



Survivable hypothermia or torpor in a wild-living rat: rare insights broaden our understanding of endothermic physiology

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Abstract

Maintaining a high and stable body temperature as observed in endothermic mammals and birds is energetically costly. Thus, it is not surprising that we discover more and more heterothermic species that can reduce their energetic needs during energetic bottlenecks through the use of torpor. However, not all heterothermic animals use torpor on a regular basis. Torpor may also be important to an individual's probability of survival, and hence fitness, when used infrequently. We here report the observation of a single, ~5.5 h long hypothermic bout with a decrease in body temperature by 12 °C in the native Australian bush rat (*Rattus fuscipes*). Our data suggest that bush rats are able to rewarm from a body temperature of 24 °C, albeit with a rewarming rate lower than that expected on the basis of their body mass. Heterothermy, i.e. the ability to withstand and overcome periods of reduced body temperature, is assumed to be an evolutionarily ancestral (plesiomorphic) trait. We thus argue that such rare hypothermic events in species that otherwise appear to be strictly homeothermic could be heterothermic rudiments, i.e. a less derived form of torpor with limited capacity for rewarming. Importantly, observations of rare and extreme thermoregulatory responses by wild animals are more likely to be discovered with long-term data sets and may not only provide valuable insight about the physiological capability of a population, but can also help us to understand the constraints and evolutionary pathways of different phenologies.

Keywords Heterothermy · Homeothermy · Native Australian rodent · Bush rat · Rewarming · Cooling

Introduction

As endotherms, mammals and birds are characterised by metabolically defending a near-constant body temperature (T_b) by regulatory feedback mechanisms in the hypothalamus (Zhao et al. 2017). The maintenance of T_b within a narrow range of optimal temperatures has several advantages, such as sustained aerobic activity, independence from environmental conditions and optimisation of enzyme activity, but endothermy comes with a high energetic cost

relative to ectothermic species (Nagy 2005). This energetic cost is particularly high for smaller species, and increases with decreasing ambient temperature (T_a) below the animal's thermal neutral zone (Bennett and Ruben 1979). Thus, given that food is often not continuously available, it is not surprising that some mammals and birds can lower their metabolically defended T_b in a controlled state known as torpor (Geiser 2004). During torpor, the metabolic rate of an animal is reduced in correspondence with the reduction in T_b and the animal is able to rapidly rewarm from its low T_b by endogenously fuelled heat production. This process is fundamentally different from unregulated hypothermia, during which T_b is equally reduced, but metabolic rate remains high as the animal is attempting to generate as much metabolic heat as possible to defend its T_b against a further decline. Torpor by so-called heterothermic endotherms, therefore, can provide a pronounced reduction of the animal's daily energy expenditure (Geiser 2004). The resulting energy saving provides these species with greater flexibility in managing the combined risks of starvation and predation under variable environmental conditions (Turbill

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et al. 2011, 2019; Turbill and Stojanovski 2018). To date, we know more than 171 species of mammals and 43 bird species that are capable of using torpor (Ruf and Geiser 2015). Numbers of heterothermic species are steadily increasing, partly because ongoing technological advances in biologing equipment (Chmura et al. 2018) allow T_b to be recorded in a greater range of wild-living animals, which are more likely to exhibit torpor compared to captive animals (Geiser et al. 2000). Notable recent additions of species using torpor in the wild include a primate—the pygmy slow loris (Ruf et al. 2015), a passerine—the superb fairy-wren (Romano et al. 2019), and the discovery of multiday torpor in response to a flood event in golden spiny mice, a species that had been described previously as undergoing only short bouts of torpor for a few hours (Barak et al. 2018). While it is relatively easy to discover and describe torpor use in species that are using torpor on a regular basis, torpor could also be important to an individual's probability of survival, and hence fitness, when used infrequently, such as in response to extreme weather events (Nowack et al. 2015), and these rare torpor bouts require long-term data sets of wild-living animals (see Nowack et al. (2020) for a recent list of species that are known to use torpor only rarely).

Australia's native rodent species are one group of mammals that might be expected to use torpor, but for which we have very little data on T_b , especially in wild-living animals. At least 40% of Australia's native mammals are known to use torpor, yet although native rodents make up approximately 25% of Australian mammal species (Geiser and Körtner 2010), only one native species, the ash-grey mouse *Pseudomys albocinereus* has been shown to be capable of employing regulated torpor in the laboratory at T_a of 20 and 25 °C (Barker et al. 2012). Hypothermic bouts have also been recorded in the sandy mouse, *Pseudomys hermannsburgensis* (Tomlinson et al. 2007), but heterothermy in *P. hermannsburgensis* is assumed to represent hypothermia (Tomlinson et al. 2007), i.e. a non-controlled, non-reversible drop in T_b . In addition, the house mouse, *Mus musculus*, an introduced species that lives in natural environments in Australia, shows daily torpor in the wild (Morton and Lee 1978) and in captivity in response to increased energy expenditure (Schubert et al. 2010) or increased perceived predation risk (Turbill and Stojanovski 2018), and a recent paper has revealed that juvenile mice use torpor during their development (Renninger et al. 2020). All other studies on thermoregulation of native Australian rodent species, such as the bush rat (*Rattus fuscipes*), so far suggest they are strictly homeothermic species that regulate their T_b within a narrow range (e.g. Glanville and Seebacher 2010). One reason for this might be a lack of field-based data. Bush rats are a particularly well-studied species, but all studies on bush rats have either been laboratory studies (Seebacher and Glanville 2010; Glanville et al. 2012) or short field studies

