

Flexible Employment of Torpor in Squirrel Gliders (*Petaurus norfolcensis*): An Adaptation to Unpredictable Climate?*

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ABSTRACT

Torpor is a highly effective response to counter various ecological and physiological bottlenecks in endotherms. In this study, we examined interrelations between thermoregulatory responses and key environmental variables in free-living squirrel gliders (*Petaurus norfolcensis*) in a habitat with drastic climatic and ecological changes across seasons. To this end, we measured body temperature (T_b) and heart rate (f_H) simultaneously throughout the year using implanted data loggers. Squirrel gliders in our study experienced fluctuations in ambient temperature (T_a) between -4.0°C and 44.1°C and expressed torpor at different times during the year. In contrast to our expectations, torpor seemed to be employed flexibly, on demand, and most frequently in spring rather than during the coldest and/or hottest periods. Torpor bouts lasted, on average, about 5 h, and T_b during torpor dropped as low as 17.9°C . The f_H during torpor decreased below 50 bpm, which is about one-third of the basal level. The ability to record f_H alongside T_b enabled us to also report periods of low f_H during thermoconforming hyperthermia at T_a 's above 35°C that likely occurred to conserve energy and water. Our findings double the

body size of Australian gliders for which data on torpor are available and advance our ecological understanding of the dynamics of torpor expression in wild mammals and of how animals cope with varying conditions. Moreover, they highlight that the flexibility of physiology and thermoregulatory responses are clearly more complex than previously thought.

Keywords: thermoregulation, physiological flexibility, torpor, heart rate, body temperature, marsupial, squirrel glider.

Introduction

Changes in ambient conditions are challenging for wild organisms, irrespective of whether these changes are natural, such as seasonal or stochastic fluctuations, or anthropogenically induced, such as global climate change or consequences of habitat alterations. Given that endothermic species must invest energy into thermoregulation to maintain a high and constant body temperature (T_b), varying food and water availability and changes in temperature can result in a mismatch between energetic costs and energy availability. A common strategy for small endotherms to decrease energy and water requirements is the expression of torpor (i.e., daily torpor and hibernation), a temporary controlled reduction in metabolic rate (MR) and typically T_b (Lyman et al. 1982; Kenagy 1989; Heldmaier and Ruf 1992; Geiser and Ruf 1995; Geiser 2004; Heldmaier et al. 2004).

Traditionally, daily torpor and hibernation have been viewed as seasonal responses restricted to species inhabiting temperate and arctic regions (Lyman et al. 1982). However, studies in recent decades have revealed an increasing number of mammals from all climate zones expressing torpor throughout the year in response to a variety of triggers, such as fire, drought, flooding, or the lunar cycle (Smit et al. 2011; Geiser and Brigham 2012; Stawski et al. 2015; Nowack et al. 2017; Barak et al. 2018; Geiser 2020; Geiser et al. 2020). Indeed, compared to patterns of heterothermy in temperate species, available data from tropical and subtropical climatic conditions have revealed diverse and unpredicted responses (Bartels et al. 1998; Dausmann et al. 2004; Lovegrove and Génin 2008; Kobbe et al. 2011; Körtner and Geiser 2011; McKechnie and Mzilikazi 2011). For example, recent evidence has shown that torpor can be employed to counter heat stress,

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especially when evaporation is impaired because of unavailability of water or high relative humidity (RH; *Molossus molossus* [O'Mara et al. 2017a]; *Macronycteris commersoni* [Reher and Dausmann 2021]). It is likely that more data will show that this facet of torpor is very important, especially as climate change is expected to have the most severe consequences for warm habitats where animals already live near the edge of their climate envelopes (Huey et al. 2012; IPCC 2013; Rodgers and Franklin 2021). However, many predictions about the effects of climate change need further evaluation, as they disregard the potential influence of phenotypic flexibility of species physiology. This is often the case because long-term data are lacking or studies are performed in captivity (Turbill et al. 2003; Turbill 2006; Geiser et al. 2007; Warnecke et al. 2007; O'Connor et al. 2017; O'Mara et al. 2017a), where it is difficult to reproduce the complexity of the thermal and ecological reality (e.g., food abundance, predation risk) experienced in the wild. As such, laboratory studies tend to underestimate the extent of torpor use in the wild and consequently underestimate its impact on energy expenditure (Geiser et al. 2000, 2007). Unfortunately, there are still only a few studies on the thermal ecology and energetics of animals in the field (but see, e.g., Körtner and Geiser 2000; Turbill et al. 2003; Dausmann et al. 2004, 2009; Liu and Karasov 2011; Speakman and Hambly 2016; Bethge et al. 2017; Aharon-Rotman et al. 2021), and they rely primarily on measures of T_b or skin temperature as proxies for energetics. The recent miniaturization of biologgers has improved our ability to directly measure multiple physiological variables in free-ranging animals (Fahlman et al. 2021). This has opened up new avenues for investigating animals' physiological variables under natural conditions, but this technology has yet to be widely applied to small heterothermic species. Flexible strategies for energy conservation have already been uncovered via heart rate (f_H) biollogging in tropical bat species (O'Mara et al. 2017a, 2017b), and the scope of this method is far-reaching, particularly when applied to species inhabiting regions that experience extreme conditions at both ends of the temperature continuum: heat waves (possibly connected to droughts) in summer and cold spells in winter.

Many small Australian mammals are heterothermic, including species of the family Petauridae (Smith and Ganzhorn 1996; Geiser and Körtner 2010). For instance, the sugar glider (*Petaurus breviceps*), a small (~130-g) arboreal marsupial, uses torpor opportunistically during inclement weather on wet, cold winter days (Körtner and Geiser 2000; Christian and Geiser 2007) or in other emergency situations (Nowack et al. 2015). However, it is not known whether the closely related squirrel glider (*Petaurus norfolcensis*, ~230 g; Kerr 1792), which is almost twice the size of *P. breviceps*, employs torpor. *Petaurus norfolcensis* has a patchy distribution along the coast in southeastern Australia but lives in a variety of habitat types, including mountainous areas that are characterized by distinct seasons: cold winters and hot summers with clear variations in food and water availability. This makes *P. norfolcensis* an excellent model organism to enhance the understanding of the physiological flexibility of Australian mammals and of their ability to cope with highly variable environments.

In this study, we investigated the thermoregulatory patterns of free-ranging squirrel gliders during varying seasonal conditions

throughout the year. At the same study site, we compared possible heterothermic responses to cold conditions (to save on costs of endothermy) and hot and dry conditions (to avoid dehydration). To this end, we measured squirrel gliders' T_b 's and f_H 's in the field in relation to key environmental conditions. The measurement of f_H alongside T_b in the field provides a more comprehensive indication of metabolism in free-ranging individuals at a fine time resolution (Currie et al. 2014; O'Mara et al. 2017a). These data will enable predictions about their capacity to endure environmental and climatic change.

