

# The influence of natural photoperiod on seasonal torpor expression of two opportunistic marsupial hibernators

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**Abstract** Many mammals use torpor throughout the year but the individual contributions of environmental variables to seasonal changes in torpor expression are often difficult to tease apart. In many mammals, torpor is most often used opportunistically in response to decreased ambient temperature ( $T_a$ ) and food availability, but information on how seasonally changing photoperiod per se influences torpor patterns is scant. Therefore, we quantified patterns of torpor use in response to natural photoperiod in captive marsupial pygmy-possums held at near-constant  $T_a$  with a stable food supply over a period of 19 months. Western pygmy-possums (*Cercartetus concinnus*) and eastern pygmy-possums (*C. nanus*) used spontaneous torpor in every month of the year; in total we measured >1100 individual torpor bouts. Torpor bout duration was >60 % longer in winter than in summer and increased with decreasing day length for both species. Interestingly, the duration of torpor appeared to be adjusted at both the beginning and end of bouts because the time of entry into and rewarming from torpor relative to sunrise and sunset, respectively, changed with season. We propose that this reflects a synchronisation of torpor timing with foraging periods in the wild, which would enable animals to maintain a high body mass year-round by maximising both energy savings via torpor and energy input via food consumption. Our study suggests that photoperiod

makes a significant contribution to the seasonal change in torpor bout duration of small hibernating mammals that use torpor throughout the year.

**Keywords** Burramyidae · *Cercartetus* spp. · Environmental cue · Temporal organisation · Season · Non-invasive method

## Introduction

Seasonal variations in torpor patterns occur in many heterothermic species from all three mammalian subclasses from diverse habitats and climatic regions. As torpor is primarily used for energy conservation when food availability is low, it is entirely restricted to winter in many rodents (Heldmaier and Steinlechner 1981; Lyman et al. 1982; Wang 1989; Boyer and Barnes 1999; Carey et al. 2003) and dwarf lemurs (Dausmann 2014). However, for other mammals such as echidnas, small marsupials, bats, elephant shrews and dormice, torpor is expressed opportunistically throughout all or most of the year (Geiser and Baudinette 1987; Nicol and Andersen 2002; Mzilikazi and Lovegrove 2004; Bieber and Ruf 2009; Stawski and Geiser 2010; Turner et al. 2012b; Hoelzl et al. 2015). Nevertheless, even in those species that use torpor in all seasons, torpor during winter conditions when ambient temperature ( $T_a$ ) is low is usually deeper and longer than in summer. Although temperature is known to strongly affect torpor expression it is not the only environmental variable that changes with season and other intrinsic or external factors are likely to be involved.

Data on dormice (*Glis glis*) and bats (*Nyctophilus bifax*) suggest that seasonal changes in torpor patterns are predominantly temperature dependent because torpor bout

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duration forms a continuum between winter and summer and is a linear function of  $T_a$  (Bieber and Ruf 2009; Stawski and Geiser 2010). Similarly, torpor bout duration is negatively correlated with  $T_a$  in other hibernators within the  $T_a$  range that they are thermoconforming (Twente and Twente 1965; Lyman et al. 1982; Geiser and Broome 1993; Buck and Barnes 2000). However, the torpor bout duration of some hibernators changes within a hibernation season even under constant laboratory conditions and can be independent of photoperiod (Morrison 1964). Usually, shorter bouts of torpor occur at the beginning of the hibernation season, followed by longer bouts in the middle and short bouts again at the end of the season (Lyman et al. 1982; French 1985; Boyer and Barnes 1999). As this type of seasonal hibernation occurs in strongly seasonal habitats within a discrete, annually occurring unit of time, these data suggest that an intrinsic biological clock determines the temperature-independent seasonal change in torpor bout duration. Furthermore, such hibernators usually spend the winter in enclosed burrows relying on stored energy reserves and are, hence, often relatively unaware of and insensitive to photoperiodic changes (Pengelley and Fisher 1963; Davis 1976). As other species inhabiting less seasonally predictable environments often exhibit torpor throughout the year, do not undergo seasonal changes in body mass and forage between torpor bouts, they may instead adjust torpor patterns in response to immediate environmental cues instead of endogenous circannual rhythms.

Photoperiod is an important signal eliciting seasonal change of many functional variables including torpor use, reproductive condition, body mass and food intake (e.g. Morrison 1964; Canguilhem et al. 1977; Heldmaier and Steinlechner 1981; Perret and Aujard 2001; McAllan et al. 2006). However, in some detailed seasonal studies of torpor expression animals were kept in outdoor enclosures, which either precluded separation of the individual contribution of  $T_a$  and photoperiod to torpor use as both change with season (Geiser and Baudinette 1987), or indicated that while photoperiod plays a prominent role in prompting torpor expression,  $T_a$  is likely also needed as a cue as animals age (Heldmaier and Steinlechner 1981). In those studies where animals were only acclimated to exclusively photoperiodic changes, exposure times were usually brief, lasting only part of the natural yearly cycle (Lynch et al. 1978; Geiser et al. 2005), or the species did not enter torpor at all under long photoperiod so torpor patterns could not be compared among seasons (Geiser and Heldmaier 1995). Therefore, data on the effects of photoperiod on patterns of torpor among all seasons, but independent of  $T_a$  effects, are scant.

