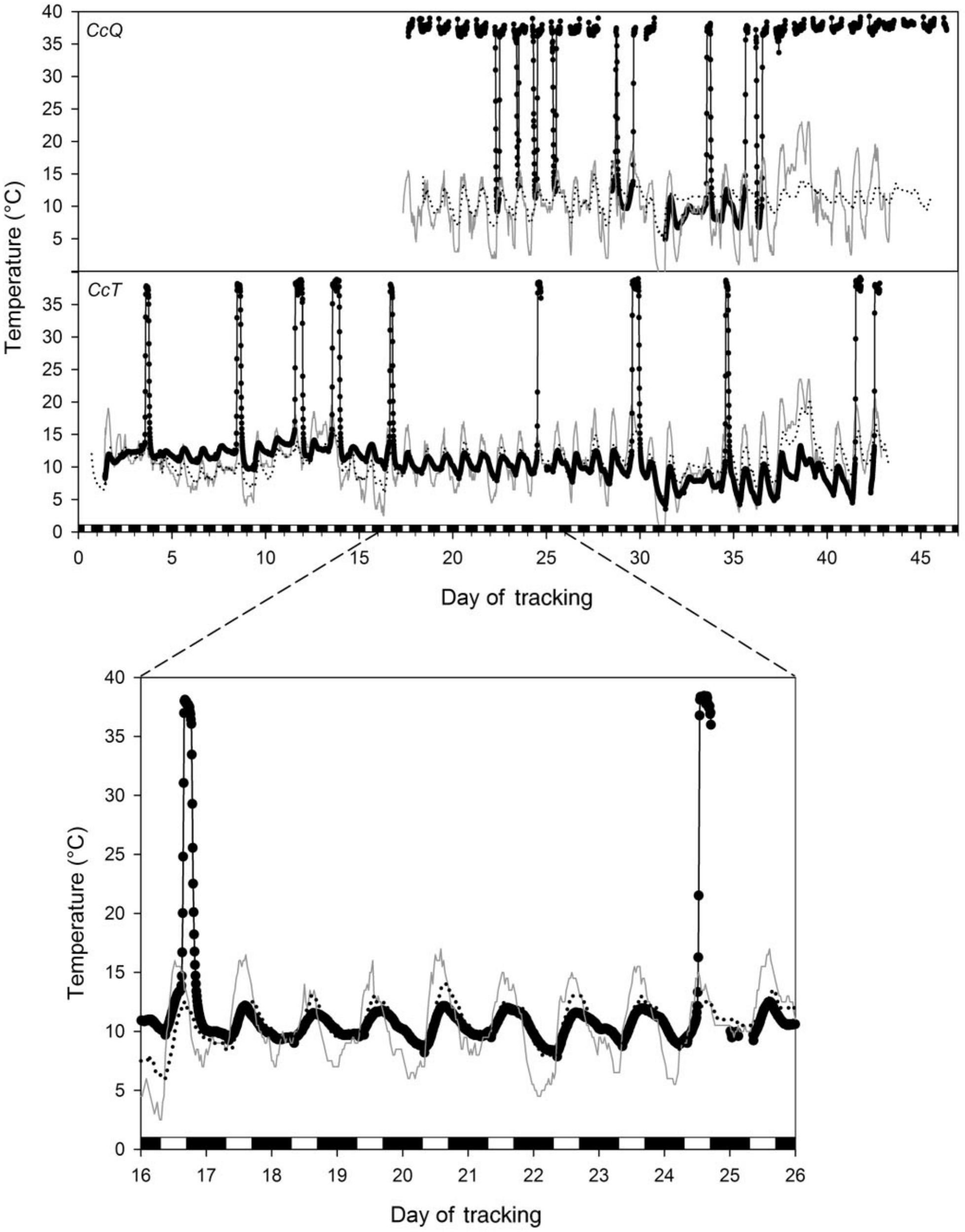

Figure 1 Body temperature (T_b, closed circles and black line) of two individual *Cercartetus concinnus* over a 6-week period (Day 1 = 9 July 2009) with ambient temperature (T_a, grey line) and nest site temperature (T_{nest}, dotted line). One animal (*CcQ*) used mostly short torpor bouts and spent an extended period of time normothermic, while the other (*CcT*) entered a period of hibernation (mean torpor bout length 4.6 ± 2.1 days). The magnified section shows detail of the longest single torpor bout measured (7.8 days); note T_b passively fluctuating with T_{nest}. Dark bars indicate the scotophase.

