

Thermobiology, energetics and activity patterns of the Eastern tube-nosed bat (*Nyctimene robinsoni*) in the Australian tropics: effect of temperature and lunar cycle

Alexander Riek^{1,2,*}, Gerhard Körtner¹ and Fritz Geiser¹

¹Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Armidale, NSW 2351, Australia and

²Department of Animal Sciences, University of Göttingen, Albrecht-Thaer-Weg 3, 37075 Göttingen, Germany

*Author for correspondence (ariek2@une.edu.au)

Accepted 23 March 2010

SUMMARY

Currently, there are no data on the thermal biology of free-ranging pteropodid bats (Chiroptera). Therefore, our aim was to investigate physiological and behavioural strategies employed by the fruit bat *Nyctimene robinsoni* (body mass ~50 g) in winter in tropical Northern Queensland in relation to ambient temperature (T_a) and the lunar cycle. Daily body temperature (T_b) fluctuations in free-ranging bats were measured *via* radio-telemetry and metabolic rate was measured in captivity *via* open-flow respirometry (T_a , 15–30°C). Free-ranging bats showed a significant 24 h circadian cycle in T_b , with the lowest T_b at the end of the rest phase just after sunset and the highest T_b at the end of the activity phase just before sunrise. Average daily core T_b ranged from 34.7±0.6 to 37.3±0.8°C (mean ± s.d.) over an average daily T_a range of 17.1±1.1 to 23.5±1.8°C. T_b never fell below 30°C but T_b was significantly reduced during the full moon period compared with that during the new moon period. T_b was correlated with T_a during the second half of the rest phase ($P<0.001$) but not during the active phase. Resting metabolic rate of bats was significantly affected by T_a ($P<0.001$, $R^2=0.856$). Our results show that tube-nosed bats exhibit reduced T_b on moonlit nights when they reduce foraging activity, but during our study torpor was not expressed. The energy constraints experienced here by tube-nosed bats with relatively moderate T_a fluctuations, short commuting distances between roosting and feeding locations, and high availability of food were probably not substantial enough to require use of torpor.

Key words: tube-nosed bat, thermobiology, body temperature, lunar cycle.

INTRODUCTION

The Eastern tube-nosed bat (*Nyctimene robinsoni* Thomas 1904) is a small to medium sized (body mass ~50 g) pteropodid bat of the suborder Yinpterochiroptera (Teeling, 2009), inhabiting sub-tropical and tropical rainforests of Australia. The distribution of this endemic species stretches along the East coast of Australia from Northern New South Wales to the Cape York peninsula. It is one of eight pteropodid bats in Australia and one of 14 tube-nosed bat species (*Nyctimene* spp.) worldwide and has the most southerly distribution of the latter. *Nyctimene robinsoni* relies on vision and smell to detect its food sources, which consist mainly of figs and other rainforest fruits (Spencer and Fleming, 1989; Hall and Pettigrew, 1995).

Small mammals like *N. robinsoni* are particularly affected by seasonal changes in climate, because of their diet and their body size, and in the case of bats also because flying is energetically demanding (Speakman and Racey, 1991; Bartels et al., 1998; Geiser and Coburn, 1999). Most small mammals forage at night and thus are usually exposed to the coolest part of the day potentially increasing their energy expenditure. Moreover, if they rely on vision for foraging like pteropodid bats, they are also likely to be affected by nocturnal illumination, such as during different phases of the moon cycle. Data from the literature suggest that during higher lunar illumination nocturnally active rodents (Lockard and Owings, 1974; Wolfe and Summerlin, 1989; Bowers, 1990; Daly et al., 1992; Abramsky et al., 1996), lagomorphs (Butynski, 1984; Gilbert and Boutin, 1991), and some neotropical and insectivorous bats (Erkert, 1978; Haeussler and Erkert, 1978; Morrison, 1978; Morrison, 1980; Lang et al., 2006) reduce their activity. This is generally explained by increased predation pressure, which seems to outweigh the

advantage that could be gained in finding food. However, to our knowledge, only limited data are available for visually foraging frugivorous pteropodid bats (Law, 1997; Elangovan and Marimuthu, 2001). Hence it remains largely unknown how the lunar cycle affects small flying mammals that exclusively forage on fruit by using vision and thus face potential tradeoffs between enhanced foraging during moonlit nights while at the same time risking increased exposure to visually oriented nocturnal predators. Data on continuous body temperature (T_b) in relation to the lunar cycle, which indicate the energetic costs for increased or decreased activity, are entirely lacking.