Environmental variables directly influencing seasonal changes in torpor expression are often difficult to tease apart, so we experimentally investigated whether natural photoperiod would cause a seasonal change in torpor

patterns of two small marsupial species under constant  $T_a$  and food supply. The western pygmy-possum *Cercartetus concinnus* and the eastern pygmy-possum *C. nanus* do not hibernate seasonally and instead enter spontaneous torpor in captivity and in the wild at any time of the year with minimum body temperatures of 2–5 °C and maximum torpor bout durations of 1–5 weeks (Geiser 1987, Turner et al. 2012a, b). Both species are opportunistic hibernators in the wild: *C. concinnus* enters torpor in response to prevailing low winter  $T_a$  (Turner et al. 2012a), whereas in *C. nanus* torpor use appears to be affected by foraging success and season (Turner et al. 2012b). As these studies were conducted in the wild any direct effects of photoperiod may have been masked.

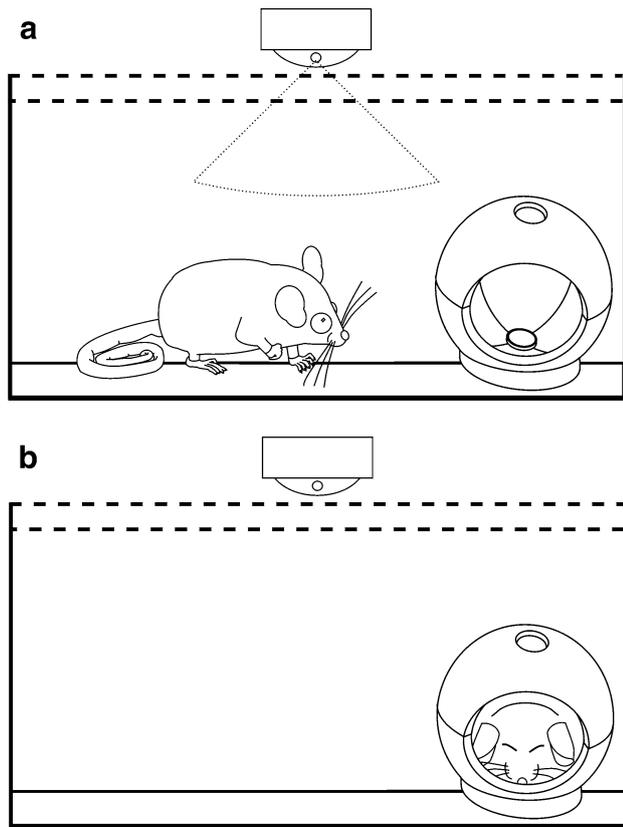
## Materials and methods

### Animals and trapping

Pygmy-possums of the genus *Cercartetus* are small, arboreal, nocturnal marsupials that use torpor year-round. They nest in leaf-and-bark dreys, tree hollows, dead stumps, vegetation thickets, disused birds' nests or beneath leaf litter (Tulloch 2004; Turner et al. 2012a, b); sites that would allow possums to perceive changes in photoperiod and  $T_a$ . Six *C. nanus* (all females) were caught using nest boxes near Dorrigo, NSW (30°22'S., 152°34'E.) in mid-2005. Five *C. concinnus* (three males, two females) were trapped using pitfall traps with drift fences in Mallee Cliffs National Park, NSW (34°15'S., 142°36'E.) in March 2007. Animals were transported to the University of New England in Armidale (30°31'S., 151°40'E.) and housed at a  $T_a$  of ~20 °C in individual plastic enclosures (44 × 34 × 23 cm) under natural photoperiod (annual day length 10.2–14.1 h). Natural light entered the holding room through windows running along the length of one side. The cryptic nature and low trapping success of pygmy-possums precluded us from housing enough animals for a control group exposed to an experimental light/dark regime. Throughout the study period animals were fed the same daily ration of apples, walnuts, sunflower seeds, rolled oats and a nectar substitute containing high-protein baby cereal, honey, a vitamin supplement, boiled eggs or protein powder and pureed fruit. Food was not provided ad libitum because pygmy-possums tend to become obese in captivity. Water was freely available.