ing time) of 0.59°C min^{-1} occurred when a pygmy-possum increased its T_b from 18.4 to 36.1°C in 30.0 min.

Torpor timing

Individuals entered torpor significantly later in the night when using short bouts (08:15 h ± 85 min; non-random distribution: $r = 1.0$, $P < 0.001$; $n = 2$, $N = 9$) compared to prolonged bouts (19:34 h ± 132 min; $r = 1.0$, $P < 0.001$; $n = 4$, $N = 12$) ($F_{1,19} = 163.4$, $P < 0.001$, Fig. 5a). In contrast, the mean time of the beginning of rewarming from torpor was similar for short (12:29 h ± 98 min; $n = 4$, $N = 21$; $r = 1.0$, $P < 0.001$) and prolonged (12:24 h ± 189 min; $n = 4$, $N = 17$; $r = 1.0$, $P < 0.001$) bouts ($F_{1,36} = 0.98$, $P > 0.5$, Fig. 5b).

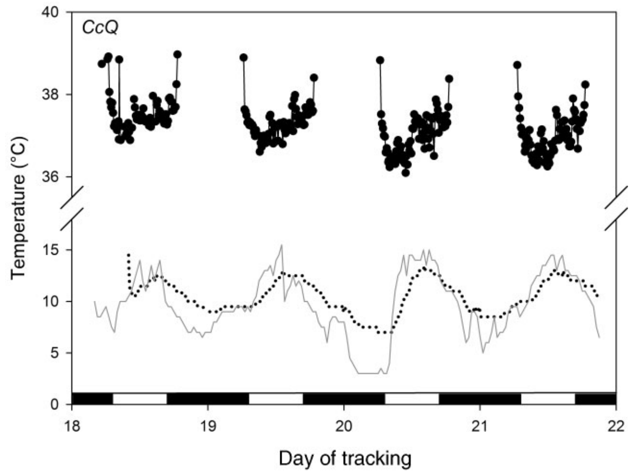

Figure 2 Body temperature (T_b, closed circles and black line) of an individual normothermic *Cercartetus concinnus* (*CcQ*) over a period of 4 days (Day 18 = 26 July 2009) with ambient temperature (T_a, grey line) and nest temperature (T_{nest}, dotted line). Dark bars indicate the scotophase.

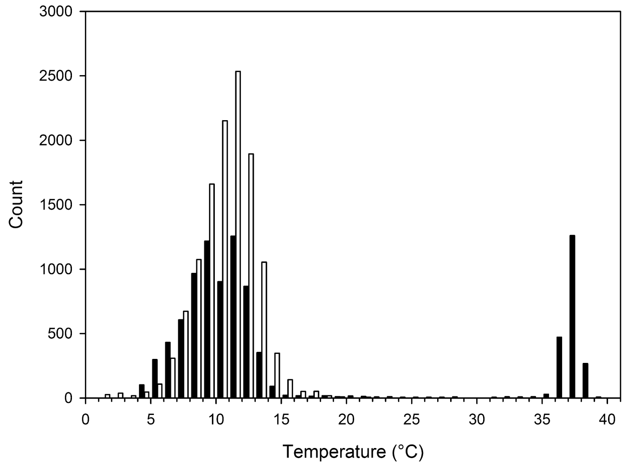

Figure 4 Frequency distribution histogram for body temperature (T_b, black bars, $n = 3$) and nest temperature (T_{nest}, white bars, $n = 3$). A clear bimodal distribution was seen for T_b, illustrating groupings of normothermic and torpid T_b.