Another challenge to small mammals in Australia's tropical regions is the seasonal changes in food availability because the climate changes substantially between the wet (summer) and the dry season (winter). In other climate zones, including arid environments, many mammals respond to such varying environmental conditions by migration or entering torpor to reduce energy demands (Coburn and Geiser, 1998; Körtner et al., 1998; Lovegrove and Raman, 1998; Cryan and Wolf, 2003). Field data show that torpor use for a reduction of energy requirements is not restricted to temperate climates but is also employed by tropical species (Schmid and Speakman, 2000; Dausmann et al., 2005). This could also apply to pteropodid bats, which, unlike insectivorous bats, were in the past believed to be mainly obligate homeotherms (Morrison, 1959; Bartholomew et al., 1964). However, some laboratory data showed that a few of the smaller (<50 g) pteropodid bats, such as the blossom bats (*Syconycteris australis*, *Macroglossus minimus*) and the common tube-nosed fruit bat (*Nyctimene albigenter*), are capable of entering daily torpor (Bartholomew et

al., 1970; Geiser et al., 1996; Bartels et al., 1998). Nevertheless, it remains unknown how often and under what conditions torpor in pteropodid bats is employed in the field, especially as recent studies indicate that thermal energetics in mammals can differ substantially between the laboratory and the field (Körtner and Geiser, 2000; Geiser et al., 2007).

Therefore, because food availability is affected by climate, and foraging by visibility and potential predation pressure we tested the hypothesis that the lunar cycle influences T_b and hence the energy balance in a small free-ranging mammal that uses night vision to find its food sources in a tropical environment. Furthermore we investigated the physiological and behavioural strategies of free-ranging *N. robinsoni* to determine how these data relate to metabolic measurements in captivity.

MATERIALS AND METHODS

Study sites

The study was undertaken from 22 July to 27 August at two adjacent privately owned fruit farms (17°54'S, 146°00'E) approximately 10 km East of Tully, and at Lacey Creek at Tam O'Shanter National Park (17°51'S, 146°03'E) 7.5 km North/West of Mission Beach in the wet tropics of Northern Queensland, Australia. The two study sites were within 30 km of each other and experienced similar weather conditions. Tam O'Shanter National Park is characterized by dense tropical rainforest. The vegetation of the two adjacent fruit farms was a mix between banana plantations and fruit orchards surrounded by dense tropical rainforest. The area where the study was undertaken has an average yearly rainfall of approximately 4500 mm of which most occurs during the wet season from December to April (Australian Government, Bureau of Meteorology).

The study was conducted under a permit from the Environmental Protection Agency Queensland (WISP06159309) and a licence from the University of New England Animal Ethics Committee (AEC09/059).

Climate data

Ambient temperature (T_a) and relative humidity (RH) at both study sites were recorded continuously throughout the study with miniature data loggers at 30 min intervals (Thermochron and Hydrochron, temperature resolution 0.06°C, humidity 0.6% hydrochron only, i-Buttons temperature resolution 0.5°C, Maxim Integrated Products, Sunnyvale, CA, USA). The T_a at the farms and at Lacey Creek was measured at several different locations in the shade at approximately 1.5 m above the ground. Moreover, T_a at Lacey Creek was measured in the shade of a tree trunk at heights of 1, 3, 6, 9 and 12 m above ground level in order to assess T_a gradients from ground level to the canopy. Rainfall was recorded daily with a rain gauge (Lacey Creek) and by a rain gauge data logger (TinytagPlus, Gemini Data Loggers Ltd, Chichester, West Sussex, UK), recording the occurrence and

the amount of precipitation every 30 min (farm) throughout the study. The lunar cycle during the time of the study was expressed as % illumination.

Trapping

Trapping was conducted by using mist nets with a length of 6–18 m. Nets were opened just before sunset at approximately 18:00 h at several locations on the farms or at Lacey creek (usually six to eight mist nets were used at a time). After sunset nets were checked every 15–30 min for 3 h until approximately 21:00 h, when they were removed.

Body temperature measurements

To measure daily T_b fluctuations, temperature-sensitive radio transmitters (1.9 g, Sirtrack, Havelock, New Zealand) were implanted into five individuals (four females and one male, Table 1). Transmitters were calibrated to the nearest 0.1°C against a precision mercury thermometer over a temperature range of 10–40°C in a water bath and sterilized before implantation. Transmitters were implanted intraperitoneally under general oxygen/isoflurane anaesthesia. The incision into the abdominal cavity was closed using Chromic Gut (2.0 metric, Ethicon, Sommerville, NJ, USA) for the muscle layer and Coated Vicryl (3.0 metric, Ethicon) for the skin. A topical anaesthetic (Ban Itch, Apex Laboratories Pty Ltd, Sommerby, NSW, Australia) and Leuko Spray Bandage (BSN medical Aust. Pty Ltd, Clayton, Vic, Australia) was applied. After surgery bats received an oral dose of liquid Children's Panadol (GSK Consumer Healthcare, Ermington, NSW, Australia) and were held for the following night and day before they were released at the site of capture on the following evening. Captive bats were kept in an outdoor tent (3 m × 3 m × 2 m) in the shade. The fabric of the tent was transparent to light and equipped with fly screens so animals were exposed to the natural photoperiod and T_a . During captivity bats had *ad libitum* access to fruits (bananas, berries) and fruit juice mixed with a high protein cereal.

After release implanted individuals were radio tracked daily with handheld radio antennas (3-element, Yagi) and receivers to their roosting sides shortly after sunrise. Roosting sides were marked and the location recorded daily with a handheld GPS (Oregon 400T, Garmin, Olath, KS, USA). For each bat, a mobile data-logging system measuring the interval between two transmitter pulses every 10 min was placed close to the roosting side (Körtner and Geiser, 1998). After several days, data were downloaded to a personal computer. Log-transformed interval data were converted to T_b values using a second-order polynomial equation based on the original calibration of the transmitter.

