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Summer and winter torpor use by a free-ranging marsupial

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ABSTRACT

Torpor is usually associated with low ambient temperatures (T_a) in winter, but in some species it is also used in summer, often in response to limited food availability. Since the seasonal expression of torpor of both placental and marsupial hibernators in the wild is poorly documented by quantitative data, we investigated torpor and activity patterns of the eastern pygmy-possum *Cercartetus nanus* (17.4 g) over two seasons. We used radio telemetry to track animals during winter (n = 4) and summer (n = 5) in a warm-temperate habitat and found that torpor was used in both seasons. In winter all animals entered periods of short-term hibernation (from 5 to 20 days) containing individual torpor bouts of up to 5.9 days. In summer, torpor bouts were always <1 day in duration, only used by males and were not related to daily mean T_a. Pygmy-possums entered torpor at night as T_a cooled, and rewarmed during the afternoon as T_a increased. Individuals interspersed torpor bouts with nocturnal activity and the percentage of the night animals were active was the same in summer and winter. Our study provides the first information on torpor patterns in free-ranging *C. nanus*, and shows that the use of torpor throughout the year is important for energy management in this species.

1. Introduction

Torpor is a physiological state characterised by a controlled reduction in body temperature (T_b) and metabolic rate that is commonly used by many mammals and birds to overcome times of low ambient temperature (T_a) and/or limited food and water availability (Lyman et al., 1982). For seasonal hibernators such as ground squirrels and marmots (Sciuridae) and hamsters (Cricetidae), torpor usually occurs exclusively in the colder winter months, and mostly in climatic zones that undergo profound yet predictable seasonal decreases in T_a and resource accessibility (Davis, 1976; French, 1985; Wang, 1989; Boyer and Barnes, 1999). For these species, food is more difficult to obtain or often completely unavailable during winter (Davis, 1976; Bronson, 1980; Wolff, 1996). Therefore before the onset of winter seasonal hibernators store energy by either fattening extensively (Mrosovsky, 1976; French, 1982) or creating food caches (Lyman, 1954). This energy storage allows animals to survive and persist for several months without leaving their hibernacula. At the end of hibernation seasonal hibernators become active and emerge to forage and reproduce, and during the summer many species do not use torpor at all (Davis, 1976; Wang, 1989; Kobbe et al., 2011).

In contrast to this strictly seasonal use of torpor, many daily heterotherms enter torpor throughout the year. The use of both winter and summer torpor has been identified in a range of species, including dasyurid marsupials (Geiser and Baudinette, 1987), numbats *Myrmecobius fasciatus* (Cooper and Withers, 2004), and golden spiny mice *Acomys russatus* (Levy et al., 2011). Torpor in both winter and summer even occurs in hibernators such as edible dormice *Glis glis* (Bieber and Ruf, 2009), short-beaked echidnas *Tachyglossus aculeatus* (Brice et al., 2002), and several vespertilionid bats (Willis et al., 2005b; Dietz and Kalko, 2006; Wojciechowski et al., 2007; Stawski and Geiser, 2011). Most of these species are insectivorous and, because of high T_a and an abundance of arthropods, summer torpor bouts are usually shorter than those used in winter. In contrast, the nectarivorous blossom bat *Syconycteris australis* employs longer torpor bouts in summer apparently in response to low nectar availability (Coburn and Geiser, 1998). It therefore appears that the expression of summer torpor is more strongly governed by food availability than T_a. Compared to the northern hemisphere, the southern hemisphere is characterised by milder but less predictable seasonal changes in T_a and food availability (e.g. Morton et al., 2011). Consequently, it is plausible that summer torpor is more commonly used in the southern than the northern hemisphere.

To investigate the influence of season on torpor use we studied the thermal biology of a small Australian mammal, the eastern pygmy-possum *Cercartetus nanus*. This insectivorous and nectarivorous marsupial of the family Burramyidae is closely related to the only two marsupial species for which data on hibernation in free-ranging individuals are available: the seasonally hibernating mountain pygmy-possum *Burramys parvus* (Körtner and Geiser, 1998), and the opportunistically hibernating western pygmy-possum *Cercartetus concinnus* (Turner et al., 2012). Under laboratory conditions *C. nanus*

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readily enters prolonged torpor at any time of the year (Hickman and Hickman, 1960; Bartholomew and Hudson, 1962; Geiser, 1993), and adjusts torpor use in response to both T_a and energy availability (Westman and Geiser, 2004). In the wild, the movements, breeding patterns and diet of *C. nanus* are also adjusted in response to food availability (Arnould, 1986; Tulloch and Dickman, 2006, 2007; Ward, 1990), and although information on torpor is limited to only incidental accounts, individuals have been found torpid in all seasons (Bladon et al., 2002). The aim of our study was to investigate whether *C. nanus* hibernates in the wild, how torpor use is affected by season, and to compare our findings with available data on *B. parvus* and *C. concinnus*. Therefore, we monitored body temperature (T_b) in free-ranging individuals during both summer and winter using radio telemetry. Based on the expression of heterothermy in related species, we expected torpor to be used more in winter than in summer.