lasting < 3 weeks (Glanville and Seebacher 2010), while longer term field data might be required to document the physiological breath of a species (Geiser et al. 2000, 2007). For example, studies comparing torpor use in sugar gliders under laboratory and field conditions have revealed differences in activity pattern as well as a difference in T_b regulation with a lower normothermic T_b and more frequent and deeper torpor bouts in the wild (Geiser et al. 2007).

We present long-term T_b data from free-ranging individuals of the native Australian bush rat (*Rattus fuscipes*), a species endemic to Australia, recorded during the austral autumn and early winter seasons. These data were collected during a broader study that aimed to test for within-individual correlations and among-individual differences in behavioural and physiological traits in wild rats. Among 1047 individual-days of T_b , we recorded a single observation of a 12 °C decrease in T_b over 5.5 h during the resting phase for one individual. This paper focusses on this unique observation and discusses its implications for our understanding of endothermic thermoregulation.

Methods

Animals

We captured a total number of 30 bush rats in walk-in live traps (Elliott traps, type A) in the Blue Mountains, approximately 60 km WNW of Sydney, Australia (S 33.60994, E 150.63809) between March and May 2016. Traps were baited with rolled oats and peanut butter in the afternoon and checked in the early morning. After capture, rats were transported to Hawkesbury Campus of Western Sydney University, where they were fitted with a subcutaneous microchip for individual identification (PIT tag; Trovan ID100 Midi-chip) and surgically implanted with a temperature-sensitive data logger before being released (ibutton; DS1922L-F5#, resolution: 0.0625 °C, accuracy improved to 0.1 °C by calibration, logging interval: every 30 min; Maxim Integrated Products, Inc., Sunnyvale, California, USA; surgery details below). Temperature loggers were waxed in Elvax and calibrated before use in a water bath to the nearest of 0.1 °C (high precision NIST traceable digital thermometer; Control Company, Texas) from 5 to 40 °C. Loggers weighed < 3 g after waxing, which is < 5% of the body mass of adult bush rats (rats weighed between 59 and 137 g). After recovery from surgery (details below), rats were released at the exact capture location. We re-captured 14 of 30 implanted rats in June and July 2016 (recapture rate: 47%) and recorded a total of 1047 individual-days of T_b data between March and June 2016 (42–87 days per animal (Table 1), $N = 14$ animals (9 m, 5 f), average body mass: 92 ± 21 g).

Table 1 Overview of data recording

Animal	Release/recording start date	Recapture/recording end date	Number of days
1	14 March	02 June	80
2	14 March	01 June	79
3	14 March	01 June	79
4	20 March	14 June	87
5	27 March	12 June	77
6	27 March	12 June	77
7	27 March	12 June	77
8	27 March	12 June	77
9	04 April	19 June	76
10	04 April	19 June	76
11	12 April	28 June	77
12	12 April	28 June	77
13	22 April	29 June	66
14	17 May	29 June	42

The table indicates the recording period as well as the total number of recording days per animal

Surgery details

Sterile transmitters were implanted intraperitoneally under general oxygen–isoflurane anaesthesia through a small (1–2 cm) abdominal incision. Pain relief was achieved by a single subcutaneous injection of a non-steroidal anti-inflammatory (carprofen). The skin and muscle fascia incisions were sutured separately using vicryl absorbable suture (Vicral Ethicon, Johnson & Johnson, Somerville, New Jersey, USA), and a topical anaesthetic (Xylocaine) and Leuko spray bandage plastic skin (BSN Medical, Clayton, Victoria, Australia) were applied. Post-surgery, animals were kept individually at 20 ± 2 °C and monitored closely. Animals were allowed to recover for up to 7 days before being released. All released animals appeared in good body condition and surgery wounds had healed well. Explantation of loggers from re-captured animals followed the same protocol as specified above.

Ambient conditions

Ambient temperature was recorded within the trapping area via temperature loggers placed in the shade at a height of 1.2 m from the ground (ibutton, DS1922L-F5#, resolution: 0.0625 °C; Maxim Integrated Products, Inc., Sunnyvale, California, USA). Rainfall and solar radiation data for the whole study duration as well as minimum and maximum T_a for 6 days for which we were lacking ibutton data (14.03 to 19.03.2016) was sourced from the nearby weather station (~ 13 km away, Richmond RAAF, Australian Government Bureau of Meteorology; Pearson correlation coefficient

was calculated to test the correlation between ibutton and weather station data and showed a high correlation for minimum ($R=0.92$) as well as maximum T_a ($R=0.90$)).