Bats were tracked until the end of the study with two exceptions. One female bat (bat no. 2, Table 1) was eaten, probably by a reptile as the temperature decreased sharply after day 8 of recording but

Table 1. Details of tube-nosed bats used in the study

Bat no.	Sex	Capture body mass (g)	Capture location	Recording period	
				T_b measurements	MR measurements
1	Female	50.0	Tam O'Shanter NP	22/7/09–23/8/09	–
2	Female	53.1	Tam O'Shanter NP	22/7/09–29/7/09	–
3	Female	53.5	Farm	03/8/09–27/8/09	01/8/09
4	Male	50.8	Farm	06/8/09–27/8/09	03/8/09 and 04/8/09
5	Female	48.3	Farm	11/8/09–27/8/09	08/8/09 and 09/8/09
6	Male	53.4	Farm	–	19/8/09 and 20/8/09
7	Male	56.8	Farm	–	24/8/09 and 25/8/09

T_b , body temperature; MR, metabolic rate.

the transmitter continued to move. The transmitter was found several days later on the ground in what were presumably snake or goanna faeces. The implanted transmitter of another female (bat no. 1) stopped transmitting after 38 days of recording probably due to exhaustion of the battery in the transmitter.

Metabolic measurements

Rates of oxygen consumption (\dot{V}_{O_2}) and carbon dioxide production (\dot{V}_{CO_2}) of five individuals (three males and two females, Table 1) were measured by flow-through respirometry over the T_a range experienced by the free-ranging bats during our study (i.e. 15–30°C). Measurements commenced in the early morning after capture at night and lasted until the late afternoon. Metabolic measurements were recorded for two T_a (~15 and 20°C) on one day and two further T_a (~25 and 30°C) on the second day. For bat no. 4 only two temperatures were recorded to facilitate early release.

Bats were placed in a metabolic chamber (11), which was situated in a temperature-controlled cabinet. Dry air, provided by an air pump (ASF, Munich, Germany), was divided, with air going to the chamber passing through an Omega FMA5698 mass flow meter (Stanford, CT, USA) and the remainder going directly to a two-way solenoid valve to give a reference air sample. Flow rate to the chamber was maintained at ~450 ml min⁻¹. Air exiting the chamber passed through a column of Drierite (CaSO₄) to remove water vapour, and a sub-sample entered an O₂/CO₂ analyser (280 Combo, David Bishop Instruments, Leamington, Warwickshire, UK). Voltage outputs from the flow meter, gas analyser and a temperature probe within the chamber were interfaced *via* a 16-bit analog to digital converter (ADC-16, Pico Technology Ltd, Cambridge, UK) with a laptop computer. Data were recorded in 3 min intervals with a custom-written program (Visual Basic for DOS). The gas analyser was placed in an insulated box to reduce temperature-related drift and a reference air sample was taken every 15 min. Prior to the measurements the gas analyser was calibrated with a precision gas mixture (BOC Gases).

At the conclusion of each day's measurement rectal T_b was measured with a thermocouple to the nearest 0.1°C immediately after the bat had been removed from the chamber.

Statistical analysis

Statistical analyses were performed with the program package SAS version 9.01 (SAS, 2001). We used mixed modelling (PROC MIXED) to control for repeated measurements from the same individuals. As the data for T_b measurements in free-ranging bats included four females and only one male, sex differences could not be determined. To test whether the lunar cycle had an effect on T_b we compared T_b occurring at moon illuminations of 51–100% ('full moon period') with T_b occurring at moon illuminations of 0–50% ('new moon period') using an integrated *post hoc* test (Tukey). Mean T_b values per 30 min intervals of the day were calculated for each day and bat. Slopes of regressions were compared with the program StatistixL (www.statistixl.com) using the integrated regression comparison feature. Summary statistics are given as means ± s.e. (unless otherwise stated), where N is the number of individuals and n is the number of measurements.

To test for the generality of the relation between body mass and basal metabolic rate (BMR) in pteropodid bats, published data [see White et al., and McNab and Bonaccorso for references (White et al., 2009; McNab and Bonaccorso, 2001)] and our results were assessed using the phylogenetic generalized least squares approach (PGLS) (Grafen, 1989; Martins and Hansen, 1996; Garland and Ives, 2000; Rohlf, 2001) in order to account for the potential lack of

independence between species, because of their shared evolutionary history (Felsenstein, 1985; Garland et al., 1992). Calculations were performed using the computer software PGLS, version 1.14, 2008 (distributed by the author: P. C. Withers, Department of Zoology, University of Western Australia, Crawley, WA, Australia). The phylogeny for the species used in the present analysis was derived from a mammalian 'supertree', which includes 4510 species with branch lengths derived from dated estimates of divergence times (Bininda-Emonds et al., 2007). This 'supertree' for mammals in Newick format was transformed to a distance matrix using the Analyses in Phylogenetics and Evolution package in R (Paradis et al., 2004) and pruned to include only the species of concern for the present analysis.