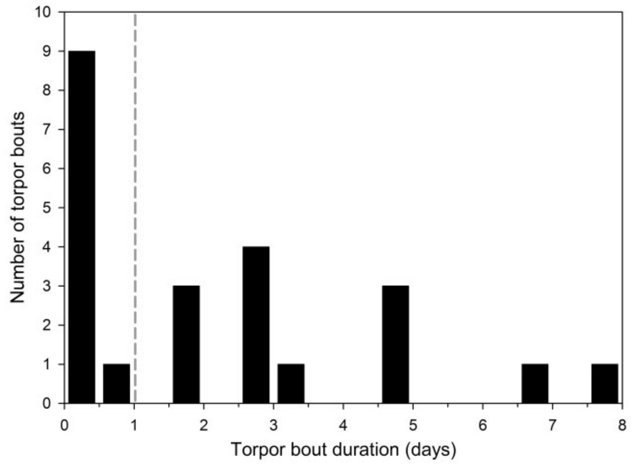

Figure 3 Frequency distribution histogram for torpor bout duration ($n = 4$). The dashed line indicates the division between short (<24 h) and prolonged (>24 h) torpor bouts.

Discussion

Our study provides the first quantitative data on opportunistic hibernation in a free-ranging marsupial. During winter, western pygmy-possums used torpor on 63% of days. Individuals employed both short and prolonged torpor bouts, as well as sequences of prolonged torpor bouts resembling 'classical' hibernation. The observed flexibility in torpor patterns, together with an influence of T_a upon torpor expression, is indicative of the opportunistic nature of winter torpor in this species.

We found considerable plasticity in torpor use among pygmy-possums inhabiting the same area of bushland as torpor bouts were rarely synchronized among individuals. Three individuals were not observed to enter torpor at all, but these were monitored for only relatively short time periods. However, variation in torpor use among individuals can also be affected by body mass, reproductive status or microclimate (Dietz & Kalko, 2006; Kobbe & Dausmann, 2009; Schmid & Ganzhorn, 2009; Kobbe *et al.*, 2011), but our small sample size does not allow further analysis.

Both short and prolonged torpor bouts were associated with low night-time T_a, which is a common trigger for torpor in many mammals (French, 1982; Geiser, 1987). However, the timing of short and prolonged torpor bouts differed. An individual was likely to remain in prolonged torpor until the local daytime T_{nest} elevated the animal's T_b to a level that initiated rewarming (~12°C), a pattern similar to that of some *Nyctophilus* spp. bats (Turbill & Geiser, 2008). Short torpor bouts always commenced at sunrise at the end of the normal activity period, while prolonged bouts were entered into after sunset at the end of the normal resting period. This distinct difference in entry times suggests that the trigger for short and prolonged torpor use may differ. Perhaps pygmy-possums employed short torpor bouts as a response to a negative energy balance accrued while active during the previous night, whereas prolonged torpor was entered into on evenings where cold T_a indicated that activity might be too energetically expensive. These different patterns of torpor use then allowed some control of the balance between energy conservation and expenditure. Nevertheless, torpor was seldom synchronized among individuals and therefore other factors such as foraging success or the presence of predators (Bieber & Ruf, 2009; Matheson, Campbell & Willis, 2010; Schubert *et al.*, 2010; Stawski & Geiser, 2010) likely contributed to the expression of torpor.

Similar to torpor entry, arousal was also affected by T_a and was more likely to occur on warmer days. Furthermore,