### Possum den construction

Individual possum dens were made from tennis balls (diameter 6.5 cm: *C. concinnus*; 10 cm: *C. nanus*). Balls were halved and a small hole was cut into the base of one



**Fig. 1** Cage setup with tennis ball dens: **a** the active animal outside its den triggers passive infrared detector (PIR) detector mounted on cage roof and temperature data logger in den base records  $T_{\text{den}}$ ; **b** when an animal is inside its den no motion is detected and data logger records  $T_{\text{skin}}$ . Not to scale

half to allow the insertion of a small temperature data logger (see below), while a second hole was cut into the top half of the ball for ventilation (Fig. 1). An entrance hole allowed animals to climb inside. The den was held together using a rubber band, a small piece of paper towel covered the top hole and the ball was placed on a cardboard ring for stability.

### Skin and ambient temperature

Skin temperature ( $T_{\text{skin}}$ ) was measured at 10-min intervals using factory-calibrated temperature-sensitive data loggers ( $\pm 0.5$  °C; DS 1921G Thermochron iButtons; Maxim Integrated Products, San Jose, CA, USA). Loggers were placed in the base of dens (Fig. 1a) so that whenever an animal was inside the spherical den shape assured that it was sitting directly on the logger. Similar methods of non-invasively monitoring surface temperature to quantify torpor expression have been successfully used for both small mammals and birds (e.g. Hiebert 1993; Willis et al. 2005;

Munn et al. 2010; Warnecke 2012). Logger data were downloaded every 2 weeks and continuous measurements were taken from April 2007 to October 2008, excluding a 2-week gap in January 2008 and a 12-week gap in late autumn/early winter 2008.

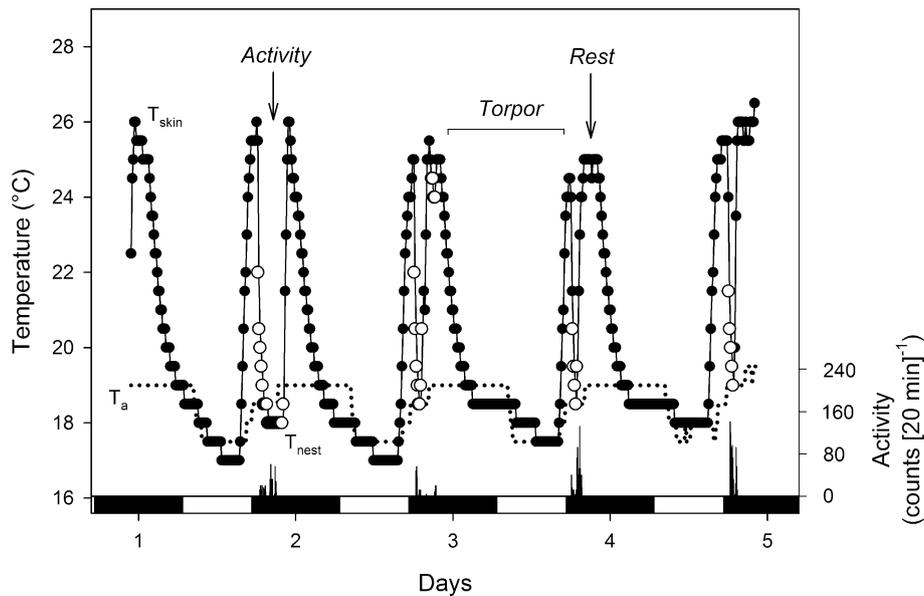
$T_a$  ( $\pm 0.5$  °C) was recorded at 10-min intervals using an iButton placed near the enclosures.

### Torpor bout identification

When an individual was outside its den (Fig. 1a) the logger recorded den temperature ( $T_{\text{den}}$ ), which was the same as  $T_a$ . When a normothermic animal was inside (Fig. 1b) the logger recorded high  $T_{\text{skin}}$ .  $T_{\text{den}}$  rapidly fell when the animal left its den (Fig. 1). When the animal entered torpor,  $T_{\text{skin}}$  slowly decreased with the cooling of the body until it was slightly above  $T_a$ . To clearly differentiate between low  $T_{\text{skin}}$  measured during a torpor bout and  $T_{\text{den}}$  when an animal was absent, activity was recorded by placing a passive infrared motion detector (PIR; LA-5017, Jaycar Electronics, Rydalmere, NSW, Australia) on top of each individual's enclosure and measuring motion events (Fig. 1). These were recorded using a custom-built data logger (Körtner and Geiser 1995) and summed over 20 min for analyses. All logger data from inside dens that were recorded during activity periods were omitted from torpor analyses. The time of entry into and rewarming from torpor was determined by visual inspection of temperature data because differences in the body position of a pygmy-possum in a den resulted in  $T_{\text{skin}}$  variability among individuals in the same state of torpor/normothermia, precluding the use of general temperature cutoff values. Therefore, torpor entry was defined as the time when elevated  $T_{\text{skin}}$  of a normothermic animal began to decrease steadily before reaching a stable minimum, when  $T_{\text{skin}} \approx T_a$ . The end of rewarming from torpor was defined as the time when  $T_{\text{skin}}$  increased to a high, normothermic level (Fig. 2).