RESULTS

Climate data

The T_a gradients between the heights of 1 and 9 m measured at Lacey Creek were not significant, but T_a measured in the canopy at a height of 12 m during the day were slightly higher because of exposure to direct sunlight. Hence T_a measured at a height of 1–2 m was deemed representative for T_a experienced by the bats. Mean daily T_a was 19.6±0.2°C, mean daily maximum T_a ($T_{a,max}$) was 23.1±0.3°C (range 19.5–26.5°C) and mean daily minimum T_a ($T_{a,min}$) was 16.7±0.2°C (range 14.5–19.0°C). The amplitude of daily T_a fluctuations during the time of the study (22 July–27 August) averaged 6.3±0.4°C (range 2.0–11.5°C) (Fig. 1). The mean daily RH was 86.8±0.6%, mean daily maximum RH (RH_{max}) was 100.5±0.2% (range 98.8–101.7%) and mean daily minimum RH (RH_{min}) was 59.0±1.5% (range 47.7–75.6%). Rainfall occurred on 8 of the 36 study days, mainly during the night. The highest rainfall occurred on 3 August (11.2 mm) and on 4 August (13.9 mm). Rainfall on the remaining 6 days ranged between 0.1 and 1.2 mm.

Body mass and distances between roost locations

The mean body mass for all bats and all recordings was 54.8±0.6 g (range 48.3–56.8 g; $N=7$) and did not differ between sexes ($F_{1,3}=1.45$, $P=0.363$).

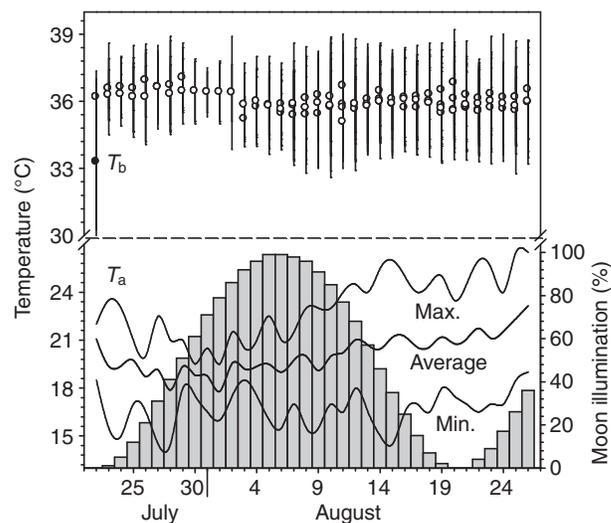


Fig. 1. Daily maximum (Max.), minimum (Min.) and average ambient temperature (T_a), daily body temperature (T_b , range and mean; filled circle indicates one bat with low T_b after release, see text for details) of *Nyctimene robinsoni* and the lunar cycle (grey bars) during the time of the study.

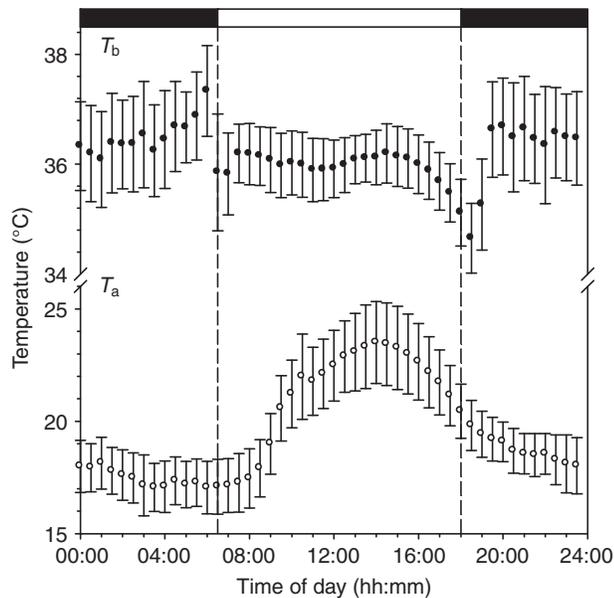


Fig. 2. Average body temperature (T_b , filled circles) of *N. robinsoni* and ambient temperature (T_a , open circles) in relation to time of day during the study period (22 July–27 August). Values are means \pm s.d. of five individuals over a total of 98 recording days. Black bars indicate scotophase.

During our study all bats stayed in close range to their initial capture location and roosted in the canopy of trees. Distances between roost locations on consecutive days for the five free-ranging bats were on average 41 ± 38 m (range: 0–397 m). The average maximum distance for each individual between any roost location for the time of our study was 254 ± 103 m (range: 105–418 m).

Body temperature

Five bats (four females and one male, Table 1) with implanted transmitters were monitored for a combined total of 98 days from which a total of 8437 measurements of T_b were obtained. Activity (19:00 h to 06:00 h, indicated by a break in continuous T_b records) and rest phase (06:30 h to 18:30 h) approximately equalled the daily night (18:30 h to 06:00 h) and day phase (06:30 h to 18:00 h) (Fig. 2).