Data analysis

Data analysis was conducted in R version 3.6.2 (R Development Core Team 2019). Data are presented as mean \pm 1 standard deviation. N denotes the number of individuals, n the cumulative days of data recorded. T_b data were analysed by assigning each T_b datum to either nighttime (active-phase) or daytime (rest-phase) following Levesque et al. (2018). Plotting the frequency distribution of all data, we found a bi-modal distribution of T_b and calculated modal T_b of daytime (resting) and modal T_b of nighttime (activity). Sunset and sunrise data for the analysis and plots were calculated using the R package ‘maptools’ (Bivand and Lewin-Koh 2019), which is using the following website: <https://www.esrl.noaa.gov/gmd/grad/solcalc/sunrise.html>. Linear mixed effects models (“lme” in package ‘nlme’, Pinheiro et al. (2021)) followed by type 1 ANOVA were used to test the influence of minimum or maximum T_a on minimum, maximum T_b and the daily amplitude. All models accounted for repeated measures by including animal ID as random effect on the intercept. Normal distribution of residuals was checked visually and using Shapiro–Wilk tests and non-normally distributed data were boxcox transformed prior to carrying out the analysis. Pearson correlation coefficient was calculated to test the correlation between daily minimum and maximum T_a . Rayleigh tests were used to determine whether circular data (timing of T_b above/below 38 °C) differed significantly from random distribution (“rayleigh.test” in package ‘circular’, Agostinelli and Lund (2017)).

Results

Ambient conditions

Mean daily T_a during the study period ranged from 5.8 to 22.6 °C, with an absolute nightly minimum of 0.6 °C at the end of May and an absolute daytime maximum of 34.6 °C at the end of March. Monthly average mean and maximum T_a decreased progressively from March to June, whereas average monthly minimum T_a was lowest in May (Table 1). Daily minimum and maximum T_a were strongly correlated ($R=0.99$). Daylength decreased from just more than 12 h (12 h 6 min) in March to less than 10 h (9 h 54 min) in June. Daily amplitude in T_a ranged from 2 to 19 °C. Rainfall was low during March to May (4.2–12.8 mm per month) but increased in June (189.2 mm per month). Daily solar radiation was highest in March (monthly average: 16.3 MJ m⁻²) and decreased continuously until June (monthly average

8.8 MJ m⁻²), with an absolute minimum during the study of 2.2 MJ m⁻² in early June.

Variation in body temperature

Daily mean T_b of bush rats ranged between 37.4 and 37.6 °C during the study period ($N=14$). T_b showed a clear bi-modal distribution with a daytime modal T_b of 36.5 °C and a nighttime modal T_b of 38.3 °C (Fig. 1A,B). Average daily maximum T_b was relatively stable and not influenced by minimum ($F_{1,1031}=3.4$, $p=0.0636$) or maximum T_a ($F_{1,1031}=1.6$, $p=0.2032$). Daily minimum T_b decreased from autumn to winter (Table 2) and was significantly influenced by minimum T_a ($F_{1,1031}=143.03$, $p<0.001$), i.e. rats had a lower T_b during colder days. Daily amplitude between minimum and maximum T_b ranged from 1.4 to 5.4 °C, with the exception of one occasion when an animal decreased its T_b by >12 °C (see below), and daily T_b amplitude was significantly positively influenced by minimum T_a ($F_{1,1031}=126.5$, $p<0.001$, Table 2), as well as by daily amplitude in T_a ($F_{1,1031}=20.5$, $p<0.001$).

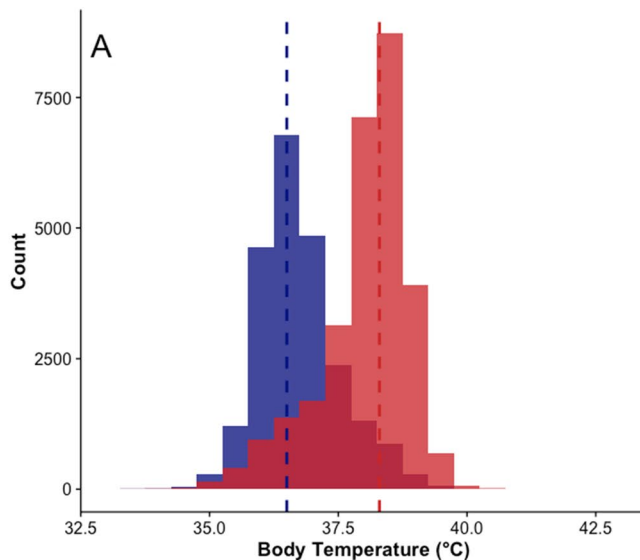
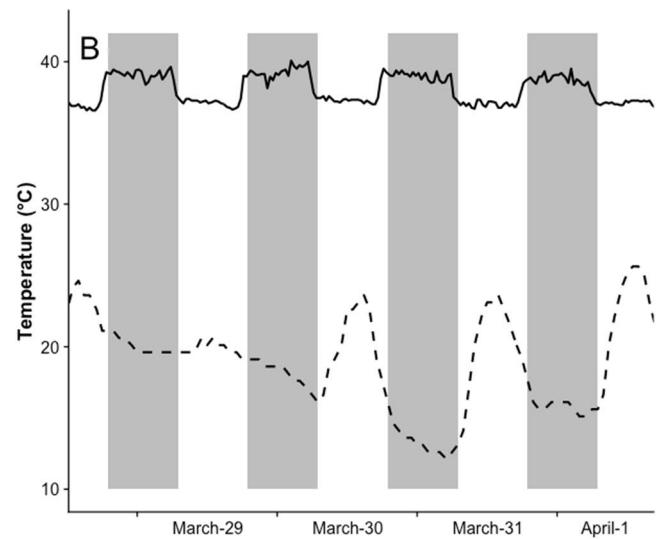