### Data and statistical analyses

We divided torpor into short (<26 h) and prolonged bouts (>37 h) based on frequency distribution tables generated using *statistiXL* v1.8; because pygmy-possums are hibernators capable of multi-day torpor we avoid the term “daily torpor” to describe bouts <26 h in duration. To test for an influence of photoperiod (i.e. day length) on body mass (BM), torpor bout duration and timing of entry into and rewarming from torpor relative to sunrise/sunset we used linear mixed effects models using the covariate “day length”, random factor “individual” and dependent variables “body mass”, “torpor bout duration”, “entry time” and “rewarming time” and tested model residuals for normality



**Fig. 2** Skin temperature ( $T_{\text{skin}}$ ; closed circles and line) over a four-day period for one individual *C. nanus* in winter 2008 showing four torpor bouts (*Torpor*). Ambient temperature ( $T_a$ ; dotted line) and activity (*Activity*; vertical bars) are also shown. When activity is registered, the data logger records den temperature ( $T_{\text{den}}$ ; open circles); when activity is not recorded the animal is inside its nest box either

at rest (i.e. with high  $T_{\text{skin}}$ ; *Rest*) or in torpor.  $T_{\text{den}}$  values higher than  $T_a$  are due to the animal moving in and out of the nest box during the activity period, temporarily warming the data logger. Some individuals also exited and re-entered the nest box during the rewarming phase, apparently using locomotion to aid rewarming. Dark horizontal bars indicate the scotophase

using a Kolmogorov–Smirnov test using SPSS v21. This analysis takes individuals into account by determining the deviance of each individual from the common regression and adjusts for repeated measures; degrees of freedom are computed from both the numbers of individuals and observations to avoid false  $p$  values caused by pseudoreplication. A conditional  $R^2$  was calculated to examine the fit of each model using the package “MuMIn” (Bartoń 2015) in R (R Core Team 2014). Linear regression tested if  $T_a$  changed with day length. The timing of torpor entry and rewarming was tested for non-random distribution using a Rayleigh’s test, after which a Watson–Williams test was used to compare times among seasons (Zar 2010). Data are presented as mean  $\pm$  1 SD;  $n$  denotes the number of individuals,  $N$  the number of measurements.

## Results

### Ambient temperature, body mass and den use

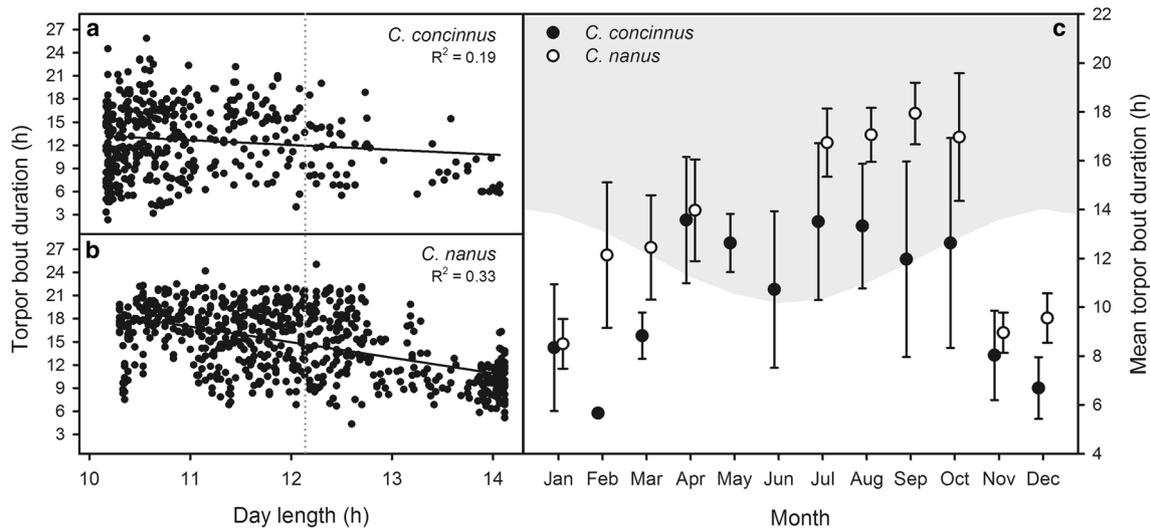
The average  $T_a$  during the study period was  $19.9 \pm 1.3$  °C (min:  $18.9 \pm 1.2$  °C, max:  $20.9 \pm 1.4$  °C). Average daily  $T_a$  increased slightly with day length ( $19.5$ – $20.5$  °C;  $R^2 = 0.10$ ,  $F_{1,362} = 38.46$ ,  $p < 0.001$ ), but this change was only 1 °C over the year and unlikely to be biologically significant.