2. Material and methods

This study was carried out in Macpherson State Forest, a semi-open sclerophyll forest in eastern New South Wales, Australia (33°16′ S., 139°9′ E.), which is characterised by warm summers and cool winters (see Fig. 1). Five *C. nanus* (2 females, 3 males; 17.0 ± 2.6 g) were trapped in November–December 2008 (herein referred to as "summer") and four (2 females, 2 males; 18.0 ± 4.3 g) in May–June 2009 ("winter"). Captures were made using wooden nest boxes, arboreal PVC pipe traps (adapted from Winning and King, 2008), and 15 × 50 cm PVC pipe pitfall traps with drift fences. Individuals were transported to a field laboratory, kept under natural photoperiod for less than one week, and fed daily with pureed and fresh fruit and a nectar substitute consisting of high protein baby cereal, honey and a vitamin supplement. Water was provided *ad libitum*.

To measure T_b we used sterilised temperature-sensitive FM radio transmitters (0.9–1.1 g BD-2TH; Holohil Systems Ltd, Canada), which were coated in an inert wax and calibrated to the nearest 0.1 °C in a water bath from 2 to 42 °C at ~7 °C increments using a mercury thermometer traceable to the national standard. Transmitters were implanted into the intraperitoneal cavity of *C. nanus* under inhalation anaesthesia of isoflurane in oxygen. All transmitters were <10% of an individual's body mass, which is within the range permitting unhindered locomotion in small terrestrial mammals (Rojas et al., 2010). The incision was sutured closed using Coated Vicryl (muscle layer; 2.0 metric, Ethicon Inc., Sommerville, NJ, USA) and Chromic Gut (skin; 2.0 metric, Ethicon Inc.). 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 to the surgical site. Animals were warmed immediately after surgery and once conscious fed a sweet analgesic (Metacam, Boehringer Ingelheim, North Ryde, NSW, Australia). Animals were allowed to recover for ~48 h after surgery and the local anaesthetic and analgesic were administered daily. Before release at sunset at the point of capture a final application of the spray bandage was issued to ensure wound integrity. Animals were not recaptured after this release.

Individuals were located daily using radio receivers (Telonics TR-4 and Icom IC-R10) with Yagi antennas (AY/C, Titley Scientific, Australia). The T_b of individual animals was measured remotely at 10 min intervals using mobile logger/receivers (see Körtner and Geiser, 1998 for details). Data were downloaded every 3–10 days. The short transmitter detection range of the logger/receivers (<20 m) required their frequent relocation and resulted in a loss of signal if an animal changed its nesting spot, so not all torpor entries were recorded. Manual T_b readings were taken using a receiver and a stopwatch several times each day. Activity periods were inferred from an absence of data recorded by the loggers.

The temperature characteristics of six out of the nine transmitters evidently drifted during the course of the study so no absolute T_b values are presented (but see below). However, the data clearly show times when animals were torpid and normothermic. Torpor bout duration was defined as the time period between the time an individual's T_b began to cool at the onset of torpor before reaching low and stable torpid values, and the time when it rewarmed to normothermia (Willis et al., 2005a). Specifically, we defined entry into torpor as the time of the first T_b measurement after the initial steep T_b decrease below normothermia (see Fig. 2). The start of rewarming from torpor was the time of the first T_b value elevated above those of stable torpor at the beginning of the characteristic steep T_b increase, and the end of rewarming was the last point of this increase before stable normothermic T_b was reached (Fig. 2). 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 without activity.

T_a was measured to the nearest 0.5 °C using small data loggers (DS 1921G Thermochron iButtons; Dallas Semiconductor, USA; n = 12 in summer, 18 in winter) that were placed ~1 m above ground in the shade in various locations in the study site that were likely to be encountered by *C. nanus*, for example near food trees or nesting sites. The mean of all logger temperature readings was used in the analyses, and is referred to as "T_a". To determine whether nest sites provided thermal buffering from daily T_a variation, additional loggers (n = 4 in both seasons) were placed inside (T_{in}) and outside (T_{out}) two occasionally used nest sites (a dead branch of a fallen tree and a small tree hollow). Additional climate data were obtained from the Australian Bureau of Meteorology (http://www.bom.gov.au).

Data analyses were conducted using *statistiXL* v1.8. Differences among means (means of means for each individual) were evaluated using one-way ANOVA (effect of time on torpor use), paired t-tests (T_{in} and T_{out} comparisons) and unpaired t-tests (T_a, activity and body mass comparisons). The frequency of torpor bouts in each season and the influence of rain on torpor use were analysed using a chi-squared test. Linear regressions were used to examine the effect of body mass, T_a and activity duration on torpor bout length. The timing of torpor entry and rewarming was tested for non-random distribution using a Rayleigh's test (significance of the mean angle using an *r*-value derived from a calculated *z*-value), after which a Watson–Williams test (*WW*; significance of a pairwise comparison using a calculated *F*-statistic) was used to compare times among these variables (Zar, 1999). Data are presented as mean ± 1 SD; *n* denotes the number of individuals, *N* the number of measurements.