Fig. 1 Body temperature pattern of bush rats **A** Body temperature distribution of bush rats ($N=14$, $n=1047$) over the total study duration (March–June). *Blue* bars represent daytime body temperature values, *red* bars nighttime values. **B** Exemplary body temperature trace

Hypothermic bout

One subadult female (76 g at first capture) showed a large decrease in T_b beginning on the 7th of May (autumn; Fig. 2A, B), reaching a minimum daily T_b of 23.8 °C and T_b remaining <30 °C for at least 5.5 h (0720 h to 1250 h; 30 min recording interval). On the day of the hypothermic bout, T_b of this individual peaked to above 39 °C at about 1.5 h before sunset and remained high for only 1.5 h before T_b was reduced to resting level (mean: 35.9 °C) and kept low until the early morning. On all other days in May, T_b only rose >38 °C after sunset (mean 1753 h, timing different from random distribution: Rayleigh test, $r=0.9529$, $p<0.001$) and dropped back to <38 °C only at a time just before sunrise (mean 0455 h, Rayleigh test: $r=0.908$, $p<0.001$). On the day of the hypothermic bout, T_b started to continuously decrease further at about 2.5 h before sunrise and reached a minimum at around 0850 h. Ambient temperature at this time was 15.2 °C (T_b-T_a differential: 8.6 °C, Fig. 2).

Cooling rate of the animal during entry into the hypothermic bout varied from 0.5 to 3.9 °C h⁻¹ measured over 10 min (i.e. <0.01 to 0.07 °C min⁻¹, Fig. 2). Maximum



over 4 days in March/April of a female bush rat. *Solid line*: body temperature, *dashed line*: ambient temperature, *shaded areas* illustrate nighttime.

Table 2 Monthly average body temperature and ambient temperature values, including number of sampling days (n)

Month	n	$T_{b,min}$ (°C)	$T_{b,max}$ (°C)	$T_{b,mean}$ (°C)	$T_{b,amplitude}$ (°C)	$T_{a,min}$ (°C)	$T_{a,max}$ (°C)
March	18	36.4 ± 0.5	39.1 ± 0.3	37.6 ± 0.4	2.8 ± 0.3	16.4 ± 3.0	27.6 ± 4.4
April	30	36.1 ± 0.3	39.1 ± 0.2	37.5 ± 0.2	3.0 ± 0.4	12.9 ± 2.0	21.9 ± 2.7
May	31	35.9 ± 0.4	39.1 ± 0.2	37.4 ± 0.3	3.2 ± 0.5	7.3 ± 2.8	19.2 ± 2.7
June	28	36.0 ± 0.5	39.1 ± 0.3	37.5 ± 0.3	3.1 ± 0.5	7.6 ± 3.1	15.0 ± 1.8