We found no evidence of free-ranging bats entering torpor on any of the days T_b was recorded. Only bat no. 1 (Table 1) showed signs of shallow hypothermia the day following its release the previous night (recorded T_b range 30.2–32.9°C at 07:11 h to 18:10 h). This lower T_b lasted until the following night when normal activity commenced. We attributed this to recovery from surgery and hence excluded these T_b data from further statistical analysis. Bats showed a distinct 24 h daily cycle in T_b with a higher T_b phase during the night than during the day (Figs 2 and 3). Time of day had a significant effect on T_b ($P < 0.001$).

When all data were pooled the average T_b over 24 h was 36.0 ± 0.01 °C ($N=5$, $n=8437$). During the activity phase T_b was 36.4 ± 0.03 °C ($N=5$, $n=1846$) and during the rest phase T_b was 35.9 ± 0.01 °C ($N=5$, $n=6591$). Daily average T_b of *N. robinsoni* during our study ranged from a mean minimum of 35.1 ± 0.1 °C to a mean maximum of 37.0 ± 0.1 °C ($n=98$), while the daily T_b range in bats was on average 3.6 ± 0.1 °C (range 1.6–6.0°C) (Fig. 1). The daily minimum T_b ($T_{b,\min}$) recorded for all animals and all observation days was 34.7 ± 0.0 °C (range: 32.6–36.7°C, $N=5$, $n=268$) at a mean T_a of 19.8 ± 0.2 °C just after sunset (18:30 h) and before the beginning

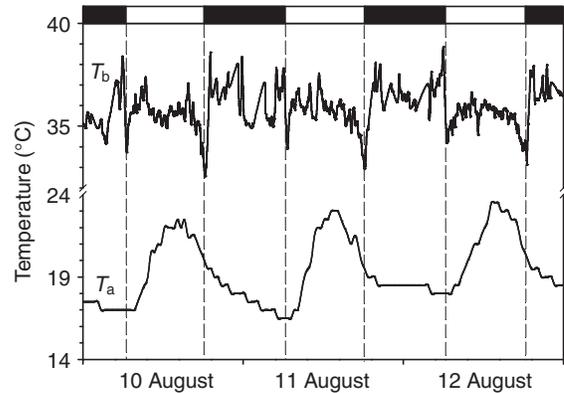


Fig. 3. Record of body temperature (T_b , thick line) and ambient temperature (T_a , thin line) for one tube-nosed bat (*N. robinsoni*) over 3 days. Black bars indicate scotophase.

of the activity phase (Fig. 2). The daily maximum T_b ($T_{b,\max}$) recorded was 37.3 ± 0.1 °C (range: 35.9–39.2°C, $n=5$, $N=177$) at a mean T_a of 17.1 ± 0.1 °C just before sunrise (06:00 h) and at the end of the activity phase.

Daily $T_{b,\max}$ and $T_{b,\min}$ were not influenced by the corresponding T_a or RH for any bat. When testing for the effect of mean daily T_a , $T_{a,\min}$, $T_{a,\max}$, mean daily RH, RH_{\min} and RH_{\max} on mean daily T_b , $T_{b,\min}$ and $T_{b,\max}$ none of the relationships were significant ($P > 0.05$). Testing for the same effects separately for the resting and active phase only, $T_{b,\min}$ during the active phase was significantly affected by mean T_a ($F_{13,25}=2.49$, $P=0.024$), which was explained by the regression equation $T_{b,\min}=37.71-0.138T_a$ (where temperature is in °C; $R^2=0.16$, $P<0.001$, Fig. 4). Furthermore, average T_a significantly affected average T_b between 10:30 and 18:30 h ($F_{66,144}$, $P<0.001$) explaining 10% of the variation when all data were included in the regression analyses ($T_b=33.17+0.115T_a$; $R^2=0.102$), with no significant differences among bats ($F_{1,67}$, $P=0.561$). When calculating mean T_b for 30 min intervals of the day over all observation days and all bats, the relationship between T_b and T_a was described by the equation $T_b=27.74+0.363T_a$ ($R^2=0.891$, Fig. 5).

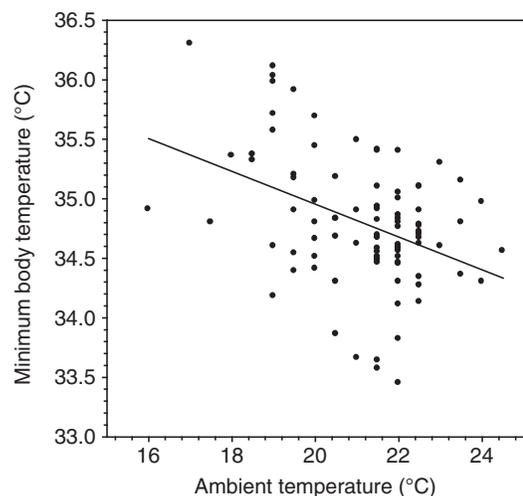


Fig. 4. Relationship between daily mean ambient temperature T_a and daily minimum body temperature $T_{b,\min}$ ($N=5$, 98 observation days) for *N. robinsoni* during the daytime (06:30 h to 18:00 h; $T_{b,\min}=37.71-0.138T_a$, $R^2=0.16$, $P<0.001$).