To allow the visualisation of T_b data despite transmitter drift, we drift-corrected a 30-day T_b trace for each season. During normothermia the average T_b at the beginning of the study for a five-day period without drift was 37.5 ± 0.3 °C (n = 2), and drifted normothermic T_b was adjusted to match. In winter, torpid T_b values were adjusted by assuming $T_b - T_a = 1.9$ °C during steady-state torpor (ΔT; Song et al., 1997). Daily T_b variation was then scaled to match the mean daily variation in T_{nest}. In summer, the minimum T_b during a torpor bout was assumed to be the same as daily minimum T_a, which is likely an overestimation of their depth because the torpor bouts were short (<5.5 h in duration), however T_{nest} was not available for the time period. T_b during entry into and rewarming from torpor was then scaled according to the corrected normothermic and torpid T_b values.

3. Results

3.1. Ambient conditions

The average daily minimum T_a during the winter tracking period (8.9 ± 2.6 °C; 2.2–12.8 °C) was significantly lower than in summer (14.1 ± 2.0 °C; range 9.0–18.6 °C; $t_{56} = 9.18$, $p < 0.001$; Fig. 1). Similarly, the average daily maximum T_a during winter (16.5 ± 2.0 °C; 13.0–20.8 °C) was lower than in summer (26.2 ± 4.7 °C; 17.5–36.1 °C; $t_{56} = 11.94$, $p < 0.001$; Fig. 1). The mean T_a of the second half of the

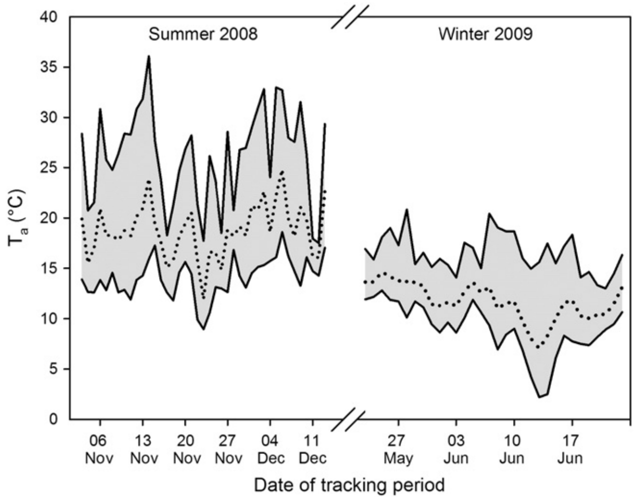

Fig. 1. Ambient temperature (T_a) at the study site during summer 2008 and winter 2009. The upper and lower solid lines indicate respectively average daily maximum and minimum T_a, the dotted lines are daily average T_a.

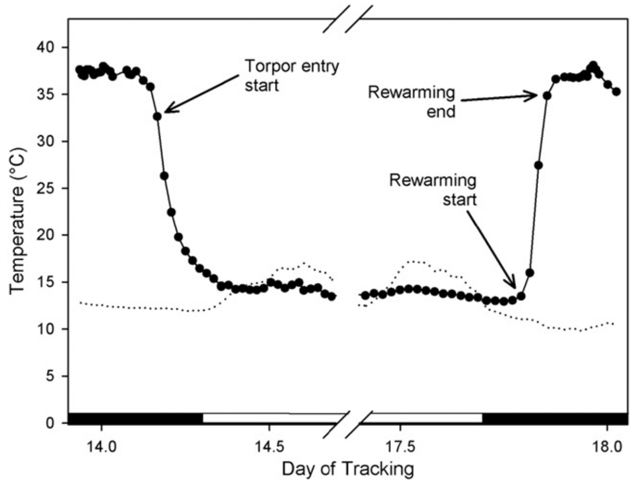

Fig. 2. Drift-corrected body temperature (T_b; circles and solid line) of the one individual during winter included in Fig. 3. Arrows point to the T_b values used for classifying the beginning of entry into torpor ("Torpor entry start"), the start of rewarming from torpor ("Rewarming start"), and the end of rewarming from torpor ("Rewarming end"). The dotted line is ambient temperature (T_a) and the dark bars indicate the scotophase.