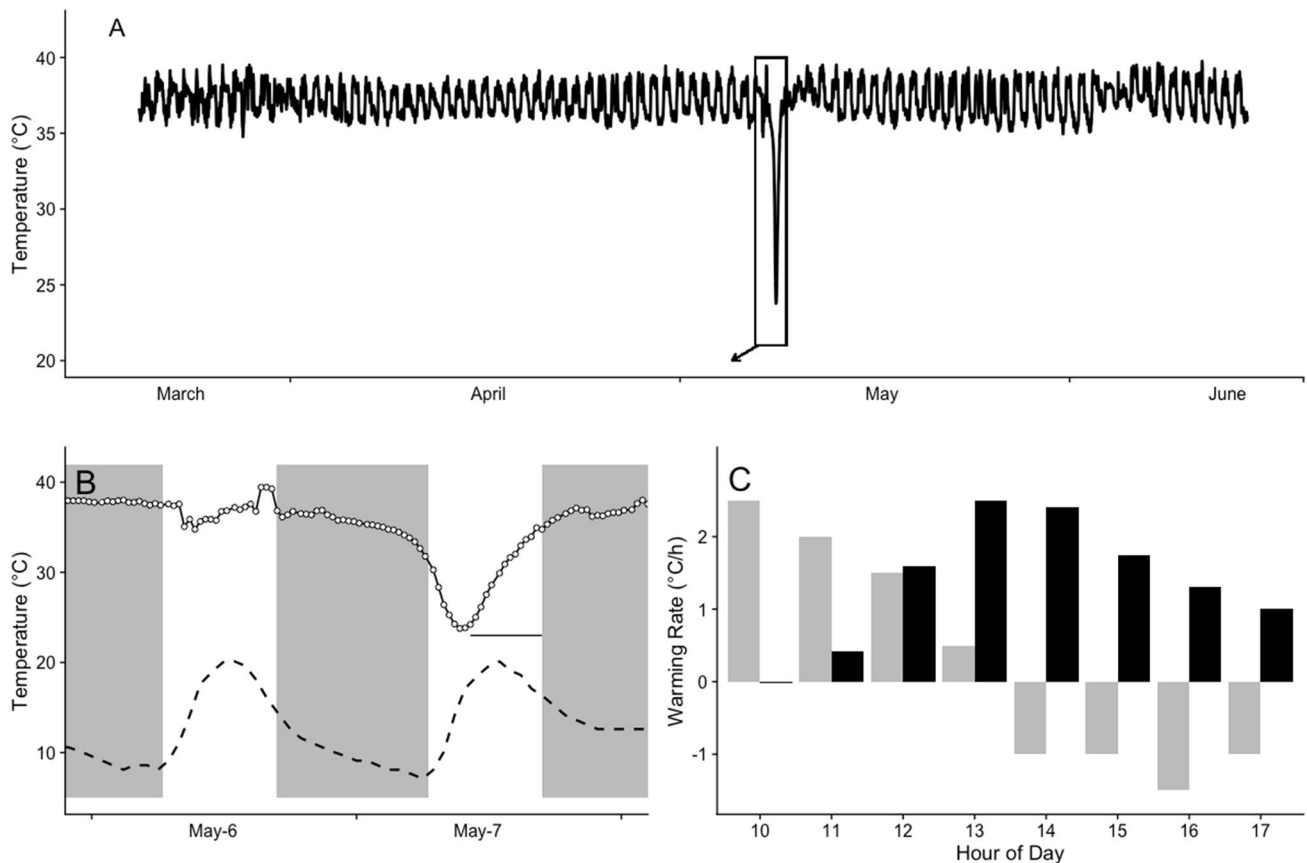


Fig. 2 Hypothermic bout of female bush rat (*Rattus fuscipes*) **A** Body temperature recording from March to June **B** Body temperature trace of the days around the hypothermic bout; *solid line*: body temperature, *dashed line*: ambient temperature, *grey*: night phase, *horizontal line* indicates the time period of warming body temperatures depicted

in C. **C** Warming rates of the animal (*black bars*) and the ambient temperature (*grey bars*). The animal started to rewarm at ~1100 h and a body temperature of ~35 °C was reached at around 1700 h, i.e. the start of the scotophase. Hourly values are calculated as the average between the previous hour and depicted hour

cooling rate was reached at a T_b of 30 °C and cooling rate slowed down again before reaching minimum T_b . Minimum T_b of around 24 °C (23.8 to 24.3 °C) was maintained for about 1.5 h. Body temperature of the animal started to increase again in the early morning, reaching > 30 °C at around midday and back to a normal resting level T_b of ~35 °C in the afternoon (after ~6 h; Fig. 2A,B). Rewarming rate of the bush rat was fastest at a T_b below 30 °C and slowed down thereafter (Fig. 2C). Maximum rewarming rate of 2.75 °C h⁻¹ (i.e. 0.05 °C min⁻¹; Fig. 3) was reached at around 1200 h and was faster than warming of the environment (Fig. 2C). Ambient temperature reached a minimum of 8.1 °C at 0600 h and warmed thereafter, with a maximum warming rate occurring between 0800 and 0900 h. After 1000 h, T_a rose between 1.5 and 2.0 °C h⁻¹ (~0.03 °C min⁻¹) until 12 pm, then by 0.5 °C h⁻¹ (<0.01 °C min⁻¹) until daytime maximum temperature of 21.7 °C was reached at 1 pm and T_a started to decrease again (Fig. 2C). The day of the hypothermic bout had no rainfall and a daily solar radiation of 13.7 MJ m⁻².

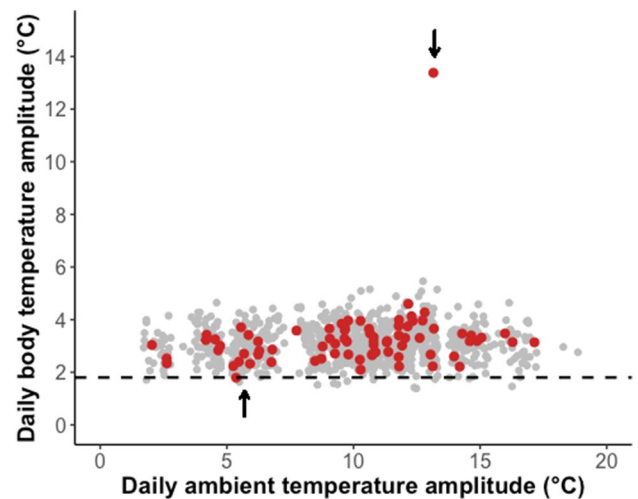


Fig. 3 Daily body temperature amplitude versus daily ambient temperature amplitude. *Grey dots* represent all 14 bush rats, *red dots* represent the individual showing the hypothermic bout. The *dotted line* marks a body temperature amplitude of 1.8 °C for comparison purposes. The arrows mark day of the hypothermic bout (daily amplitude > 12 °C) and the day following the bout (1.8 °C)