BM during the ~19-month measurement period was  $16.8 \pm 4.9$  g for *C. concinnus* and  $43.7 \pm 9.8$  g for *C. nanus*. BM did not change with day length for *C. concinnus* ( $F_{1,183.0} = 1.08$ ,  $p = 0.301$ ) but increased with increasing day length for *C. nanus* ( $41.3$ – $47.1$  g;  $F_{1,181.3} = 8.80$ ,  $p = 0.003$ ).

*Cercartetus concinnus* used dens on 1479 out of total of 1805 possum-days ( $82.5 \pm 11.6$  %,  $n = 5$ ); *C. nanus* used dens on 1566 out of 1753 possum-days ( $88.5 \pm 11.7$  %;  $n = 6$ ).

### Torpor bout duration

The  $T_{\text{skin}}$  of a torpid animal inside its den was easily differentiated from  $T_{\text{den}}$  when the animal was outside by omitting values recorded during times of activity (Fig. 2). 438 spontaneous torpor bouts were recorded in their entirety for *C. concinnus*. Average short torpor bout duration was  $12.6 \pm 4.6$  h (range 2.3–25.8 h;  $n = 5$ ,  $N = 410$ ) and prolonged torpor lasted  $63.6 \pm 19.3$  h (range 37.7–102.7 h;  $n = 4$ ,  $N = 28$ ). For *C. nanus*, we recorded a total of 692 torpor bouts. Average short torpor bout duration was  $14.9 \pm 4.4$  h (range 4.3–25.0 h;  $n = 6$ ,  $N = 688$ ) and  $42.1 \pm 3.8$  h for prolonged torpor (range 37.0–45.8 h;  $n = 2$ ,  $N = 4$ ). Owing to the low number of prolonged torpor bouts expressed by both species, only short torpor bouts were used for statistical analyses. For



**Fig. 3** The negative relationship between day length and short torpor bout duration for *C. concinnus* (a;  $n = 5$ ) and *C. nanus* (b;  $n = 6$ ); solid trendlines are shown. The dotted line indicates the median day length. c Torpor bout duration (means of individual monthly

mean  $\pm$  SD from the entire 19-month study period) plotted over a single year for *C. concinnus* (closed circles) and *C. nanus* (open circles); the grey area indicates the scotophase

**Table 1** Timing of entry into and the end of rewarming from torpor for *C. concinnus* and *C. nanus*, including results of the Rayleigh’s tests

Season	$n$ ( $N$ )	Entry ( $h$ )	$r$	$z$	$p$	Rewarming ( $h$ )	$r$	$z$	$p$
<i>C. concinnus</i>									
Summer	5 (9)	5:51	0.98	8.67	<0.001 <sup>b</sup>	12:56	0.94	7.92	<0.001 <sup>b</sup>
Autumn	5 (97)	2:53	0.64	39.59	<0.001 <sup>a</sup>	15:28	0.63	38.83	<0.001 <sup>a</sup>
Winter	5 (220)	3:00	0.63	87.90	<0.001 <sup>a</sup>	15:26	0.72	113.59	<0.001 <sup>a</sup>
Spring	5 (82)	3:07	0.72	42.37	<0.001 <sup>a</sup>	15:03	0.87	61.81	<0.001 <sup>a</sup>
<i>C. nanus</i>									
Summer	4 (138)	5:43	0.86	102.48	<0.001 <sup>b</sup>	16:35	0.92	115.79	<0.001 <sup>b</sup>
Autumn	6 (173)	3:13	0.75	98.26	<0.001 <sup>c</sup>	16:56	0.94	153.24	<0.001 <sup>a</sup>
Winter	6 (212)	0:14	0.79	132.66	<0.001 <sup>a</sup>	17:11	0.94	188.30	<0.001 <sup>a</sup>
Spring	6 (163)	0:07	0.60	59.01	<0.001 <sup>a</sup>	17:02	0.94	143.52	<0.001 <sup>a</sup>

For each species, seasons with the same superscript letter did not differ significantly from one another after a Watson–Williams test ( $p > 0.2$ ); all others were significantly different ( $p < 0.05$ )