Methods

All procedures were approved by the Animal Ethics Committee of the University of New England (protocol AEC19-025) and were conducted under permits from the National Parks and Wildlife Service (permit SL100791).

Study Site

The study was carried out in Warrumbungle National Park (31°27'6"S, 148°9'82"E) in inland New South Wales, Australia. The climate of this region changes drastically with seasons. It is characterized by hot summers between November and March, which regularly experience heat waves with temperatures peaking above 40°C, and cold winters from May to September with a frequent occurrence of frost, making it one of the coldest habitats occupied by *Petaurus norfolcensis*. Average daily minimum ambient temperature (T_a) in summer is higher than average daily maximum T_a in winter (fig. 1). Because of climate change, the occurrence of heat waves is increasing, and the area is predicted to be one of the most severely impacted by climate change in Australia (Australian Bureau of Meteorology; <http://www.bom.gov.au>). The whole state of New South Wales had been impacted by an extensive 3-yr drought at the time of the study.

Study Species

The squirrel glider (*P. norfolcensis*) is a small to medium-sized marsupial (body length: ~210 mm; body mass: ~230 g; Quin 1995; van der Ree 2002) endemic to Australia, where it has a patchy distribution along the eastern coast of the continent. It occurs in a variety of habitat types, including dry sclerophyll forest and woodland from sea level up to 1,200 m (Goldingay and Jackson 2004; Winter et al. 2016), indicating that this species is physiologically and ecologically flexible. It is nocturnal and rests in tree hollows during the day in family groups of 2–10 individuals, generally comprising one male, at least two females, and juveniles (Suckling 1995; Quin 1995). Reproduction is seasonal, likely reflecting food availability, and birthing peaks in late autumn/early winter (Quin 1995; Millis and Bradley 2001; Sharpe and Goldingay 2010). The species eats mostly nectar and invertebrates but also eats tree sap, and thus, food sources are likely to fluctuate on a seasonal basis and to be temperature dependent (Smith 1982; Racey and Swift 1985; Menkhorst and Collier 1987; Sharpe and Goldingay 1998). Because of the large distribution range and

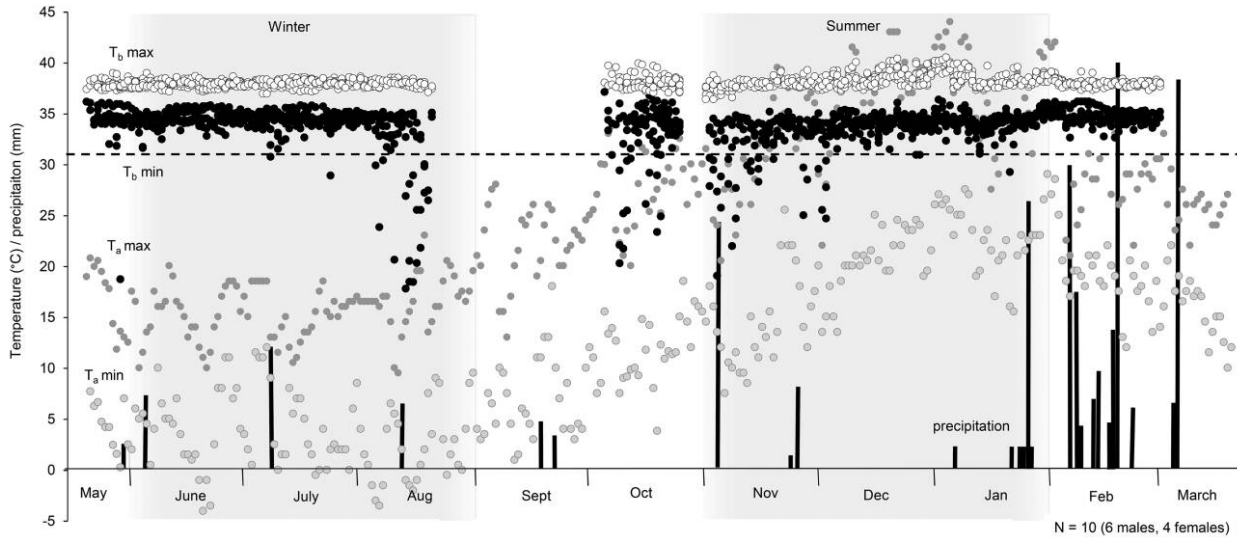


Figure 1. Body temperature (T_b) of all studied *Pettaurus norfolcensis* individuals across the year. Because of storage limitations of the loggers, there are no T_b data available from the middle of August to the beginning of October. White circles indicate daily maximum T_b , black circles indicate daily minimum T_b , dark gray circles indicate daily maximum ambient temperature (T_a), and light gray circles indicate daily minimum T_a . The dashed line signifies torpor cutoff at 31°C. Black bars denote precipitation, and gray blocks denote winter and summer months.

occurrence in several protected areas, *P. norfolcensis* is currently classified as a species of least concern by the International Union for the Conservation of Nature. However, it is listed as vulnerable in New South Wales, where its population is decreasing as a result of habitat loss and fragmentation, a lack of suitable hollows in most habitats, and predation by feral and domestic cats (Woodd et al. 2006; Winter et al. 2016).

Trapping, Housing, and Implantations

Squirrel gliders were captured at different locations within Warumbungle National Park with live traps (30 traps, 40 cm × 15 cm × 15 cm) and in nest boxes (checked with an inspection camera; Brite Star, Pinewood, Australia). Traps were covered with jute; baited with oats, honey, and raspberry jam; and checked in the early mornings (less than 2 h after sunrise). Captured animals were transferred into cotton bags and transported to the research station. Captured squirrel gliders were weighed, sexed, and individually marked with passive identification transponders (Trovan, EURO ID Usling, Weilerswist, Germany). They were housed individually or with their social partner in aviaries equipped with branches for climbing and a nest box with bedding. Food (special glider mix made from baby food [Farex], honey, and vitamin powder; fresh fruit; and raspberry jam) and water were provided ad lib. The squirrel gliders were implanted intraperitoneally with data loggers (DST micro-HRT, Star-Oddi; 3.3 g), which recorded T_b and f_H simultaneously. The loggers had a battery life of 3 mo and thus needed to be implanted shortly before each season. Additionally, individuals were equipped intraperitoneally with temperature-sensitive radio transmitters (PIP2SM, BioTrack; 3.5 g) for the localization of resting sites and, at the end of the season, for logger and transmitter removal, as well as for additional T_b

data via the signal interval. Before implantation, signal intervals were calibrated in a water bath to temperatures between 8°C and 42°C in steps of 3°C with a thermometer traceable to a national standard (R^2 always > 0.999). The mass of both devices combined was <3% of squirrel gliders' body masses and thus was well below the maximum of 5% body mass suggested for wild animals (Sikes et al. 2011). Only adult individuals, as identified by size and body mass, were used for the study.