winter tracking period (10.4 ± 1.6 °C) was cooler than the first (13.0 ± 1.1 °C; $t_{30}=5.45$, $p<0.001$), but this was not observed in summer ($t_{36}=0.56$, $p=0.582$). In both seasons *C. nanus* were usually found nesting in the hollow stumps of dead trees or in dead branches of living *Angophora costata*, *Banksia serrata* or *Eucalyptus* spp. In winter T_{in} fluctuated significantly less (daily amplitude = 7.0 ± 2.5 °C) than T_{out} (9.8 ± 4.5 °C; $t_{30}=6.74$, $p<0.001$), and the same pattern was observed in summer (T_{in} daily amplitude = 11.3 ± 4.5 °C, $T_{out}=14.7\pm5.4$ °C; $t_{40}=9.21$, $p<0.001$). One individual used a nest site containing T_{in}/T_{out} data loggers on a single occasion but gave no indication that it was disturbed by any ultrasonic noise that may have been emitted by the devices (see Willis et al., 2009). In winter rain was recorded on 74% of tracking-days (7.0 ± 10.2 mm day^{-1}) and 51% in summer (6.7 ± 9.9 mm day^{-1}). Sunrise and sunset during winter were at 07:40 h ± 5 min and 17:44 h ± 2 min, respectively (day/night length 10.1/13.9 h), and during summer were 05:33 h ± 6 min and 19:27 h ± 11 min (13.9/10.1 h).

3.2. Torpor expression

Individual *C. nanus* were radio-tracked for 28.5 ± 5.4 days in winter and 34.8 ± 5.4 days in summer (Table 1). Torpor bouts were easily identified despite the drifting transmitters (Fig. 2) and torpor was used in both winter and summer (Fig. 3). In winter, animals were found torpid on 63.2% of possum-days ($n=4$, $N=72$), but only on 10.3% in summer ($n=3$, $N=18$; Table 1, Fig. 4), and we found that torpor was employed more often in winter compared to summer ($\chi^2=89.42$, $p<0.001$). We measured 13 complete torpor bouts in winter, six in summer, and observed 47 individual bouts in total (the time of torpor entry could not be determined for some bouts when an animal had changed nest sites the night before). All individuals entered torpor in winter ($n=4$, $N=29$), but in summer only the males used torpor ($n=3$, $N=18$). During both seasons torpor patterns were variable among individuals as different animals were often either torpid or normothermic on the same day (16/27 days when torpor was used in winter, 12/13 in summer; Figs. 4 and 5). In winter both short torpor bouts (duration <24 h; $N=11$) and prolonged torpor bouts (duration >24 h; $N=18$) were used (Figs. 3 and 5), whereas in summer *C. nanus* only entered short torpor bouts ($N=18$; Figs. 3 and 5). In winter the length of an additional two torpor bouts could not be classified as short or prolonged because torpor entries were not recorded. The number of days torpor was used did not differ between the first and second halves of the study periods in either winter ($F_{2,5}=3.15$, $p=0.130$; $n=4$) or summer ($F_{2,3}=5.96$, $p=0.090$; $n=3$), suggesting no effect of date on torpor use within a season. In winter, individuals were more likely to enter

Table 1
Torpor variables for pygmy-possums radio-tracked in winter and summer.

Season	Winter				Summer				
ID	*CnU*	*CnV*	*CnW*	*CnX*	*CnC*	*CnD*	*CnE*	*CnF*	*CnG*
Sex	f	f	m	m	f	f	m	m	m
Mass (g)	24.0	15.4	14.4	18.2	14.4	21.1	15.3	17.4	16.8
Days tracked	26	33	22	33	26	40	36	38	34
Total torpor bouts	6	11	6	6	0	0	6	6	6
Short bouts	2	6	1	1	0	0	6	6	6
Prolonged bouts	4	4	4	5	0	0	0	0	0
Unclassified bouts	0	1	1	0	0	0	0	0	0
Days torpor used (%)	50.0	45.5	100.0	66.7	0	0	16.7	15.8	17.6

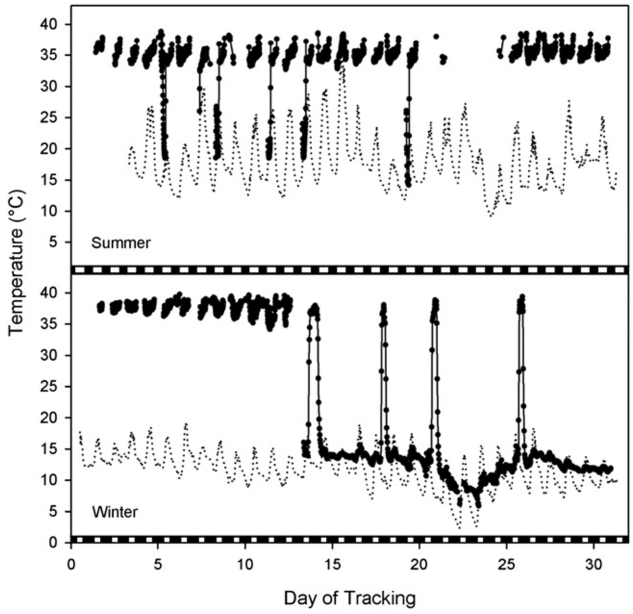

Fig. 3. Drift-corrected body temperature (T_b; circles and solid line) for one individual each during summer (upper panel) and winter (lower panel), with ambient temperature (T_a; dotted line). In summer, Day 1 of the tracking period is 31st October 2008, in winter Day 1 is 21st May 2009. Dark bars indicate the scotophases.