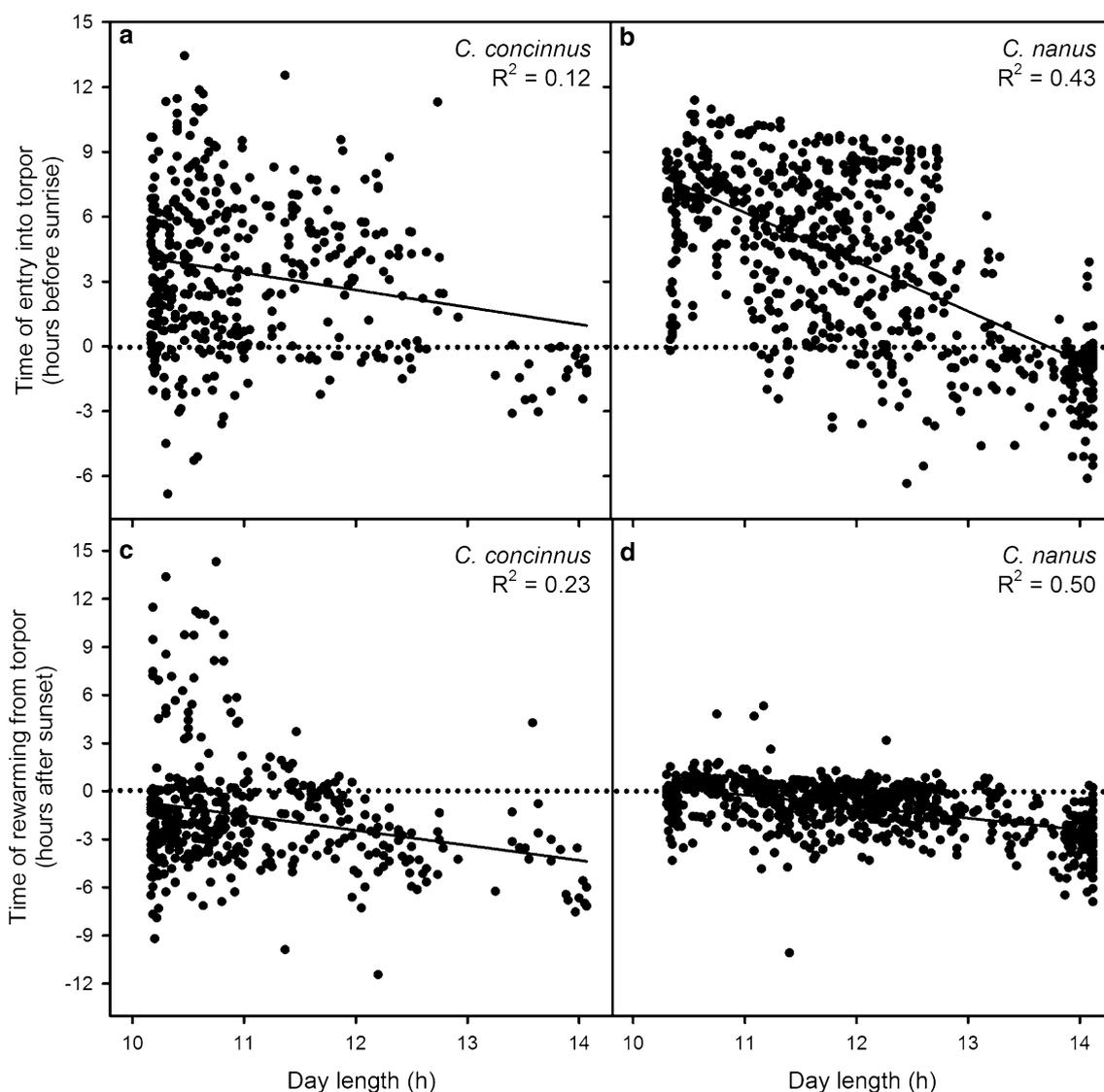
*C. concinnus*, most prolonged bouts occurred in winter: July ( $N = 11$ ), August ( $N = 16$ ) and September ( $N = 1$ ); for *C. nanus* in March ( $N = 1$ ) and September ( $N = 3$ ). 81 % of torpor bouts occurred in the darker half of the year (i.e. between the Autumnal and Vernal equinoxes: March 21st–September 23rd; including late autumn, winter and early spring) for *C. concinnus*, and 59 % for *C. nanus* (Fig. 3).

Torpor bout duration decreased with increasing day length for both species (*C. concinnus*:  $F_{1,404.8} = 4.41$ ,  $p = 0.036$ ; *C. nanus*:  $F_{1,681.2} = 160.02$ ,  $p < 0.001$ ; Fig. 3). Although the models were highly significant, the conditional  $R^2$  for *C. concinnus* was relatively weak ( $R^2 = 0.19$ , slope =  $-0.47$ ), and only slightly stronger for *C. nanus* ( $R^2 = 0.33$ , slope =  $-1.66$ ).

**Torpor timing**

The timing of both entry and rewarming from short torpor was non-randomly distributed in all seasons for both species (Table 1). Entry into torpor occurred in the early morning and the end of rewarming in the afternoon. For *C. concinnus*, torpor started later in the night in summer compared to all other seasons ( $p < 0.02$ ), and finished earlier ( $p < 0.05$ ; Table 1). For *C. nanus*, torpor entry was earlier in winter and spring than in summer and autumn ( $p < 0.001$ ) and also ended earlier in summer ( $p < 0.05$ ; Table 1).