Surgery was performed under general oxygen/Isoflurane anesthesia (~3%–4% for induction, 0.5% for maintenance). The effectiveness of the anesthetic was confirmed by touch and by observation of breathing. Fur from the lower abdomen was removed, and the site was sterilized with ethanol. A small incision (~1.5 cm) along the ventral midline was made with surgical scissors, and the sterile logger and wax-coated transmitter were inserted intraperitoneally. Muscle layer and skin were sutured separately with dissolving sutures. The abdomen was then cleaned with Betadine, a topical anesthetic (Xylocaine 10%) applied to reduce discomfort, and the wound was sealed with a spray-on bandage. Recovery from anesthesia was under 100% oxygen until the animal regained consciousness. The animal was then placed in a clean cage and monitored continuously over the following hours. The duration of the surgery was a maximum of 20 min, and animals were kept on a heating pad throughout surgery. After recovery, the individuals were released at the capture site after dark.

There were three trapping periods. Squirrel gliders were first captured before winter (May 2019) for implantation. The second trapping period was conducted just before summer (October 2019) for removal of old devices and implantation of new devices in recaptured individuals and for implantation in newly captured individuals. The last capture period took place after summer

(March 2020) for removal only. Despite extensive efforts, only a limited number of individuals were captured (five males/two females before winter; five males/four females before summer [five recaptures]; four males/two females after summer [all recaptures]).

Resting Sites, Group Compositions, and Environmental Conditions

Before recapture and in the days following release, resting sites of the squirrel gliders and group compositions of tagged individuals were determined with the radio transmitters. T_a was recorded at eight locations throughout the study site and every 30 min throughout the year with temperature data loggers (Thermochron iButtons, DS1922L, Maxim Integrated Products, San Jose, CA; resolution: $\pm 0.5^\circ\text{C}$) attached 2 m aboveground to the (shady) southern side of trees with known resting sites of squirrel gliders. Three of these loggers, distributed across the study site, also recorded RH (Hygrochron iButtons, DS1923L, Maxim Integrated Products; resolution: $\pm 0.5^\circ\text{C}$). We also equipped nest boxes, which had been used multiple times by squirrel gliders, with temperature data loggers to record temperatures directly within the resting sites. However, as squirrel gliders used nest boxes only infrequently and likely even avoided some of them on hot days because of their north-facing location on the trees, we are not confident how closely these data reflect actual resting site temperatures and thus do not include them in the analyses. Rainfall data were retrieved from the Australian Bureau of Meteorology for the nearest weather station (Miegunyah) and included all forms of precipitation that reach the ground, such as rain, drizzle, hail, and snow (<http://www.bom.gov.au>).

Measurement of Body Temperature

Implanted data loggers stored T_b in intervals of 10 min, starting 2 wk after implantation until the internal storage capacity was exhausted after about 3 mo. Five individuals (three males/two females) were successfully recaptured after the winter season, and loggers were removed, yielding long-term continuous T_b and f_H data (see below); six individuals (four males/two females; table 1) were successfully recaptured after the summer season.

Additionally, ad hoc T_b data were recorded from all individuals during the resting site controls via the implanted transmitters. Self-constructed (G. Körtner) automated receivers/loggers were placed near the resting sites to record T_b every 10 min during the resting phase (between 1 and 15 d) in May 2019, October 2019, and March 2020. These data were the only data available for the individuals that were not recaptured.

Measurement of Heart Rate

The f_H loggers were initially implanted intraperitoneally with no anchoring suture and therefore likely drifted within the body cavity, affecting the quality of f_H recordings. Following this, during the second round of implantations, a single suture anchored the logger to the body wall and thus improved electrocardiogram (ECG) signal. The f_H was recorded at a sampling frequency of

Table 1: Overview of individuals and number of days with body temperature (T_b) records

ID	Sex	No. of days with T_b records		
		Total	Winter	Summer
A	F	190	88 (-)	102 (2)
B	M
C	M	10	10 (1)	...
D	F	104	88 (0)	16 (2)
E	M	226	88 (6)	138 (11)
F	M	96	88 (10)	8 (4)
G	M	182	88 (6)	94 (13)
H	M	105	...	105 (1)
I	F	129	...	129 (11)
J	F	9	...	9
K	M	131	...	131 (1)
Total		1,182 (67)	450 (23)	732 (44)

Note. The number of days where torpor bouts were observed is given in parentheses. Winter includes May to August, and summer includes October to February. F = female; M = male.

either 300 or 700 Hz. Given the technical limitations of the Star-Oddi loggers to collect 600 samples total per f_H recording, the maximum recording period was approximately 2 s; therefore, the minimum f_H that we were able to detect was 32 bpm (at least two heartbeats were detected within the sampling window).

The validity of f_H recordings was confirmed via secondary analysis of intermittent ECG recordings (fig. S1). Because ECG recordings were programmed to occur primarily during the rest phase, it was not possible to assess the validity of f_H 's above 600 bpm. As it is also likely that f_H 's > 600 bpm coincided with activity and greater electrical artifacts, which could lead to inaccurate f_H measurements, all f_H 's above this were excluded from analysis. Star-Oddi provides a quality index (QI 0–3) that classifies f_H measurements based on a number of qualifiers, including f_H variability and artifacts within recordings. Following our own quality assurance measures, we considered any f_H measurement classified as QI = 3 that could not be verified by ECG as inaccurate and discarded it. This extensive filtering procedure resulted in a drastic reduction in the number of f_H measurements included in further analysis (95,512 of a total 151,697 recordings) and disrupted the continuity of our f_H data. Overall, f_H was more likely to be overestimated than underestimated by loggers, leading us to consider low f_H to be the most accurate. Figure S2 demonstrates the quality of the ECG recordings for f_H calculations.

Data Analyses

Patterns of thermal state and occurrences of heterothermy were examined in all T_b data gathered, related to T_a and RH, and compared between seasons. As triggers for torpor use could differ between seasons, winter and summer data were analyzed separately. Because of storage limitations of the loggers, there are no T_b data available from the middle of August to the beginning of

October. Torpor was defined as any T_b below 31°C , as this is the temperature when the left-skewed frequency distribution of minimum T_b values around the mean deviates from a normal distribution (fig. S3). The use of a torpor threshold from only f_H data was not deemed suitable, as f_H data were not continuous for all animals. In addition, f_H can vary greatly at rest, and without developing a model for the relationship between f_H and MR under each physiological state, this would be potentially misleading (see Currie et al. 2014). Instead, we used the T_b threshold and compared recorded f_H to basal f_H , as predicted from allometry for an

average 230-g marsupial (158 bpm; Kinnear and Brown 1967). Resting f_H was calculated from data where T_b was $>32^\circ\text{C}$, the difference between T_b and T_a was $>1^\circ\text{C}$, and f_H was above 158 bpm. This was done in an attempt to exclude data that may represent phases of sleep or thermoconforming, which could confound the results. The relation between occurrence of torpor and weather variables was analyzed in SPSS by comparing minimum T_a and maximum T_a , minimum RH (RH_{\min}) and maximum RH (RH_{\max}) on nights with torpor and on nights without torpor in separate generalized linear mixed effects models (GLMMs), including