The individual maintained a stable T_b on the day after the hypothermic bout with a daily amplitude of only 1.8 °C (Fig. 3). Body temperature did not drop below 34.8 °C on the other 76 days for which we recorded T_b in the field for this individual. The animal was re-captured in good body condition (body mass gain of +12 g since last March) at the end of June.

Discussion

Our data show that bush rats at our field site in Eastern Australia mostly kept their T_b within a narrow range, with a higher T_b during the nocturnal activity phase and a lower rest-phase T_b . Minimum T_b of bush rats was lower on colder days and the amplitude between resting T_b and active T_b was largest during days with lower nightly minimum temperature. These data are largely in line with a previous field-based study of this species over a relatively short period of <3 weeks per season that found a winter decrease in mean T_b and an increase in daily amplitude from 3.0 °C in summer to 3.6 °C winter (Glanville and Seebacher 2010). T_b levels varied slightly between both study populations and mean daily T_b was 0.6 °C to 0.8 °C higher in our study than in the previous study, potentially due to local habitat adaptations. However, in contrast to the strict homeothermic T_b regulation that the previous study has found (Glanville and Seebacher 2010), our data revealed a single hypothermic bout in one subadult individual in late autumn. This observation is the greatest daily reduction of T_b recorded under field conditions in the genus *Rattus* and provides evidence for either a survivable bout of profound hypothermia or a controlled bout of torpor in these endemic Australian bush rats.

Does the heterothermic bout represent a torpor bout?

The observed decrease in T_b to a minimum of 23.8 °C was >12 °C greater than the normal diurnal variation observed in this population and poses the question of whether we have observed a bout of torpor—as defined by a temporary, reversible and controlled reduction of metabolic rate and, at T_a less than T_b , a corresponding reduction in T_b from normothermic values—or a bout of survivable hypothermia, which, in contrast to a torpor bout, involves high levels of metabolic heat production that nevertheless are insufficient to counter rates of heat loss, leading to an involuntary drop in T_b (Geiser et al. 2014).

Timing of entry and rewarming from low T_b was approximately corresponding with the early rest phase and thus similar to what has been reported for other daily heterotherms (Körtner and Geiser 2000). However, the early increase in T_b before sunset, i.e. during the normal resting time and

the later maintenance of a resting level T_b during the active phase before the rather slow entry into the hypothermic bout are unusual for an otherwise nocturnal species. This almost certainly indicates that the individual did not exhibit activity and possibly did not forage for food during the night, and eventually was either not able to metabolically defend a high T_b and entered hypothermia or voluntarily dropped T_b to save energy during torpor.

Cooling and rewarming rates differ between regulated torpor and unregulated hypothermia: entry into hypothermia is slow at first, because of the high rate of metabolic heat production, and only becomes more rapid at lower T_b , matching the exponential negative effect of temperature on enzyme activity (Geiser et al. 2014). Warming from hypothermia begins passively with rising T_a , and hence usually slowly, and rewarming rate then increases with increasing T_b as metabolic activity is increased (Geiser et al. 2014). Based on this criterion, cooling in the bush rat resembles entry into hypothermia, because the rate increased only after the body had started to cool. Nevertheless, maximum cooling rate was comparable to cooling rates recorded during torpor entry in the much smaller ash-gray mice, *P. albocinereus*, the only native Australian rodent species for which torpor has been confirmed via T_b and metabolic rate data (Barker et al. 2012). Maximum cooling rate in ash-grey mice was 2.7 °C h⁻¹, which is less than the maximum of 3.9 °C h⁻¹ recorded for the individual bush rat, even though the bush rat was more than twice the body mass of *P. albocinereus* (15–40 g; Barker et al. 2012). However, cooling rates are difficult to compare between the studies, because it is also dependent on the T_a - T_b differential, which was less for *P. albocinereus* at a T_a of 20 °C compared to that likely experienced by the bush rat.

The minimum T_b of the bush rat during torpor was maintained at ~24 °C for about 1.5 h, which was ~9 °C above external T_a at this time. This could suggest that T_b was maintained at a temporarily lowered set-point level such as found during regulated torpor (Heller and Collier 1974), although it has to be considered that the microclimate surrounding the animal inside its nest might be buffered from the daily minimum T_a causing a lower T_a - T_b differential. Further, the phase during which T_b was maintained at minimum level (i.e. the maintenance phase), might appear relatively short, but short maintenance phases during daily torpor are routinely observed in daily heterotherms, such as yellow footed antechinus, *Antechinus flavipes*, (Stawski et al. 2017; Reher et al. 2018) or the African lesser bushbaby, *Galago moholi* (Nowack et al. 2013b), and in some hibernating species, such as the Malagasy bat, *Macronycteris commersoni* (Reher et al. 2018).