The timing of entry into and rewarming from torpor was significantly and negatively correlated with day length: pygmy-possums entered torpor earlier during short-day photoperiod and rewarmed later during long-day



**Fig. 4** The effect of day length on time of entry into torpor (**a, b**) and time of the end of rewarming from torpor (**c, d**) for *C. concinnus* (**a, c**;  $n = 5$ ) and *C. nanus* (**b, d**;  $n = 6$ ). On the y-axes Time = 0 is

sunrise (*upper panels*) or sunset (*lower panels*), indicated by a *dotted line*. Times before sunrise and after sunset are positive integers. *Solid trendlines* are shown

photoperiod (Fig. 4; *C. concinnus* entry:  $F_{1,405.6} = 17.25$ ,  $p < 0.001$ ,  $R^2 = 0.12$ , slope =  $-0.75$ ; rewarming:  $F_{1,404.8} = 24.32$ ,  $p < 0.001$ ,  $R^2 = 0.23$ , slope =  $-0.85$ ; *C. nanus* entry:  $F_{1,675.8} = 327.24$ ,  $p < 0.001$ ,  $R^2 = 0.43$ , slope =  $-1.98$ ; rewarming:  $F_{1,685.4} = 218.21$ ,  $p < 0.001$ ,  $R^2 = 0.50$ , slope =  $-0.68$ ).

## Discussion

Our data suggest that a seasonal change in photoperiod causes measurable adjustments in torpor expression in two opportunistic hibernators that use torpor throughout the year. The only environmental cue experienced by the

pygmy-possums that communicated a change in seasons was photoperiod; nevertheless, both species showed significant variation in torpor bout duration among seasons. A shortened photophase has been demonstrated to induce torpor use in mammals inhabiting seasonally distinct environments in Palaearctic (Heldmaier and Steinlechner 1981), Nearctic (Geiser et al. 2007) and Afrotropical regions (Perret and Aujard 2001). However, in the more variable Australasian climate, photoperiod acclimation has not been found to strongly affect torpor use (Geiser et al. 2005), even in the only seasonally hibernating marsupial, the alpine mountain pygmy-possum (*Burramys parvus*; Körtnner and Geiser 1995). The response in torpor use observed here in *Cercartetus* spp. suggests that photoperiod is one of

the important factors determining seasonal torpor patterns in these species.

The seasonal change in torpor expression of pygmy-possums in our study is reminiscent of that in northern hemisphere hibernators during a winter hibernation season, but instead torpor duration changed gradually over the entire year and was not only restricted to the cold season. In northern hibernators, the mechanism for spontaneous lengthening and shortening of torpor bouts with season is not clearly understood, although it is often viewed to reflect an innate yearly rhythm (French 1985) that is likely entrained by photoperiod in some species (Morrison 1964). We acknowledge that the low sample size and absence of a control group in our study means that we are unable to conclusively say that photoperiod alone affected torpor expression; it is possible that an endogenous circannual rhythm was also involved. To tease these factors apart and determine whether a Type I/II (partially/entirely endogenously influenced) or Type III (purely exogenous) rhythm is present it would be necessary to expose animals to constant and reversed photoperiods and examine torpor patterns (Prendergast et al. 2002). However, we argue that the seasonal change in torpor bout duration in *C. concinnus* and *C. nanus* we observed is unlikely to be the result of an endogenous circannual rhythm. Circannual torpor rhythms are usually expressed in seasonally predictable environments by obligate placental hibernators, which only use torpor during the winter hibernation season, such as ground squirrels and chipmunks (Morrison 1964; Joy and Mrosovsky 1983; Kawamichi 1996). An exception such as the edible dormouse *Glis glis*, for example, may extend its hibernation season into summer in non-reproductive years in response to food availability/quality, previous reproductive effort and predation risk (Bieber and Ruf 2009; Hoelzl et al. 2015). As both short and prolonged torpor use in *C. concinnus* and *C. nanus* is opportunistic and can occur at any time of the year (Geiser 1987; Turner et al. 2012a, b), as long as environmental conditions are suitable, a circannual rhythm is not likely responsible. The closely related but seasonally hibernating alpine mountain pygmy-possum (*Burramys parvus*) loses its annual cycle of hibernation and body mass when held in captivity, even if maintained under simulated natural photoperiod and  $T_a$ , suggesting that natural climate and food availability, rather a circannual rhythm, govern seasonal functional changes in this similar species (Körtner and Geiser 1995).