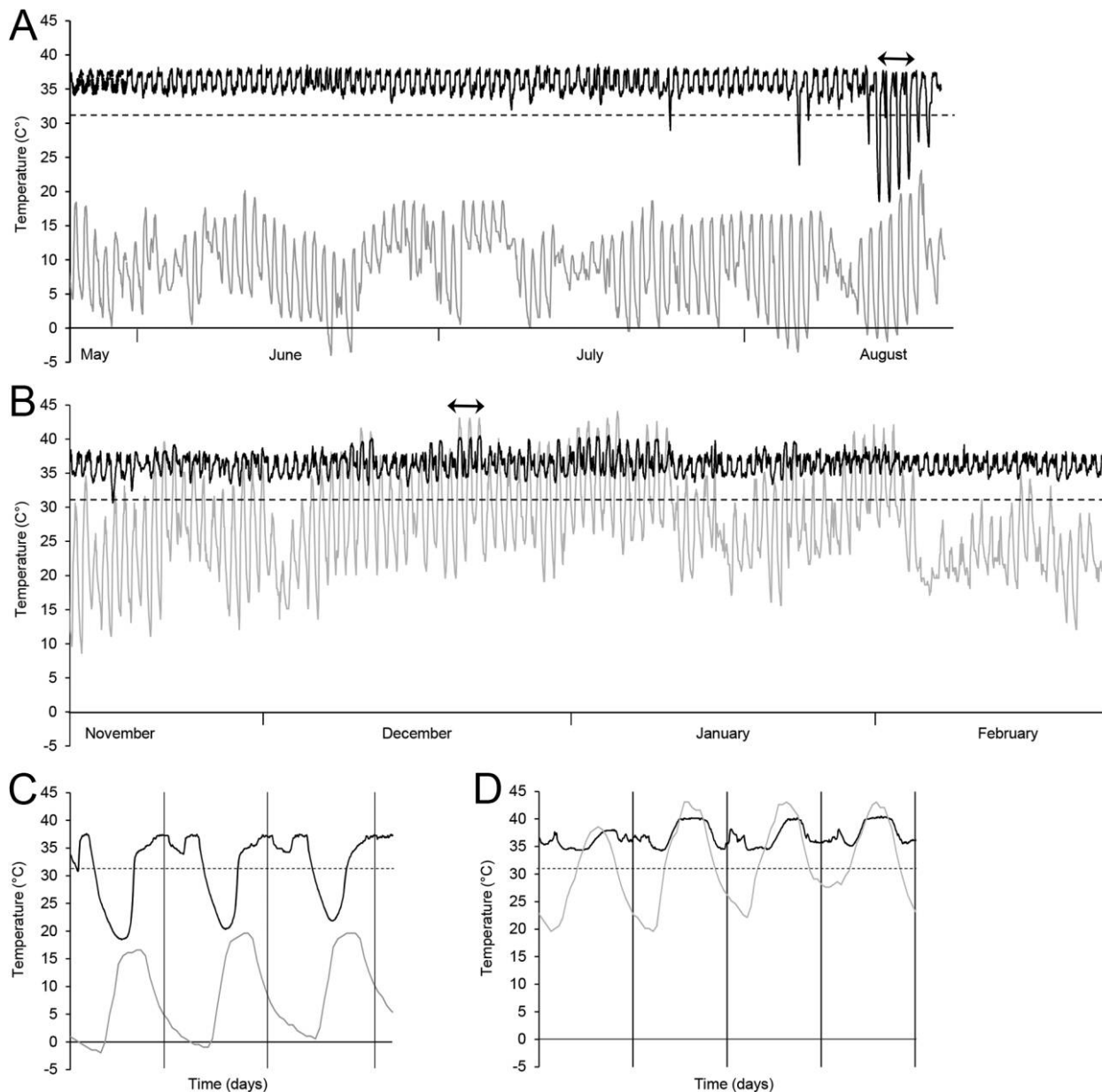


Figure 2. Body temperature of a free-ranging *Petaurus norfolcensis* over 3 mo in winter (A) and in summer (B), detail of torpor bouts from A on August 15 to August 17, 2019 (C), and detail of thermoconforming hyperthermic episodes from B on December 19 to December 22, 2019 (D). Inserts are indicated by arrows. The black line represents body temperature, the gray line represents ambient temperature, and the dashed line represents torpor cutoff at 31°C .

individual ID as a random factor. Changes in glider body mass between the three field seasons were analyzed with a Kruskal-Wallis test. Influence of precipitation could not be assessed statistically, as it rarely rained throughout the study period.

The relationship between f_H and torpor bout duration was assessed via a linear mixed effects model (LME; package nlme, R ver. 4.1.1), where individual ID was included as a random factor. In addition, difference in minimum f_H during torpor between summer and winter was determined via a *t*-test.

Data from both sexes were pooled for the analyses. Numeric values are presented as mean \pm SD for the number of individuals (*N*) measured; *n* refers to the number of measurements. We did not calculate second-order means for T_b and torpor variables, as environmental conditions had a greater influence on the variation of the data than the identity of the individuals.

Results

Environmental Conditions

During our study period, T_a dropped below 5°C on 82 d and below 0°C on 14 d, mainly in the winter months of June and August (fig. 1). Mean daily maximum T_a in winter (June–August) was 15.8°C \pm 2.7°C, and mean daily minimum T_a was 3.7°C \pm 3.9°C (*n* = 92; absolute minimum T_a : -4.0°C; absolute maximum T_a : 23.1°C). Daily maximum T_a surpassed 35°C on 59 d and 40°C on 21 d, mainly in the summer months of December and January. Mean daily maximum T_a in summer (November–January) was 35.3°C \pm 5.3°C, and mean daily minimum T_a was 19.5°C \pm 5.1°C (*n* = 92; absolute minimum T_a : 29.1°C; absolute maximum T_a : 44.1°C). Heavy rain (>25 mm) occurred on 3 d throughout the whole study period; all 3 d occurred in the last 5 wk.

Group Sizes and Body Masses

Group sizes of gliders at our study site were small (up to two adults, sometimes accompanied by dependent young), and group composition was dynamic. We also found single individuals and two adult individuals of the same sex (males and females) together at resting sites. Breeding seemed to be fairly synchronous and seasonal, as all reproductive females had pouch young of comparable ages (only a few weeks apart) during spring.