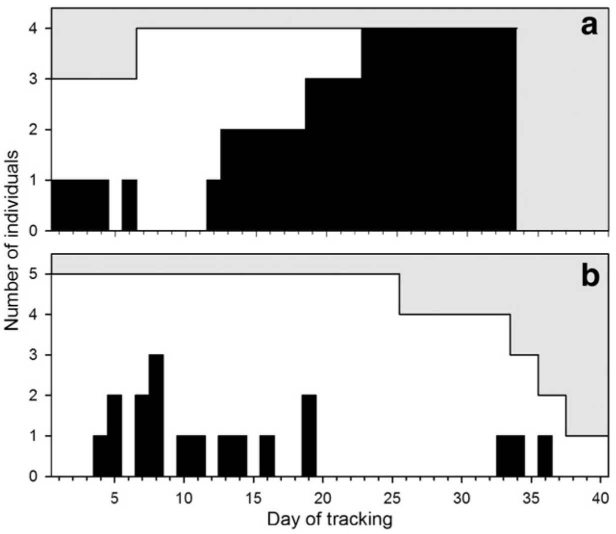

Fig. 4. The number of animals being radio-tracked at any given time during the study period (black line bordered by grey area) in a) winter and b) summer. The number of animals which entered torpor per day is shown in black vertical columns, and those that remained normothermic in white (e.g. on Day 19 in summer, two individuals enetred torpor and three remained normothermic).

torpor on days without rain ($\chi^2=4.84$, $p=0.028$), but rainfall had no effect on torpor use in summer ($\chi^2=1.61$, $p=0.205$).

The average duration of short torpor bouts in winter of 7.3 ± 3.7 h (range 3.7–12.7 h; n = 2, N = 6) was longer than the duration of short bouts in summer (3.8 ± 1.4 h; 2.3–5.5 h; n = 3, N = 6; $F_{1,6}=9.74$, $p=0.021$). The length of the prolonged bouts in winter was 101.1 ± 37.2 h (41.6–140.9 h; n = 2, N = 7). Body mass at the time of capture did not differ between seasons ($t_7=0.43$, $p=0.677$) and had no discernible effect on maximum torpor bout duration ($R^2=0.002$, $F_{1,5}=0.011$, $p=0.922$). In winter, all animals entered periods of short-term hibernation (between two and five successive prolonged torpor bouts) of up to three weeks, without leaving their nest sites (Figs. 3 and 5).

Short torpor bouts were always preceded by a period of activity, although no significant relationship was found between the length of the activity period and the duration of the ensuing torpor bout ($R^2=0.019$, $F_{1,7}=0.14$, $p=0.722$; n = 5, N = 9). Activity preceded a prolonged torpor bout on four occasions (n = 3), and each individual used a short torpor bout the day before a period of hibernation (n = 4, N = 5). Within a period of hibernation the duration of normothermic periods, after animals had periodically rewarmed from torpor, was 3.3 ± 1.2 h (range 1.7–5.8 h; n = 4, N = 11).

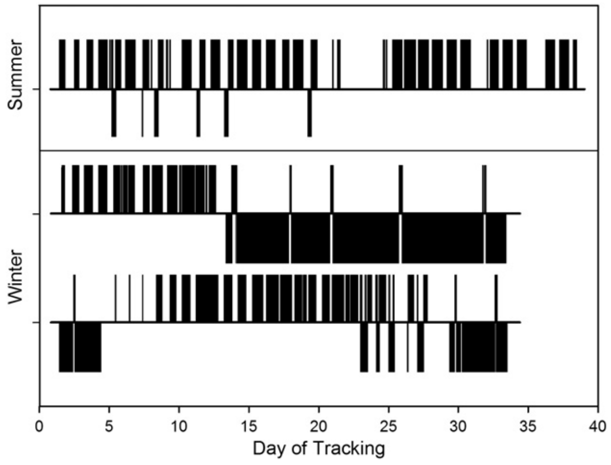

Fig. 5. Body temperature (T_b) pattern of one individual in summer (upper plot) and two in winter (lower plots). In each plot, bars above the horizontal line indicate normothemic T_b, bars below indicate torpid T_b. Gaps between the normothermic T_b bars that do not correspond with torpor show either activity or a gap in data from when an animal moved nest sites and the torpor entry was missed. In summer Day 1 is 31st October 2008, in winter Day 1 is 21st May 2009.