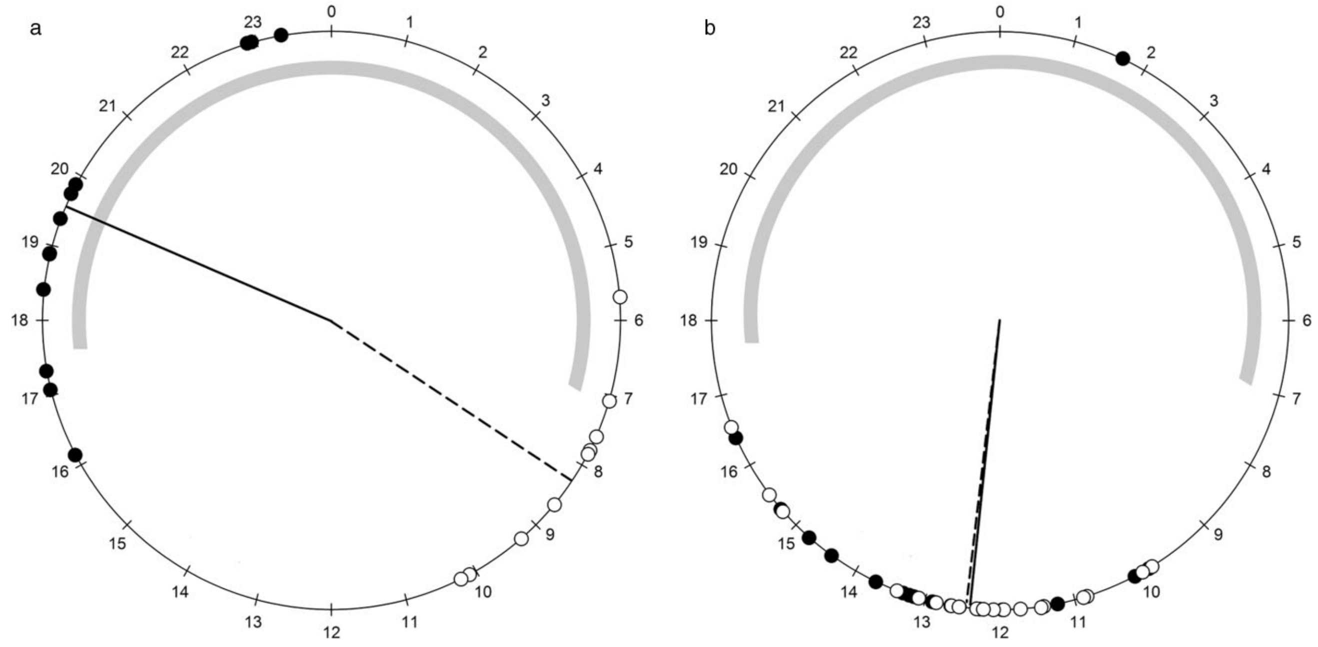

Figure 5 Times of (a) torpor entry ($n = 4$, $N = 21$) and (b) torpor rewarming ($n = 4$, $N = 38$) for short (open circles, $n = 4$, $N = 30$) and prolonged (closed circles, $n = 4$, $N = 29$) torpor bouts with averages for short (dashed line) and prolonged (solid line) bouts. The grey line indicates the scotophase.

rewarming from short as well as from prolonged torpor always occurred in the early afternoon when T_{nest} increased towards its daily maximum. Although it remains unresolved whether the pygmy-possums in our study actively selected nest-sites for their thermal properties, this rise in nest temperature permitted a small amount of passive rewarming from torpor (~9% of the total T_b increase). Passive rewarming appears to be common among heterotherms living in warmer climates (e.g. Mzilikazi & Lovegrove, 2004; Kobbe *et al.*, 2011), and can result in significant reductions in energy expenditure (Lovegrove, Körtner & Geiser, 1999; Warnecke & Geiser, 2010). This might be of particular importance for small marsupials, which likely do not possess brown adipose tissue, which is used for nonshivering thermogenesis in placental mammals (Hayward & Lisson, 1992; Nicol, Pavlides & Andersen, 1997; Cannon & Nedergaard, 2004).