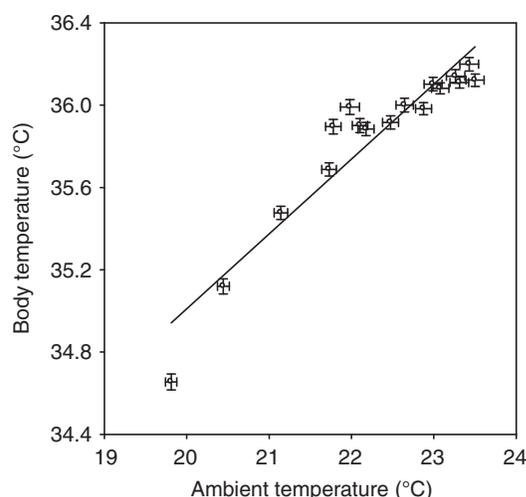


Fig. 5. Relationship between ambient temperature T_a and body temperature T_b averaged over 30 min intervals ($N=5$, 98 observation days) between 10:30 and 18:30 h for *N. robinsoni* ($T_b=27.74+0.363T_a$, $R^2=0.891$, $P<0.001$).

Separating the T_b data into T_b measured on days at moon illuminations of 51–100% (full moon period) and those measured at moon illuminations of 0–50% (new moon period) revealed that for the night hours of 22:30 h to 04:30 h, T_b during the full moon period was significantly lower ($P<0.001$) than that during the new moon period, with no differences between individuals ($F_{1,523}=0.76$, $P=0.385$; Fig. 6); the maximum difference in mean T_b was 1.1 °C at 03:00 h.

Metabolic rate

Resting metabolic rate (RMR) of bats was significantly affected by T_a ($F_{3,11}=82.9$, $P<0.001$) but not by sex ($F_{1,3}=3.01$, $P=0.181$). When regressing each bat separately for RMR against T_a slopes for the individuals did not differ ($F_{4,9}=1.33$, $P=0.331$), hence the common regression line was $\text{RMR}=2.89-0.062T_a$ (where RMR is in $\text{ml O}_2\text{g}^{-1}\text{h}^{-1}$; $P<0.001$, $R^2=0.856$, $N=5$, $n=19$, Fig. 7). Data on \dot{V}_{CO_2} followed the same pattern as \dot{V}_{O_2} and therefore \dot{V}_{CO_2} data are not presented separately here. The lowest RMR at T_a 29–31 °C ($1.00\pm 0.09\text{ ml O}_2\text{g}^{-1}\text{h}^{-1}$ or $54.7\text{ ml O}_2\text{h}^{-1}$; body mass 54.8 g) was assumed to reflect BMR. The mean respiratory quotient (RQ) was 0.83 ± 0.02 (range 0.67–0.97) and did not differ between sexes ($F_{1,3}=0.17$, $P=0.707$) or T_a ($F_{3,11}=1.08$, $P=0.396$).

Extrapolation of metabolic rate to zero (Scholander et al., 1950) gave the theoretical T_b of 46.6 °C which is 10.6 °C higher than the normothermic T_b (36.0 °C). Similarly, excluding BMR from the regression analysis gave the theoretical T_b of 42.8 °C which is 6.8 °C higher than the normothermic T_b . When calculating conductance (C) from the equation $C=\text{BMR}/(T_b-T_a)$ (Bartholomew et al., 1970) the resulting C values were $0.299\pm 0.014\text{ ml O}_2\text{g}^{-1}\text{h}^{-1}\text{ }^\circ\text{C}^{-1}$ at $T_a=30^\circ\text{C}$ ($N=4$, $n=4$) and $0.115\text{ ml O}_2\text{g}^{-1}\text{h}^{-1}\text{ }^\circ\text{C}^{-1}$ at $T_a=20^\circ\text{C}$ ($N=2$, $n=2$).

DISCUSSION

Our study provides the first evidence that moon illumination results in a substantial reduction in T_b , which has implications on foraging and energy expenditure. However, *N. robinsoni* did not display torpor in the mild winter examined here when food was plentiful.

Body temperature

The continuous long-term T_b measurements in this free-ranging pteropodid bat reveal a 24 h daily cycle in T_b with a higher T_b phase

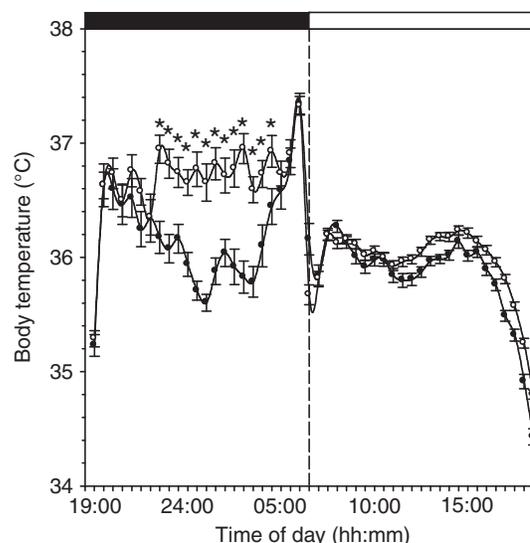


Fig. 6. Body temperature T_b of *N. robinsoni* during the new moon period (open circles, moon illumination of 0–50%) and the full moon period (filled circles, moon illumination of 51–100%). Values are means \pm s.e. of five individuals over a total of 98 recording days. Asterisks indicate significant differences between means (Tukey *post hoc* test, $P<0.001$) and the black bar indicates the scotophase.