Circadian cycles of activity and torpor use, on the other hand, are strong in pygmy-possums and appear entrainable to photoperiod (Körtner and Geiser 1995). Both *C. concinnus* and *C. nanus* entered into and rewarmed from short torpor bouts at approximately the same time relative to sunrise and sunset, respectively, in the wild (Turner et al. 2012a, b) and captivity (this study). Thus, the strong

influence of photoperiod on the energy budgeting of these species is evident not only among seasons over the course of an entire year, but also within seasons on a finer day-to-day scale. In the wild, the two species appear to enter torpor for slightly different immediate reasons: *C. concinnus* enters torpor in response to low  $T_a$  experienced the previous night (Turner et al. 2012a), whereas *C. nanus* probably uses torpor in response to foraging success and seasonal  $T_a$  patterns (Turner et al. 2012b). The number of torpor bouts we recorded in the darker half of the year (81 % for *C. concinnus* versus 59 % for *C. nanus*) is consistent with these findings from free-ranging animals and suggests that photoperiod can convey the small annual changes in  $T_a$  and food resource type present in their habitats (Huang et al. 1986; Pestell 2005). In the absence of high seasonal food and  $T_a$  variability, the tighter correlation of torpor variables with day length (i.e. higher  $R^2$ s) for *C. nanus* may indicate that this species also uses photoperiod as a cue for torpor use in the wild, as has been suggested previously (Turner et al. 2012b). Additionally, the more scattered torpor patterns of captive *C. concinnus* may indicate that  $T_a$  variability is still important for torpor use in free-ranging individuals, as the colony  $T_a$  of 19.9 °C was higher than the threshold  $T_a$  of ~12 °C, above which pygmy-possums rewarmed from torpor (Turner et al. 2012a). Nevertheless, our identification of the relationship between torpor use and photoperiod for *C. concinnus*, and the use of prolonged torpor mostly in winter indicates that photoperiod still plays a partial role in seasonal activity.

The changes to torpor entry and rewarming times to prolong torpor in *Cercartetus* spp. were likely related to a naturally increased concentration of circulating melatonin during exposure to short-day photoperiod (Goldman and Darrow 1983; Carter and Goldman 1983). Melatonin is released during the dark phase and thus circulates for longer time periods in winter than in summer; administration can mimic short photoperiod acclimation and increase daily torpor use in white-footed mice (*Peromyscus leucopus*; Lynch et al. 1978). Additionally, melatonin treatment induces earlier daily torpor entry and later rewarming in some individual Djungarian hamsters (*Phodopus sungorus*; Ruf et al. 1989), similar to our observations, and the selection of low  $T_b$  in lizards (Rismiller and Heldmaier 1987). Therefore, the exposure to naturally changing photoperiod that these pygmy-possums received probably produced both an ecological (foraging timing) and physiological (hormonal) response, thereby influencing torpor use. Interestingly, the timing of torpor entry and rewarming was not random and the duration of torpor bouts in the pygmy-possums was adjusted both at the beginning and end of bouts. In winter, torpor entry in pygmy-possums was earlier and rewarming occurred later than in summer. This is in contrast to species such as kangaroo mice (*Microdipodops pallidus*), which

adjust entry but not rewarming times in response to food rationing (Brown and Bartholomew 1969) or Cape rock elephant shrews (*Elephantulus edwardii*) which changed cooling rates but not timing of torpor (Geiser and Mzilikazi 2011). Developing dunnarts (*Sminthopsis macroura*) adjust both the beginning and end of daily torpor bouts to alter torpor bout duration as body mass increases during growth (Geiser et al. 2006). As both our pygmy-possum species hibernate opportunistically, they do not undergo large seasonal changes in body mass and must, therefore, forage regularly. Thus, entering torpor in the second half of the night and rewarming shortly before sunset would enable them to maximise both the time spent torpid and the time spent foraging, similar to patterns observed for hibernating bats (Park et al. 2000; Czenze and Willis 2015).

Torpor in mammals and birds is generally associated with winter because  $T_a$  is low and food is scarce (Lyman et al. 1982; Wang 1989); however, in more unpredictable environments, without striking seasonal changes in  $T_a$ , food availability and photoperiod, torpor can also occur in summer (Lovegrove 2000; Turbill et al. 2003; McKechnie and Mzilikazi 2011; Turner et al. 2012b). Australian mammals are often exposed to unpredictable fluctuations in rainfall and food availability and employ torpor to deal with these challenges (Munn et al. 2010; Warnecke 2012). The food supply of the animals in our study did not change, yet they still used torpor in every month of the year. This suggests that torpor use in *C. concinnus* and *C. nanus* is a routine part of their everyday energy budgeting regardless of  $T_a$  or energy availability. Torpor in pygmy-possums was used to save energy even when it is not essential for survival, and is probably a strategy to maintain body mass and fat content at an optimum, to be used as an energy source when conditions become unfavourable.

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