The highly plastic torpor expression we observed in the pygmy-possums is probably a reflection of the moderate environmental conditions experienced, which allowed intermittent foraging during winter. For example, even seasonal hibernators such as echidnas, prairie dogs and woodchucks show different patterns of torpor use along a latitudinal gradient (Grigg & Beard, 2000; Gummer, 2005; Zervanos *et al.*, 2010). Especially in the southern hemisphere, the milder winter T_a and large daily T_a fluctuations appear to encourage the opportunistic expression of torpor and hibernation. Consequently, food is intermittently available year-round in the pygmy-possums' habitat. While no information is available on their torpor use during other seasons or in different habitats, it is possible that pygmy-possums are capable of long-term hibernation in more severe environments, as closely related species enter seasonal hibernation in the wild (*B. parvus*, Körtner & Geiser, 1998), or even yearlong hibernation in captivity (*C. nanus*, Geiser, 2007). It is also plausible that summer torpor occurs on occasions, for example in response to drought conditions which are a regular feature in the semi-arid environments inhabited by western pygmy-possums in southern Australia. Additional field studies with larger numbers of individuals may help answer these outstanding questions. However, even with this small sample size, we were able to demonstrate that pygmy-possums have the phenotypic flexibility to alternate between normothermia and short or prolonged torpor bouts on a day-to-day basis, in addition to entering periods of hibernation. The ability to adjust energy expenditure in this manner enables pygmy-possums to invest energy into foraging and reproduction when environmental conditions allow.

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References

Bieber, C. & Ruf, T. (2009). Summer dormancy in edible dormice (*Glis glis*) without energetic constraints. *Naturwissenschaften* **96**, 165–171.

Bladon, R.V., Dickman, C.R. & Hume, I.D. (2002). Effects of habitat fragmentation on the demography, movements and social organisation of the eastern pygmy-possum (*Cercartetus nanus*) in northern New South Wales. *Wildl. Res.* **29**, 105–116.

Cannon, B. & Nedergaard, J. (2004). Brown adipose tissue: function and physiological significance. *Physiol. Rev.* **84**, 277–359.

Carthew, S.M., Cadzow, B.R. & Foulkes, J.N. (2008). Western pygmy-possum *Cercartetus concinnus*. In *The mammals of Australia*: 215–217. Van Dyck, S. & Strahan, R. (Eds). Chatswood: Reed New Holland.

Cory Toussaint, D., McKechnie, A.E. & van der Merwe, M. (2010). Heterothermy in free-ranging male Egyptian free-tailed bats (*Tadarida aegyptiaca*) in a subtropical climate. *Mamm. Biol.* **75**, 466–470.

Dausmann, K.H., Glos, J., Ganzhorn, J.U. & Heldmaier, G. (2005). Hibernation in the tropics: lessons from a primate. *J. Comp. Physiol. B.* **175**, 147–155.

Dietz, M. & Kalko, E.K.V. (2006). Seasonal changes in daily torpor patterns of free-ranging female and male Daubenton's bats (*Myotis daubentonii*). *J. Comp. Physiol. B.* **176**, 223–231.

French, A.R. (1982). Effects of temperature on the duration of arousal episodes during hibernation. *J. Appl. Physiol.* **52**, 216–220.

Geiser, F. (1987). Hibernation and daily torpor in two pygmy-possums (*Cercartetus spp.*, Marsupialia). *Physiol. Zool.* **60**, 93–102.

Geiser, F. (1993). Hibernation in the eastern pygmy possum, *Cercartetus nanus* (Marsupialia: Burramyidae). *Aust. J. Zool.* **41**, 67–75.

Geiser, F. (2007). Yearlong hibernation in a marsupial mammal. *Naturwissenschaften* **94**, 941–944.

Geiser, F., Holloway, J.C., Körtner, G., Maddocks, T.A., Turbill, C. & Brigham, R.M. (2000). Do patterns of torpor differ between free-ranging and captive mammals and birds? In *Life in the cold: 11th international hibernation symposium*: 95–102. Heldmaier, G. & Klingenspor, M. (Eds). Heidelberg: Springer-Verlag.

Geiser, F. & Körtner, G. (2004). Thermal biology, energetics, and torpor in the possums and gliders. In *The biology of Australian possums and gliders*: 186–198. Goldingay, R.L. & Jackson, S.M. (Eds). Chipping Norton: Surrey Beatty and Sons.