during the night (i.e. activity phase) than during the day (i.e. rest phase), which is a prominent feature in many nocturnally active mammals (Refinetti, 1999). The highest T_b was observed towards the end of the activity phase and decreased towards the end of the rest phase (Fig. 2). While it has been shown that heterothermy is widespread in free-ranging insectivorous bats, with T_b well below 30 °C during the rest phase (Maloney et al., 1999; Turbill et al., 2003; Dietz and Kalko, 2006; Jacobs et al., 2007; Turbill et al., 2008; Turbill, 2009; Stawski et al., 2009), quantitative data on torpor in frugivorous pteropodid bats are only available for captive animals and then only for a few small (<30 g) species such as *N. albigularis*, *Paranyctimene raptor*, *S. australis* and *M. minimus* (Bartholomew et al., 1970; Geiser et al., 1996; Bartels et al., 1998). Contrary to anecdotal reports on captive individuals (Hall and Pettigrew, 1995), free-ranging *N. robinsoni* in our study showed no signs or tendency to enter even shallow torpor (with the exception of one bat after surgery as mentioned in Results). Evidently, like in other species, thermal energetics in mammals can differ substantially between the laboratory and the field (Körtner and Geiser, 2000; Geiser et al., 2007).

During our study in the tropical winter, daily T_a fluctuations were relatively small with the daily minimum T_a usually not falling below 15 °C (Figs 1 and 2) which would result in only a 2-fold increase of RMR over BMR (see below). Furthermore, although we did not explicitly collect data on food availability, fruit from various fruit trees such as *Ficus nodosa* were plentiful at all study sites. Bats travelled only very short distances between feeding sites and different roost locations, which is in accordance with earlier observations (Spencer and Fleming, 1989). These observations indicate that in contrast to a range of other pteropodid bats of various sizes, such as *S. australis* (~20 g), *Pteropus alecto* (~750 g), *P. conspicillatus* (~690 g) or *P. vampyrus* (~700 g), that travel long distances between their roost and feeding sites (Law, 1996; Palmer and Woinarski, 1999; Parsons et al., 2006; Epstein et al., 2009), *N. robinsoni* uses comparatively little energy for travelling, saving

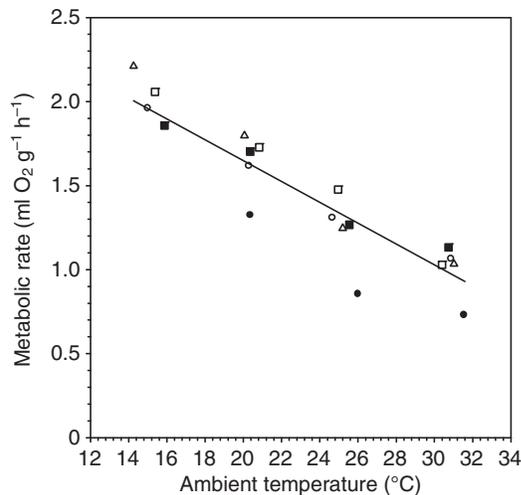


Fig. 7. Metabolic rate (RMR) measured as the rate of oxygen consumption of five tube-nosed bats (filled circles, bat 1; open squares, bat 2; open circles, bat 3; filled squares, bat 4; triangles, bat 5) in relation to ambient temperature ($RMR=2.89-0.062T_a$; $F_{1,17}=101.2$; $P<0.001$; $R^2=0.856$; $N=5$; $n=19$).

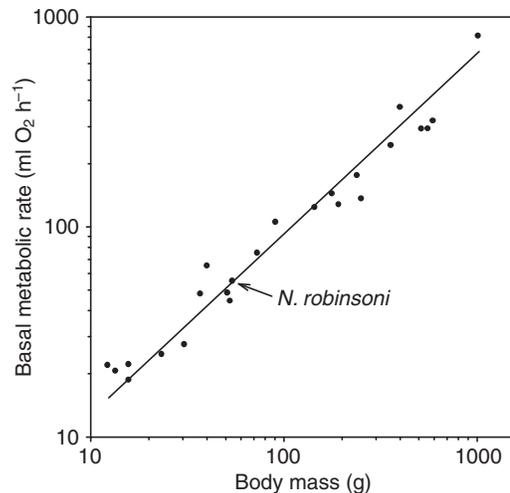


Fig. 8. Relationship between basal metabolic rate (BMR) measured as the rate of oxygen consumption and body mass (BM) for 24 pteropodid bats (including our data on *N. robinsoni*). The phylogenetically corrected allometric relationship is $BMR=1.76BM^{0.86\pm 0.05}$ ($F_{1,22}=406.5$, $P<0.001$, $R^2=0.949$, $N=24$) (see text for details).