During winter, the mean T_a of nights on which animals entered torpor (9.9 ± 0.7 °C; n = 4) did not differ from those when they did not (11.1 ± 0.8 °C; n = 3; $t_5=2.17$, $p=0.082$), and there was no difference in T_a between nights animals entered short (10.2 ± 2.0 °C; n = 4) or prolonged torpor bouts (10.1 ± 1.2 °C; n = 4; $t_3=0.06$, $p=0.957$). In summer the average T_a of nights that *C. nanus* entered torpor (16.1 ± 0.6 °C; n = 3) did not differ from those where they remained normothermic (16.1 ± 0.2 °C; n = 3; $t_2=0.03$, $p=0.981$). Torpor bout duration and mean minimum daily T_a were not correlated in summer ($R^2=0.067$, $F_{1,4}=0.29$, $p=0.620$; n = 3, N = 6) or winter ($R^2=0.02$, $p=0.693$; n = 4, N = 13). In winter the mean T_a of days that animals rewarmed from prolonged torpor (13.7 ± 1.0 °C; n = 4,) did not differ from those where they remained torpid (12.9 ± 0.9 °C; n = 4; $t_3=1.80$, $p=0.170$), nor did it differ between rewarming from short (14.1 ± 1.1 °C; n = 4,) and prolonged torpor bouts (13.7 ± 1.0 °C; n = 4; $t_3=0.35$, $p=0.747$).

3.3. Torpor timing

The time of torpor entry was non-randomly distributed for prolonged winter bouts (22:05 h ± 200 min; z = 4.68, r = 0.68, $p=0.006$; n = 4, N = 10) and short winter bouts (02:40 h ± 176 min; z = 3.89, r = 0.75, $p=0.015$; n = 3, N = 7), but not for short summer bouts, although it was close to significance (06:29 h ± 198 min; z = 2.84, r = 0.69, $p=0.052$; n = 3, N = 6; Fig. 6a). Entry times did not differ between summer and winter for short bouts ($F_{1,11}=4.17$, $p>0.05$, *WW*), but did differ between short and prolonged bouts in winter ($F_{1,15}=7.88$, $p<0.025$, *WW*).

The time of initiation of active rewarming from torpor had a non-random distribution for short bouts in summer (10:14 h ± 124 min; z = 8.20, r = 0.86, $p<0.001$; n = 3, N = 11) and prolonged bouts in winter (15:07 h ± 135 min; z = 8.49, r = 0.84, $p<0.001$; n = 4, N = 12), but not for short winter bouts (10:51 h ± 274 min; z = 1.91, r = 0.49, $p=0.149$; n = 4, N = 8; Fig. 6b). The timing did not differ between the summer and winter short bouts ($F_{1,17}=0.13$, $p>0.5$, *WW*), but occurred later for prolonged bouts than short bouts in winter ($F_{1,18}=6.22$, $p<0.025$, *WW*). Animals took longer to rewarm from short torpor bouts in winter (1.3 ± 0.5 h; n = 3, N = 7) than summer (53.7 ± 10.3 min; n = 3, N = 11; $F_{6,11}=4.03$, $p=0.022$). There was no difference in rewarming duration between short and prolonged (1.9 ± 0.8 h; n = 4, N = 12) bouts during winter ($F_{1,5}=1.36$, $p=0.296$).

3.4. Activity

Animals were nocturnal and left their nest sites 14.4 ± 56 min after sunset in winter (n = 4, N = 44), and 7.1 ± 47 min in summer (n = 5, N = 125). They arrived back at their nest sites 2.9 ± 2.4 h before sunrise in winter (n = 4, N = 32), and 1.3 ± 1.2 h in summer (n = 5, N = 158). On days when torpor was not used, the percentage of the night animals were active did not differ between winter (79.3 ± 10.6%; n = 3, N = 26) and summer (82.5 ± 5.2%; n = 4, N = 12; $t_5=0.52$, $p=0.624$). Accordingly, the total time animals were active was longer in winter (11.0 ± 1.5 h) than in summer (8.3 ± 0.6 h; $t_5=3.36$, $p=0.020$).

4. Discussion

Our study provides the first quantitative information on torpor use by free-living *C. nanus*, and is one of the few documenting torpor patterns of any species in both summer and winter in the wild. We observed flexibility in torpor use, as different individuals were often