The maximum rewarming rate of the bush rat was at 0.05 °C min⁻¹ far less than expected for a similar-sized heterothermic species actively rewarming from torpor

($0.3\text{ }^{\circ}\text{C min}^{-1}$ for a 72 g animal) (Geiser and Baudinette 1990) and correspondingly, the duration of rewarming of 6 h was longer than would be expected. However, unlike rewarming from hypothermia (Geiser et al. 2014), the maximum rewarming rate of the bush rat was faster at the beginning and slowed down later during the rewarming process. Slower rates of rewarming than those expected on the basis of body mass have been reported for some species that evidently underwent regulated torpor, such as in the primate *G. moholi* (Nowack et al. 2013b), the native Australian rodent *P. albocinereus* (Barker et al. 2012), and the monotreme echidna *Tachyglossus aculeatus* (Nicol et al. 2009). Indeed, maximum rewarming rates in bush rats were about twice as fast as those recorded for *P. albocinereus* ($2.75\text{ }^{\circ}\text{C h}^{-1}$, or $0.05\text{ }^{\circ}\text{C min}^{-1}$ for the bush rat vs. $1.5\text{ }^{\circ}\text{C h}^{-1}$ or $0.025\text{ }^{\circ}\text{C min}^{-1}$ for *P. albocinereus*) (Barker et al. 2012), even though the bush rat is larger than the ash-gray mouse and should thus rewarm slower.

The animal could also have passively rewarmed with T_a , which increased in time with the initial period of rewarming of T_b . If the animal has been in a buffered resting site, the increase in T_a might also have been delayed by a few hours. However, external T_a was $\sim 9\text{ }^{\circ}\text{C}$ lower than the animal's T_b and the increase in T_a was slower than the maximum rewarming rate of the animal. Hence, passive rewarming of T_b by rising T_a alone could not have been entirely responsible for warming of the hypothermic animal. However, it is possible that an increasing T_a could have made active arousal easier by reducing the T_b - T_a differential, especially during the earlier phase of rewarming. We think it highly unlikely the animal was exposed to direct solar radiation, because bush rats normally use underground burrows or ground nests under dense grass trees (Collins 1973; Frazer and Petit 2007). Basking in the sun should also have led to faster rewarming rates than those recorded. For example, dunnarts (*Sminthopsis* spp.) basking in sunlight can have a maximum passive arousal rates of up to $0.7\text{ }^{\circ}\text{C min}^{-1}$ (Warnecke et al. 2008). Furthermore, two-step rewarming processes as observed in species that make use of passive rewarming normally start with an initial slow passive part and are followed by a faster active proportion after a certain T_b was reached (e.g. Schmid 2000). Rewarming in the bush rat followed the opposite pattern.

The question whether the recorded drop in T_b represents a controlled torpor bout or an unregulated bout of hypothermia unfortunately cannot be answered unequivocally based on the available data. Some aspects, such as the timing of entry and arousal and the successful rewarming suggest torpor, whereas others, such as the cooling process and the unusual low rewarming rate suggest it might instead have been a survivable bout of uncontrolled hypothermia.

Implications of the hypothermic bout

Regardless of whether the bush rat was in a state of uncontrolled hypothermia or a controlled state of torpor, our field observation do show that bush rats are able to survive a drop in T_b to below $30\text{ }^{\circ}\text{C}$ for ~ 5.5 h, and are able to rewarm, albeit slowly, from a T_b of $\sim 24\text{ }^{\circ}\text{C}$ with little if any reliance on external heat sources and without any apparent physiological damage. Small mammals have to cope with a high energy expenditure due to their small body size and high mass-specific rates of heat loss and they cannot survive for long without food intake while maintaining normothermic thermoregulation, especially when heat loss is increased at low T_a (Howard 1951). Allowing T_b to decrease can thus be beneficial and allow the animal to save energy, so long as the animal is able to rewarm again. Even lowering T_b by $1.2\text{ }^{\circ}\text{C}$ leads to an energy saving of 6% of resting metabolic rate in a ~ 126 g marsupial mammal (i.e. sugar glider; Christian and Geiser 2007). The use of deep regulated torpor can even reduce energy expenditure to as little as to 1% of energy expenditure during normothermic conditions (data for a 18 g hibernating marsupial pygmy possum at $T_a \geq 5\text{ }^{\circ}\text{C}$; Geiser 1987), which can markedly increase an individual's survival chances without access to food. Thus, the reduction in T_b observed in the bush rat would have reduced energy consumption, and such rare torpor bouts can be important for surviving exceptional circumstances during which foraging activity is impaired, such as unpredictable weather events (Nowack et al. 2017). However, the particular day was comparatively warm, with medium cloud cover (i.e. solar radiation) and no rainfall and thus the hypothermic bout observed for the bush rat cannot be explained by climatic conditions.