Body masses of the squirrel gliders fluctuated throughout the year and decreased slightly from May to October (over winter) from an average of 212.1 \pm 23.8 g (*N* = 7) to 206.2 \pm 23.8 g and then increased over summer to 247.4 \pm 4.6 g in March. However, these changes were not significantly coupled to season (Kruskal-Wallis test, *H* = 8.84, *P* = 0.12). As we measured body mass only during the few days of captivity and body masses changed considerably over the study period, we could not analyze the relationship between body masses and torpor bout frequency.

General Thermoregulatory Patterns

Of 10 individuals, nine entered a low- T_b torpor bout at least once (six males/four females; figs. 1, 2A, 2C), with torpor frequency

varying considerably between individuals. Five individuals entered torpor only once or twice, while the other four individuals entered torpor 11 or more (up to 19) times (fig. S4). The only individual (a female) for which torpor was not detected had the least data available (only 9 d during October; table 1, individual J, no recapture); therefore, torpor bouts may have been missed.

Torpor was observed on 67 of 1,182 total monitoring days (5.7%, *N* = 10; fig. 1; table 1). Thus, on 16% of calendar days (39 of 243) at least one individual became torpid. The average torpor bout duration was 308 min (\pm 207 min, *n* = 66) and varied considerably. The shortest torpor bout lasted for only 30 min (with a minimum T_b of 30°C), whereas the longest torpor bout lasted for 1,040 min from 2250 hours to 1610 hours the next day; thus, torpor bouts always lasted for less than 24 h. Squirrel gliders usually entered torpor in the early mornings (0717 hours \pm 2 h 40 min, *n* = 66), when they had ceased nightly activity and T_a was low, allowing T_b to drop quickly. Most torpor bouts ended shortly after noon (1222 hours \pm 2 h 23 min, *n* = 67), several hours before nightly activity started and when T_a had increased and passively raised the thermoconforming T_b (fig. 2C). The earlier in the night a torpor bout commenced, the longer it lasted and the lower T_b dropped (fig. 3). In general, minimum T_b decreased with torpor bout length (linear regression: *P* < 0.001, *R*² = 0.52; fig. 4A). The same was true for f_H only when the longest torpor bout, an outlier with a very different general pattern, was removed (LME: *P* = 0.049; fig. 4B).

Body Temperature and Heart Rate during Torpor

The average minimum T_b during low- T_b torpor episodes was 26.7°C \pm 3.8°C (*N* = 9, *n* = 67), which occurred at an average time of 1017 hours \pm 2 h 40 min. The lowest T_b reached during a torpor bout was 17.9°C, resulting in the maximal daily amplitude of T_b at 20°C (maximum T_b on this day: 37.9°C). Average amplitude of T_b during torpor bouts (difference between maximum and minimum T_b on torpor days) was 11.0°C \pm 3.8°C (*N* = 9,

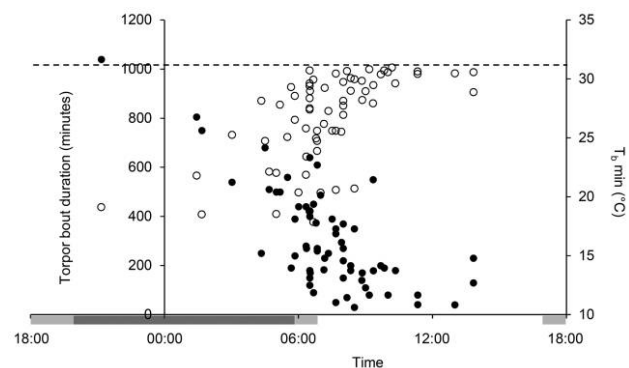


Figure 3. Influence of time of torpor entry on duration of torpor bouts (min; black circles) and minimum body temperature (T_b , min) during torpor bouts (°C; white circles). Gray bars indicate the dark phase, and light gray bars indicate the seasonal shifts in sunrise and sunset. The dashed line represents torpor cutoff at 31°C.

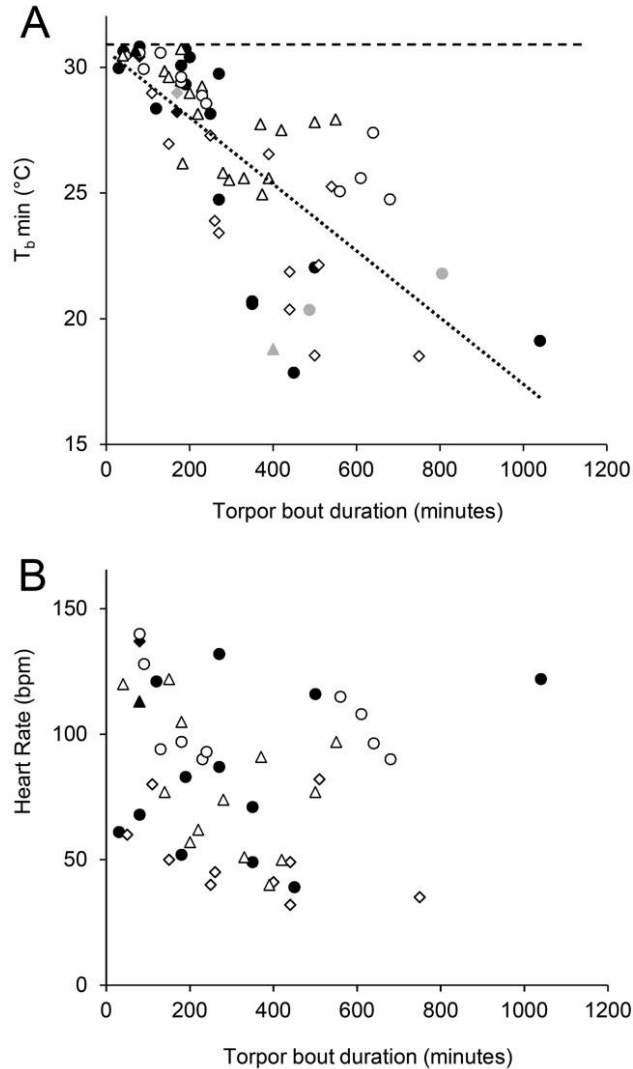


Figure 4. Minimum body temperature (T_b min; A) and heart rate (f_H ; B) during torpor bouts versus duration of torpor bouts. The longer the torpor bout was, the more T_b min decreased; this relationship was not as pronounced for f_H . The regression line is dotted, and the dashed line represents torpor cutoff at 31°C. Different symbols indicate different individuals.

$n = 67$). f_H during torpor remained extremely variable even during steady-state torpor (32–140 bpm) but in general appeared to decrease with corresponding T_b to a minimum of 32 bpm at $T_b = 23.3^\circ\text{C}$ (fig. 5). Interestingly, f_H at minimum T_b (17.9°C) was relatively high (103 bpm) compared to the absolute minimum f_H (32 bpm). On days when torpor was used, the average resting f_H was 285 ± 111 bpm ($T_b = 35.8^\circ\text{C} \pm 1.6^\circ\text{C}$, $N = 6$, $n = 1,570$), giving an average daily scope of 193 ± 58 bpm ($N = 6$, $n = 50$).