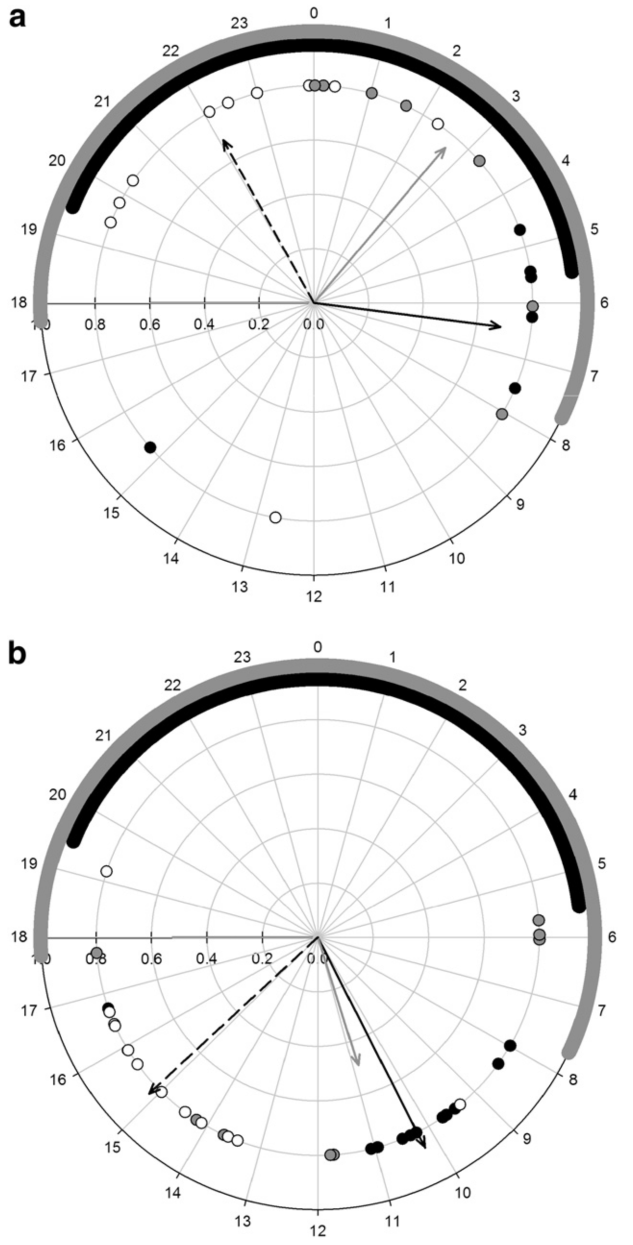

Fig. 6. Circular distribution of the time of day (00 h) for a) start of entry into torpor and b) start of rewarming from torpor. Times are for prolonged winter bouts (n = 4 for both entry and rewarming; white circles), short winter bouts (entry n = 3, rewarm n = 4; grey circles) and short summer bouts (n = 3 for both; black circles). Also displayed are the vectors of the means derived from the Rayleigh's test for each bout type (dashed, grey and black arrows for prolonged winter, short winter and short summer torpor bouts, respectively). The radial axis is a proportional scale (i.e. 0–1) as vector length (r) is a measure of dispersion from the mean, but the position of the circles is nominal and for display purposes. The average scotophase is indicated by the thick grey (winter) and black (summer) lines.

torpid and normothermic on the same day (Figs. 3 and 4). Torpor was used more extensively in winter than in summer. In winter we observed periods of hibernation lasting in excess of 18 days, containing individual torpor bouts of up to 5.9 days.

Laboratory studies have suggested that *C. nanus* is an opportunistic hibernator. Torpor bouts of captive animals increased in duration and depth with decreasing T_a, with a torpid ΔT of ~1–2 °C, and individuals entered bouts of prolonged torpor at any time of the year (Bartholomew and Hudson, 1962; Geiser 1993; Song et al. 1997). Indeed, when held under cold conditions with food withdrawal fat individuals hibernated for up to a year, the longest period of hibernation recorded for any mammal (Geiser, 2007). In free-ranging individuals we observed broad seasonal differences in torpor expression as expected: the shorter torpor bouts in summer and longer bouts in winter were consistent with this species' response to T_a in captivity. Interestingly, we did not see a finer scale influence of T_a on torpor use. The nights that animals entered torpor were about the same T_a as those where they remained normothermic, in both seasons. Further, in winter the T_a of days that *C. nanus* rewarmed from torpor did not differ from those days they remained in prolonged torpor. This differs from the closely related *C. concinnus*, which entered torpor on nights that were colder than those when it did not employ torpor (Turner et al. 2012). Additionally, *C. concinnus* rewarmed from prolonged torpor once nest site temperature reached a T_a threshold (Turner et al., 2012), similar to some bats (*Nyctophilus* spp.; Turbill and Geiser, 2008). This indicates that, unlike *C. concinnus*, day-to-day T_a fluctuations were not an important factor influencing the torpor patterns of *C. nanus*.

Even though average T_a *per se* did not seem to influence torpor expression, entry into torpor always took place at night as T_a cooled, and rewarming from torpor occurred during the day as T_a increased towards the daily maximum. Individuals rewarmed from short torpor bouts late morning and prolonged torpor in the early afternoon. Allowing torpid T_b to increase with T_a is a strategy often used by heterotherms to reduce energy expenditure (Lovegrove et al., 1999; Schmid et al., 2000; Warnecke and Geiser, 2010), however since the animals in our study selected nest sites that were buffered from daily T_a variation, passive rewarming did not appear to be of particular importance. The amount of time required for animals to rewarm from torpor appeared to be more dependent on T_a (and probably T_b) than torpor bout length because it took longer to rewarm from short torpor bouts in winter than summer. This is most likely because individuals lowered their T_b and metabolic rate during torpor further in winter, when T_a was lower, compared to summer. This resulted in deeper torpor bouts and therefore an increased time required for rewarming to normothermia (Song et al., 1997). Additionally, the time it took to rewarm did not differ between short and prolonged torpor in winter. The similar rewarming times suggest that *C. nanus* is able to quickly achieve large energy savings by cooling T_b to just above T_a, which it can do during torpor bouts as short as 3 h (Song et al., 1997).