Unregulated hypothermia on the other hand can be lethal. When metabolic rate is not sufficient to maintain a stable elevated T_b , T_b cools, and the high metabolic rate required for rewarming becomes impossible. Interestingly, even heterothermic species that can enter regulated torpor, such as the small marsupial antechinus (*Antechinus stuartii*), can become hypothermic when food deprived, i.e. they enter an unregulated state of hypothermia from which they cannot actively rewarm (Geiser 1988).

Laboratory studies report that at least some homeothermic rodents, i.e. species that are not known to undergo torpor, are able to survive periods of low T_b if they are subsequently warmed by external heat sources. Popovic (1960) found that adult laboratory rats were able to recover from hypothermia with a T_b as low as $15\text{ }^{\circ}\text{C}$, but only when hypothermia did not last more than 5.5 h (similar to our observation for the bush rat). When hypothermia lasted longer, rats were able to survive in a lethargic state at low T_b but did not survive being warmed up to normothermic values, which seemed to have been related to changes in blood pressure (Popovic 1960). Furthermore, animals exposed to severe

hypothermia typically develop cardiac arrhythmia and/or fibrillation (e.g. Björck and Johansson 1955). The native Australian sandy mouse, *Pseudomys hermannsburgensis*, can survive extended hypothermia for up to 32.5 h with a minimum T_b of 17.3 °C at a T_a of 15 °C, when rewarmed passively (Tomlinson et al. 2007). In contrast, humans seem to be unable to survive deep hypothermia and generally maintain T_b in very strict boundaries (reviewed in Shi et al. 2021). Juvenile animals are usually better in surviving episodes of low T_b . Hypothermic rat pups (*Rattus norvegicus*) can survive about 6 h of T_b below 30 °C under laboratory conditions, but need to be passively rewarmed (Geiser et al. 2014).

How does this observation broaden our understanding of endotherm physiology?

So far, we know of at least four species that are physiologically able to undergo regulated torpor but seem to not use torpor on a regular basis. These include the sandy inland mouse, bushbabies, sugar glider (*Petaurus brevices*; Christian and Geiser (2007)) and feathertail glider (*Acrobates pygmaeus*; Jones and Geiser (1992)) and these observations of rare torpor use seem thus to be restricted to non-Holarctic species (Nowack et al. 2020). Unpublished evidence also suggests that the native Australian swamp rat (*Rattus lutreolus*) can survive a decrease in T_b to 28 °C and seems able to rewarm spontaneously (C. Stawski, personal communication). Interestingly, at least two of the four species mentioned above also have low rewarming rates. As detailed above, rewarming rates for the bush rat are higher than those recorded for the sandy inland mouse, a species for which additional metabolic rate data have confirmed torpor use (Barker et al. 2012). Furthermore, the low rewarming rates from torpor observed in the African lesser bushbabies, *Galago moholi*, has led to the suggestion that bushbabies use torpor as a last resort strategy when energy reserves are low (Nowack et al. 2010, 2013b, a).

The finding of several mammal species that rarely use torpor with relatively low rewarming rates suggests these species can tolerate cold T_b but are not adapted to rewarm by massively increasing metabolic rate at low T_b like species that more regularly use torpor. While controversially discussed in the past (e.g. Geiser 2008), it is now assumed that ancestral mammals were largely heterothermic, i.e. had a high degree of thermoregulatory flexibility and survived periods of temporarily reduced T_b (Lovegrove 2012; Ruf and Geiser 2015), and that heterothermy may have played an important role in the evolution of endothermy (Wacker et al. 2017; Geiser et al. 2017). Torpor and hibernation are widespread across mammalian orders, yet not all recent mammal lineages are able to undergo torpor or to survive longer

periods of hypothermia (Ruf and Geiser 2015), which means that the ability to express heterothermy must have been lost multiple times in the course of mammalian evolution, while other lineages apparently evolved the more regulated form of torpor use. Thus, observations of rare torpor events in species that otherwise appear to be strictly homeothermic could be heterothermic rudiments, i.e. an intermediate form of torpor that involves survivable hypothermia with limited capacity for rewarming. Those data are only coming to light with long-term datasets of animals that capture their rare and extreme responses. Our data also emphasise the value of additionally recording metabolic rate (e.g. via heart rate; Currie et al. 2014) along with T_b , which would allow to make assumptions about energy expenditure during the cooling period and rewarming process and can thus be helpful to differentiate between unregulated hypothermia and torpor use.

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Author contributions All authors designed and planned the study. JN conducted the fieldwork, analysed the data and wrote the first version of the manuscript. CT edited the manuscript and provided resources and logistical support.

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Data availability Data are available on request.

Declarations

Conflict of interest The authors declare no competing interests/conflicts of interest.

Ethical approval The study was approved by the institutional animal care and ethics committee (ACEC number: A11402) and a scientific licence from the NSW National Parks and Wildlife Service (Scientific Licence number: SL101679).

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