Seasonal Occurrence of Torpor

Surprisingly, torpor episodes were not concentrated on the coldest or hottest days of the year. Although some did occur at T_a 's below freezing, most squirrel gliders remained euthermic on very

cold days (figs. 1, 6A, 6B, solid squares). On the other hand, torpor was also used on comparatively warm days with minimum T_a 's above 15°C (figs. 1, 6A, dashed square). Minimum T_a was significantly lower on days when squirrel gliders used low- T_b torpor in both winter ($N = 6$, $n = 449$, log likelihood [logLik] = 2,443.7, $P < 0.001$) and summer ($N = 9$, $n = 729$, logLik = 4,420.2, $P < 0.001$). Maximum T_a was significantly higher on torpor days in winter (GLMM: linear, $N = 6$, $n = 450$, logLik = 2,167.6, $P = 0.02$), but it was lower in summer (GLMM: linear, $N = 9$, $n = 729$, logLik = 4,614.4, $P < 0.001$). This suggests that torpor was expressed on clear days in winter (colder nights, hotter days) but on overcast days in summer (cooler nights and days). Minimum recorded f_H in low- T_b torpor was $\sim 50\%$ lower on average during winter (54 ± 15 bpm, $N = 3$, $n = 23$) than in summer (106 ± 18 bpm, $N = 5$, $n = 27$; $t = 11.253$, $df = 47.841$, $P < 0.001$), which was also true for the corresponding T_b despite an only 1.5°C difference between the seasons (winter: $27.4^\circ\text{C} \pm 2.52^\circ\text{C}$, $N = 3$, $n = 23$; summer: $28.9^\circ\text{C} \pm 2.59^\circ\text{C}$, $N = 5$, $n = 27$; $t = 2.1013$, $df = 47.123$, $P = 0.04$). As f_H data were not consistently available for all stages of a torpor bout, this difference might be explained by the longer torpor bouts in winter increasing the chance of capturing a valid f_H . Frequently, euthermic squirrel gliders during winter showed small, but clear, multihour decreases in T_b during the middle of the night (their active phase), possibly entering intermediate resting phases that could be sleep or perhaps torpor (fig. 2C). During this time, f_H fell to levels similar to those observed during torpor, with mean values ranging from 93 to 192 bpm and mean T_b 's ranging from 33.5°C to 34.8°C .

While in summer RH_{\min} or RH_{\max} did not differ between days with and without torpor, in winter RH_{\min} was lower on days with torpor, as is the case on clear days, thus matching our results for

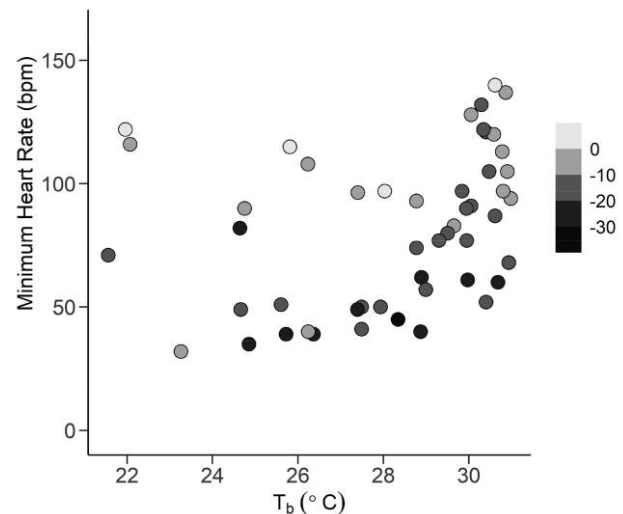


Figure 5. Minimum heart rate during a given torpor bout versus the corresponding body temperature (T_b). Shading of each data point corresponds to the difference between the T_b conditions and ambient temperature (T_a) conditions. Even during relatively shallow torpor (T_b near 30°C) and with a large difference between T_b and T_a (10°C – 20°C difference), heart rate is reduced close to 50 bpm during torpor.

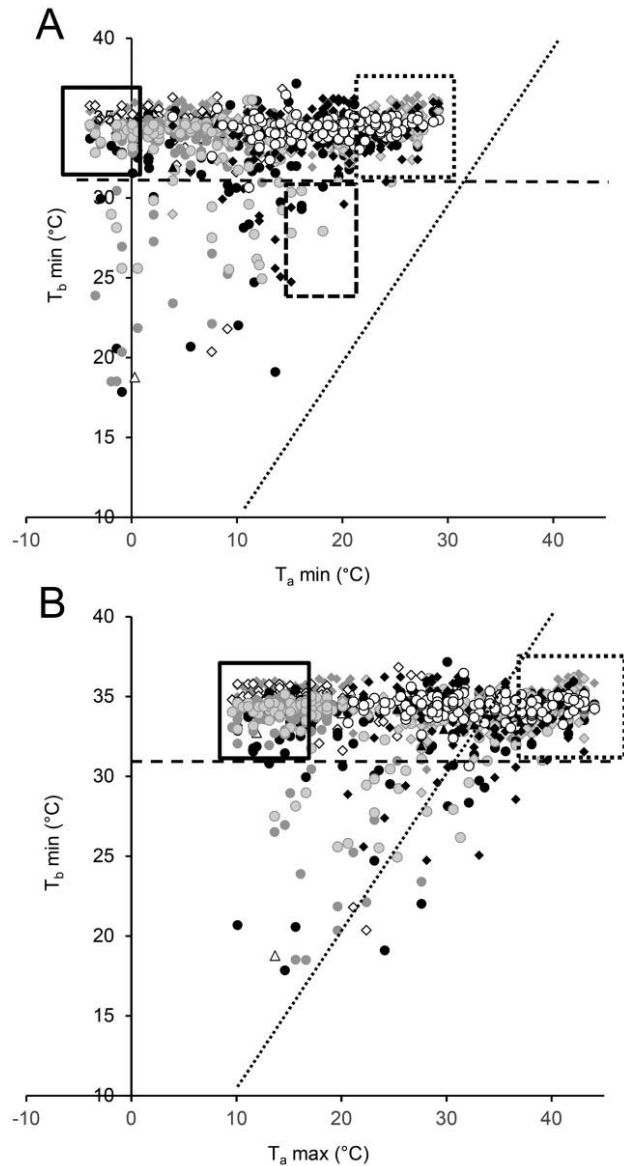


Figure 6. Daily minimum body temperature (T_b min) versus minimum ambient temperature (T_a min; A) and maximum ambient temperature (T_a max; B). Torpor episodes of *Petaurus norfolcensis* were not concentrated around the hottest or the lowest T_a . Different symbols indicate different individuals. The dashed line represents torpor cutoff at 31°C, and the dotted line represents the line of equality between T_b and T_a . Solid squares show range of euthermia on cold days, the dashed square shows range of torpor on comparatively warm days, and dotted squares show range of euthermia on hot days.

temperature (RH = 33% ± 17% [$n = 426$] vs. RH = 51% ± 13% [$n = 23$]; RH_{min} in winter, GLMM: linear, $N = 6$, $n = 449$, logLik = 3,562.9, $P < 0.001$; RH_{max} in winter, GLMM: linear, $N = 6$, $n = 450$, logLik = 3,152.4, $P = 0.09$; RH_{min} in summer, GLMM: linear, $N = 9$, $n = 729$, logLik = 6,150.3, $P = 0.22$; RH_{max} in summer, GLMM: linear, $N = 9$, $n = 729$, logLik = 6,553.6, $P = 0.57$).