Grigg, G.C. & Beard, L.A. (2000). Hibernation by echidnas in mild climates: hints about the evolution of endothermy? In *Life in the cold: 11th international hibernation symposium*: 95–102. Heldmaier, G. & Klingenspor, M. (Eds). Heidelberg: Springer-Verlag.

Gummer, D.L. (2005). *Geographic variation in torpor patterns: the northernmost prairie dogs and kangaroo rats*. PhD thesis, University of Saskatchewan at Saskatoon.

Hayward, J.S. & Lisson, P.A. (1992). Evolution of brown fat: its absence in marsupials and monotremes. *Can. J. Zool.* **70**, 171–179.

Jones, C.J. & Geiser, F. (1992). Prolonged and daily torpor in the feathertail glider, *Acrobates pygmaeus* (Marsupialia: Acrobatidae). *J. Zool. (Lond.)* **227**, 101–108.

Kemp, L.F. & Carthew, S.M. (2004). Nest site selection by the western pygmy-possum *Cercartetus concinnus*. In *The biology of Australian possums and gliders*: 186–198. Goldingay, R.L. & Jackson, S.M. (Eds). Chipping Norton: Surrey Beatty and Sons.

Kobbe, S. & Dausmann, K.H. (2009). Hibernation in Malagasy mouse lemurs as a strategy to counter environmental challenge. *Naturwissenschaften* **96**, 1221–1227.

Kobbe, S., Ganzhorn, J.U. & Dausmann, K.H. (2011). Extreme individual flexibility of heterothermy in free-ranging Malagasy mouse lemurs (*Microcebus griseorufus*). *J. Comp. Physiol. B.* **181**, 165–173.

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

Lovegrove, B.G. & Génin, F. (2008). Torpor and hibernation in a basal placental mammal, the lesser hedgehog tenrec *Echinops telfairi*. *J. Comp. Physiol. B.* **178**, 691–698.

Lovegrove, B.G., Körtner, G. & Geiser, F. (1999). The energetic cost of arousal from torpor in the marsupial *Sminthopsis macroura*: benefits of summer ambient temperature cycles. *J. Comp. Physiol. B.* **169**, 11–18.

Lyman, C.P. (1982). Who is who among the hibernators. In *Hibernation and torpor in mammals and birds*: 12–36. Lyman, C.P., Willis, J.S., Malan, A. & Wang, L.C.H. (Eds). New York: Academic Press.

Matheson, A.L., Campbell, K.L. & Willis, C.K.R. (2010). Feasting, fasting and freezing: energetic effects of meal size and temperature on torpor expression by little brown bats *Myotis lucifugus*. *J. Exp. Biol.* **213**, 2165–2173.

McKechnie, A.E. & Mzilikazi, N. (2011). Heterothermy in Afrotropical mammals and birds: a review. *Int. Comp. Biol.* **51**, 349–363.

Menkhorst, P.W. & Knight, F. (2001). *A field guide to the mammals of Australia*. Melbourne: Oxford University Press.

Misso, G.E. (1997). *Nesting sites and habitat of the western pygmy-possum*, Cercartetus concinnus. BSc Honours thesis, University of Adelaide at Adelaide.

Morrant, D.S. & Petit, S. (2011). Nest use by western pygmy-possums (*Cercartetus concinnus*) (Marsupialia :

Burramyidae) at Innes National Park, South Australia. *Aust. Mammal.* **33**, 28–32.

Mzilikazi, N. & Lovegrove, B.G. (2004). Daily torpor in free-ranging rock elephant shrews, *Elephantulus myurus*: a year-long study. *Physiol. Biochem. Zool.* **77**, 285–296.

Nicol, S.C. & Andersen, N.A. (2002). The timing of hibernation in Tasmanian echidnas: why do they do it when they do? *Comp. Biochem. Physiol. B.* **131**, 603–611.