We assume that torpor and activity patterns in *C. nanus* were an indirect result of T_a influencing food availability, similar to other small hibernating species (e.g. Wojciechowski et al., 2007; Turbill and Geiser 2008). In most Australian habitats the seasonal change in weather and food availability is less severe than those occupied by seasonal hibernators on other continents, and can be highly variable within and among years. The primary food items of *C. nanus* are nectar and invertebrates (Turner, 1985; Arnould, 1986; Huang et al., 1986), which are available year-round, but usually decrease in abundance in winter because of the lower T_a (Smith, 1982; McFarland, 1985). The proportion of the night that individuals spent active was similar to *C. concinnus* (Turner et al., 2012), and agrees with the relationship between body mass, prey item energy content and activity suggested by Jackson and Johnson (2002) for possums. Even though *C. nanus* can potentially find food during any season, negating the need for extensive autumnal fattening and extended seasonal hibernation, it can be inferred that lower winter T_a affected foraging success and as a result, torpor was triggered more often in winter (Matheson et al., 2010; Schubert et al., 2010). Conversely, summer torpor was infrequent because food resources were likely more abundant. This ability to opportunistically adjust torpor use in response to food availability is likely to be crucial for energy management.

Interestingly, in summer only the males entered torpor, whereas in winter both sexes did. Although our small sample size demands caution, we will discuss potential implications. We suggest that the males in summer may have invested considerable time searching for females instead of food, resulting in decreased nightly energy acquisition and hence the need for torpor. This hypothesis seems plausible based on year-round male fertility (Ward, 1990), combined with a larger male home range size (Laidlaw and Wilson, 1996; Harris et al., 2007), which can be attributed to a larger effort made by males to find mates (Moraes and Chiarello, 2005). The lack of summer torpor in some female bats (Dietz and Kalko, 2006) and hedgehogs (Fowler, 1988) may be attributed to pregnancy and ensuring rapid foetal development (Racey, 1969), however pregnancy and torpor are not always mutually exclusive (Audet and Fenton, 1988; Kurta and Kunz, 1988; Körtner et al., 2008). More *C. nanus* births occur in summer than winter, which appears to correlate with increased female body mass and therefore food availability (Turner, 1985; Ward, 1990; Bladon et al., 2002). The females in our study did not appear pregnant (all were in non-breeding condition; after Turner, 1985), however the use of torpor by females only in winter may be an attempt to maintain a high body mass for reproduction at a time when food resources are reduced and T_a is lower.

Our study presents only the third example of marsupial hibernation in the wild. Interestingly, when comparing our results with those of the other two pygmy-possum species for which data on free-ranging individuals are available (*B. parvus* and *C. concinnus*), it appears that *C. nanus* uses a torpor strategy intermediate between the two. In winter *B. parvus* hibernates seasonally in snow-covered alpine boulderfields where T_a remains low and food is largely unavailable (Körtner and Geiser, 1998). Individuals fatten before hibernation onset, after which they employ long torpor bouts in hibernacula that remain stable at ~2 °C. Brief activity periods occur occasionally in most animals after rewarming from torpor, but are not likely used for foraging. Conversely, *C. concinnus* uses more open habitat with a variable thermal climate and hibernates opportunistically in winter in direct response to T_a (Turner et al., 2012). Individuals do not fatten seasonally as food is available year-round, and they are regularly active between torpor bouts. As torpor use is adjusted on a day-to-day basis, animals may spend several weeks at a time either hibernating or remaining normothermic, weather permitting. Similar to *B. parvus*, the *C. nanus* in the present study used periods of short-term hibernation in response to generally colder T_a experienced in winter compared to summer, however they were also regularly active, likely foraging, throughout the winter like *C. concinnus*. Although torpor use of *C. concinnus* was directly related to prevailing T_a, we suggest that the immediate trigger for torpor in *C. nanus* is probably more related to T_a-affected seasonal differences in food availability. This likely affected the nutritional status of individuals after a period of activity, resulting in individual flexibility in torpor employment independent of T_a. Hence, in addition to broad seasonal changes in torpor expression, *C. nanus* also has the ability to employ torpor opportunistically on a finer scale. This is a strategy likely beneficial for energy conservation, which would aid the survival of such a small and vulnerable species in an area where introduced predators and habitat destruction are threats.

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