Based on T_b changes, we could not detect any torpor bouts on very hot days when daily minimum T_a was above 21°C or

daily maximum T_a was above 37°C (figs. 1, 6A, 6B, dotted squares). However, during periods of the day when T_a was above 35°C, squirrel gliders thermoconformed (T_b was within 0.5°C of T_a) between 24% and 30% of the time (figs. 1, 2B, 2D). When squirrel gliders were thermoconforming at high T_a 's, mean f_H 's were 213 ± 144 bpm ($N = 6$, $n = 553$), with individual minima ranging from 82 to 109 bpm ($N = 6$, $n = 6$), which equates to between 52% and 69% of basal f_H (158 bpm; Kinnear and Brown 1967). When T_a increased beyond 40°C, gliders started to defend T_b near 40°C and were no longer considered thermoconforming (fig. 2D). At the mean maximum T_b of 39.8°C in these individuals defending T_b at this level, mean f_H was comparable to those of thermoconforming individuals with lower T_b 's (216 ± 86 bpm, $N = 6$, $n = 9$).

The amplitude of daily fluctuations of T_b on euthermic days changed with season and was higher in summer with 6.4°C ± 4.8°C ($N = 6$, $n = 445$) than in winter with 3.6°C ± 0.9°C ($N = 6$, $n = 373$; fig. 1; GLMM: linear, logLik = 3,658.2, $P < 0.001$). Accordingly, maximum T_b in winter was significantly lower than in summer (GLMM: linear, logLik = 1,477.9, $P < 0.001$), and maximum T_b above 40°C occurred only on days with maximum T_a approaching or exceeding 40°C (fig. 7, solid square). Average resting f_H was also lower on euthermic days in summer than in winter (summer: 264 ± 111 bpm, $N = 6$, $n = 22,864$; winter: 294 ± 104 bpm, $N = 6$, $n = 33,224$; $t = -32.54$, $df = 46,972$, $P < 0.001$).

Body Temperature of Euthermic Females

In females, there seem to be recurrent periods of considerably reduced daily amplitude of T_b not detectable in males (fig. S5). Daily minimum amplitude of T_b never decreased below 2.2°C

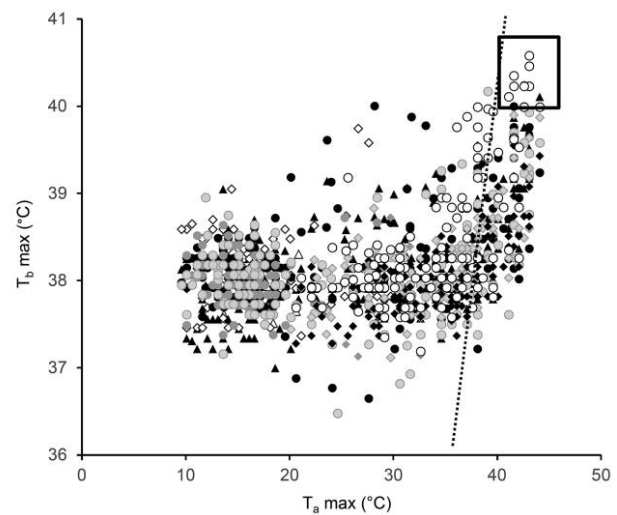


Figure 7. Daily maximum body temperature (T_b max) versus maximum ambient temperature (T_a max). Different symbols indicate different individuals. The dotted line represents the line of equality between T_b and T_a , and the square shows the range where T_b max above 40°C occurred on days with T_a max approaching or exceeding 40°C.

in males on euthermic days, whereas it frequently dropped below 2°C in females during these periods and was as low as 1.1°C. We observed only one female with several periods of reduced daily amplitude of T_b during data collection (fig. S5), and these were each about 30 d apart, suggesting a relatively fixed interval.

Discussion

In one of the first field studies that measured T_b and f_H at the same time, we evaluated the thermal biology and torpor expression of free-ranging squirrel gliders (*Petaurus norfolcensis*). We documented, for the first time, torpor expression in this species, uncovering another heterotherm within the genus *Petaurus*. *Petaurus norfolcensis* is almost twofold larger than any other gliders in this genus for which data on torpor are available, although there is anecdotal evidence that the considerably heavier congener, the yellow-bellied glider (*Petaurus australis*; 600 g), may also use torpor (Geiser and Körtner 2010).

Torpor bouts in squirrel gliders lasted on average about 5 h, and T_b during torpor dropped as low as 17.9°C, enabling substantial savings in energy and water expenditure. The f_H during torpor often decreased below 50 bpm, which is about one-third of the estimated basal level. This substantial reduction in f_H occurred even when T_b was relatively high (close to 30°C; fig. 6) during torpor. As isolated perfused hearts of other small marsupial species have been found to beat closer to 200 or 300 bpm when at 30°C (Geiser et al. 1989), our results suggest that active suppression of f_H could be occurring for periods of time to generate the very low f_H values we present here. Because f_H data were not consistently available for all stages of a torpor bout, and 32 bpm was the minimum f_H that our loggers were capable of detecting (see “Methods”), these values may not reflect the true minimum f_H of torpid squirrel gliders, which could in fact be lower. Nevertheless, f_H remained extremely variable, even during steady-state torpor. Our results, with simultaneous recording of both f_H and T_b over multiple seasons, show that the natural variation in f_H is greater than what might have been expected for this species and may indicate mechanisms by which individuals cope under heat stress. Data for f_H in marsupial heterotherms during torpor are limited to only one other species, the eastern pygmy possum (*Cercartetus nanus*; 35 g), in which f_H fell to a similar value of 32 ± 3 bpm at $T_b = 24^\circ\text{C}$ (Swoap et al. 2017).

Although almost all squirrel gliders employed daily torpor, they did so only occasionally and clearly not as a fixed, regular (e.g., seasonal) response. Surprisingly, torpor was most frequently expressed in spring (August/October), which is unusual among heterothermic species. Unfortunately, our loggers stopped recording at the end of August (shortly after torpor bouts started) because of limited storage capacities. When we implanted the new loggers at the beginning of October, torpor bouts also occurred. However, we can neither exclude nor verify that torpor was exhibited throughout all spring months.