Nicol, S.C., Pavlides, D. & Andersen, N.A. (1997). Nonshivering thermogenesis in marsupials: absence of thermogenic response to β3-adrenergic agonists. *Comp. Biochem. Physiol.* **117A**, 399–405.

Pestell, A.J.L. & Petit, S. (2007). Methods and ethical considerations of pitfall trapping for the western pygmy possum (*Cercartetus concinnus* Gould) (Marsupialia: Burramyidae), with observations on capture patterns and nest sites. *Wildlife Res.* **34**, 296–305.

Rojas, A.D., Körtner, G. & Geiser, F. (2010). Do implanted transmitters affect maximum running speed of two small marsupials? *J. Mammal.* **91**, 1360–1364.

Scantlebury, M., Lovegrove, B.G., Jackson, C.R., Bennett, N.C. & Lutermann, H. (2008). Hibernation and non-shivering thermogenesis in the Hottentot golden mole (*Amblysomus hottentottus longiceps*). *J. Comp. Physiol. B.* **178**, 887–897.

Schmid, J. & Ganzhorn, J.U. (2009). Optional strategies for reduced metabolism in gray mouse lemurs. *Naturwissenschaften* **96**, 737–741.

Schubert, K.A., Boerema, A.S., Vaanholt, L.M., de Boer, S.F., Strijkstra, A.M. & Daan, S. (2010). Daily torpor in mice: high foraging costs trigger energy-saving hypothermia. *Biol. Lett.* **6**, 132–135.

Song, X., Körtner, G. & Geiser, F. (1997). Thermal relations of metabolic rate reduction in a hibernating marsupial. *Am. J. Physiol.* **273**, R2097–R2104.

Stawski, C. & Geiser, F. (2010). Fat and fed: frequent use of summer torpor in a subtropical bat. *Naturwissenschaften* **97**, 29–35.

Stawski, C., Turbill, C. & Geiser, F. (2009). Hibernation by a free-ranging subtropical bat (*Nyctophilus bifax*). *J. Comp. Physiol. B.* **179**, 433–441.

Superina, M. & Boily, P. (2007). Hibernation and daily torpor in an armadillo, the pichi (*Zaedyus pichiy*). *Comp. Biochem. Physiol. A.* **148**, 893–898.

Tulloch, A. (2001). *Distribution, abundance and habitat use of the eastern pygmy possum in Royal and Heathcote National Parks, New South Wales*. BSc Honours thesis, University of Sydney at Sydney.

Turbill, C. & Geiser, F. (2008). Hibernation by tree-roosting bats. *J. Comp. Physiol. B.* **178**, 597–605.

Wakefield, N.A. (1970). Notes on Australian pigmy-possums (*Cercartetus*, Phalangeridae, Marsupialia). *Vic. Nat.* **87**, 11–17.

Wang, L.C.H. (1978). Energetic and field aspects of mammalian torpor: the Richardson's ground squirrel. In *Strategies in cold: natural torpidity and thermogenesis*: 109–145. Wang, L.C.H. & Hudson, J.W. (Eds). New York: Academic Press.

Wang, L.C.H. (1989). Ecological, physiological, and biochemical aspects of torpor in mammals and birds. In *Advances in comparative and environmental physiology*: 361–401. Wang, L.C.H. (Ed.). Berlin: Springer-Verlag.

Warnecke, L. & Geiser, F. (2010). The energetics of basking behaviour and torpor in a small marsupial exposed to simulated natural conditions. *J. Comp. Physiol. B.* **180**, 437–445.

Willis, C.K.R. (2007). An energy-based body temperature threshold between torpor and normothermia for small mammals. *Physiol. Biochem. Zool.* **80**, 643–651.

Zar, J.H. (1999). *Biostatistical analysis*. 4th edn. Upper Saddle River, NJ: Prentice-Hall.

Zervanos, S.M., Maher, C.R., Waldvogel, J.A. & Florant, G.L. (2010). Latitudinal differences in the hibernation characteristics of woodchucks (*Marmota monax*). *Physiol. Biochem. Zool.* **83**, 135–141.