Although, in general, the propensity to enter torpor seems to be enhanced by lower minimum T_a and low RH, as found on clear days (in winter), torpor bouts were the most frequent on neither the coldest period (temperatures did frequently drop be-

low 0°C during June–August, and daily minimum T_a was usually just above freezing) nor the hottest period of the year. Thus, torpor does not seem to be necessarily triggered by either very low T_a (to save on costs of endothermy; Nicol and Andersen 1996; Geiser 2004, 2021; Heldmaier et al. 2004) or high T_a (to decrease evaporative water loss while avoiding overheating; O’Mara et al. 2017a; Reher and Dausmann 2021). However, in summer, maximum T_b increased on hot days with T_a ’s above 40°C, and the amplitude of daily T_b fluctuations of euthermic squirrel gliders almost doubled. Thus, they might be tolerating higher T_b ’s and adaptive hyperthermia during the hot hours of the day to conserve water by avoiding evaporative cooling, analogous to the camels (*Camelus dromedarius*) in Schmidt-Nielsen’s landmark study (Schmidt-Nielsen et al. 1956) but also to others, such as oryx (*Oryx leucoryx*; Ostrowski et al. 2003), kangaroos (*Macropus giganteus* and *Macropus rufus*; Dawson et al. 2007), gerbils (*Gerbillus pusillus*; Buffenstein and Jarvis 1985), and tree-roosting microbats (*Scotorepens greyii* and *Mormopterus* sp. 3; Bondarenko et al. 2014).

On average, f_H during these hyperthermic episodes was similar to predicted basal levels, yet minimum f_H during thermoconforming hyperthermia was almost half of basal f_H , and this could point to some short-term inhibition akin to periods of reduced f_H found for a frugivorous bat species (O’Mara et al. 2017b). Given that a 30% reduction in f_H over periods of only 5–7 min was considered to provide a 10% energy savings for this bat species (O’Mara et al. 2017b), the almost 70% reduction in f_H that we reported here could possibly entail even more substantial energy savings. Yet without simultaneous measures of MR and f_H under these conditions, we cannot be certain. Nevertheless, simultaneous recording of f_H and T_b enabled us to uncover variability in cardiac scope between seasons and novel insights into the potential mechanisms by which these animals cope under heat stress.

In winter, reproductive activity may have inhibited torpor use. Torpor is employed during reproductive activity by some mammals, such as bats (Geiser et al. 2005; Willis et al. 2006; Canale et al. 2012; Dzal and Brigham 2013) and some marsupials (mulgaras, *Dasyercus blythi* [Körtner et al. 2008]; fat-tailed dunnarts, *Sminthopsis crassicaudata* [McAllan and Geiser 2014]), but reproductive efforts are inhibitive to torpor expression in others (Csada and Brigham 1994; Fietz et al. 2004). Species that enter torpor during reproduction are often found in unpredictable habitats and rely on food that can be unpredictable or strongly seasonal (McAllan and Geiser 2014), making squirrel gliders a promising candidate. Regular periods of considerably reduced daily amplitude of T_b in female squirrel gliders (not detectable in males) might possibly have been due to receptive periods. If occurring multiple times, they did so in about 1-mo intervals, which correspond to the timing of estrous cycles in marsupial gliders (Woodd et al. 2006; Raftery 2015). It is nevertheless surprising how synchronously—within a couple of days—the squirrel gliders suddenly started showing torpor bouts in the middle of August. This suggests some external, triggering event, such as a sudden decrease in food availability (Geiser and Brigham 2012; Nowack et al. 2017). If reproduction were a decisive factor, one would expect shifted constraints and thus shifted torpor

patterns between the sexes (Fietz et al. 2004; Körtner et al. 2008) and between birth dates.

At our study site, T_a 's followed a seasonal cycle, but energetic challenges related to spurious rainfall and flowering and thus food availability were somewhat unpredictable and also subject to catastrophic events, such as droughts and fires. Moreover, 2019/2020 might have been an especially harsh year for squirrel gliders because of the long-lasting drought and thus likely low food and water availability in spring. The torpor use in August/October might have been an emergency response to survive, as found in African bush babies (*Galago moholi*; Nowack et al. 2013), sugar gliders (*Petaurus breviceps*; Christian and Geiser 2007), and gerbils (*G. pusillus*; Buffenstein 1984).

Group sizes with no more than two adults were much smaller in our study population than in previous studies (Quin 1995; Suckling 1995), although the dynamic nature of group affiliation suggests a fission-fusion society, such as found in dolphins, chimpanzees, and elephants (Couzin 2006), while still having social cliques. Perhaps inland habitats are generally less productive than coastal forests (Millis and Bradley 2001; van der Ree 2002); therefore, population densities are lower. It is also likely that the aftermath of the severe 2013 bushfire that decimated wildlife and burned >95% of the park's vegetation (McInnes-Clarke et al. 2013; General Purpose Standing Committee No. 5 2016), in particular, mature trees, still resonates with the current glider population. Regardless, because of the small group sizes, huddling could not be employed at its full potential as a means of thermoregulation. During daily increases in T_b , from arousals both from torpor episodes and in the regular euthermic T_b cycle, squirrel gliders used the increasing T_a for passive thermoregulation, if T_a reached accordingly high levels.

In conclusion, there is growing evidence that torpor is a much more flexible response than previously thought (Geiser and Brigham 2012; Nowack et al. 2017) and that additional physiological mechanisms may enable heterotherms to conserve energy outside of the traditional torpor paradigm. Torpor does not seem to be a general seasonal adaptation in squirrel gliders, and it seems to be employed flexibly and on demand. Specific parameters triggering torpor episodes remain elusive, but most likely a combination of endogenous and exogenous conditions comes into play. Low T_a seems to foster employment of torpor, but torpor is not obligatory, even when temperatures drop below freezing. Flexibility in torpor timing and thus the potential to save energy and possibly water might indeed give squirrel gliders an advantage during unforeseen unfavorable conditions and dramatic environmental change. The intriguing question remains: whether small group size, the expression of torpor, and the general flexibility of energy budgeting are features of the Warrumbungle population or whether squirrel gliders living in different habitats along the eastern coast respond in the same way to unfavorable conditions. In general, it is important to acknowledge that a wide distribution of a species over broad environmental ranges does not necessarily imply a wide adaptation spectrum of all individuals of this species, as distinct populations may be locally adapted (Geiser and Ferguson 2001; Dunbar and Brigham 2010;

Violle et al. 2012; Richardson et al. 2014; Reher et al. 2022a). Variation in responses between populations may arise from genetic adaptation, developmental plasticity, or phenotypic flexibility, and only the latter allows relatively immediate compensatory responses (Reher et al. 2022b). Thus, taking the whole species' response repertoire into account might be misleading when assessing specific populations' adaptive scopes in the face of climate change and rapidly changing habitats.

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