energy for other activities. Consequently, the energy constraints experienced by free-living *N. robinsoni* in our study were probably not substantial enough to require a significant reduction in T_b and thus the use of torpor for energy conservation. Nevertheless, T_b in roosting (inactive) free-ranging *N. robinsoni* decreased from 36.2°C (06:30 h to 14:30 h) to the lowest daily average of 34.7°C (14:30 h to 18:30 h) and then sharply increased with the start of the active phase to 36.7°C in 1 h (18:30 h to 19:30 h). Although during the rest phase T_b remained initially high and was not affected by T_a , T_b was clearly correlated with T_a from approximately 10:30 h onwards until the active phase commenced (Fig. 5). *Nyctimene robinsoni* roosts mainly solitarily in the canopy of trees (Spencer and Fleming, 1989) (present data) exposed to natural fluctuations in T_a . This predicts a stronger correlation between T_b and outside T_a during the entire rest phase in contrast to bats which select roost sites with buffered microclimates such as caves or hollows. However, the initial stable T_b during the rest phase might result from the heat produced by digestion as bats most likely had full guts upon arrival at their roosting sites. Thus the short distances could mean that bats were potentially still digesting when reaching their roosting sites and consequently T_b remained high during the beginning of the rest phase. Furthermore, our T_b data show that bats were active right until the end of the night indicating foraging activity, as it has been observed previously for *N. robinsoni* (Spencer and Fleming, 1989).

Effect of the lunar cycle

The present study is the first investigating the effect of the lunar cycle on long-term T_b in a mammal. In our study moonlight had a significant effect on T_b . During the brighter full moon phase bats had significantly lower T_b at night than during the darker new moon phase (Fig. 6). These T_b differences during the lunar cycle probably reflect changes in the intensity of activity (Körtner and Geiser, 1995). It has been shown for many nocturnally active animals that with changing light conditions during the lunar cycle activity changes either due to predation risk or food/prey availability (e.g. Morrison, 1978; Daly et al., 1992; Brigham et al., 1999; Lang et al., 2006). As *N. robinsoni* is nocturnally active and relies on vision and smell

to detect its food sources (Spencer and Fleming, 1989; Hall and Pettigrew, 1995) it is possible that the lower T_b during the full moon period reflect a more efficient foraging due to better illumination. Thus using less energy for flying results in reduced T_b during the active phase. Alternatively, the lower T_b measured in *N. robinsoni* during the full moon period compared with the new moon period could also reflect a reduction in activity to avoid visually hunting predators (Lang et al., 2006; Presley et al., 2009), such as owls (e.g. *Tyto multipunctata*) (Law, 1997) and to a lesser extent snakes. For example, reduced activity during the full moon phase has been reported for frugivorous bats (Erkert, 1978; Haeussler and Erkert, 1978; Morrison, 1978; Morrison, 1980; Law, 1997; Presley et al., 2009; Elangovan and Marimuthu, 2001) and insectivorous bats (Lang et al., 2006). However, in insectivorous bats the relationship between activity and the lunar cycle seems to be more complex as they are both predator and prey (Lang et al., 2006). In contrast, frugivorous pteropodid bats rely on fruiting trees which attract a high number of bats, thus making them a predictable source for predators. By avoiding these areas during brightly illuminated full moon periods, bats may reduce their risk from predators. Although the two hypotheses on better vision for foraging or predator avoidance are not mutually exclusive, bat island populations do not seem to alter their activity in response to the lunar cycle in the absence of visually orientated predators (Gannon and Willig, 1997). Thus the predator avoidance hypothesis appears more likely for our study. Irrespective of the underlying reasons, the reduction of T_b to near-resting values will result in a reduction of energy expenditure during moonlit nights.

Metabolic rate

The measured BMR for *N. robinsoni* of 54.7 ml O₂ h⁻¹ is in the range of BMR values reported for similar-sized pteropodid bats (Bartholomew et al., 1964; Bartholomew et al., 1970; McNab, 1989; McNab and Bonaccorso, 2001) and was 98%, 86% and 84% of the predicted value from equations developed for Australian bats (Geiser, 2006), bats (Hayssen and Lacy, 1985) and mammals (White and Seymour, 2003), respectively. However, these equations do not

account for the phylogenetic signal in the bat data. Furthermore, to accurately predict values of missing species it is necessary to add the missing species into the tree (phylogeny) and then predict its value using the phylogenetic model. Therefore a new equation was developed for 24 pteropodid bat species [including values compiled by McNab and Bonaccorso (McNab and Bonaccorso, 2001) and our results on *N. robinsoni*] that controls for phylogeny using the PGLS approach. The resulting equation ($BMR=1.76BM^{0.86\pm 0.05}$, where BM is body mass) explains 95% of the variation in BMR and the predicted value for *N. robinsoni* ($55.1\text{ ml O}_2\text{ h}^{-1}$) was only 1% higher than the actual value ($54.7\text{ ml O}_2\text{ h}^{-1}$) (Fig. 8). The allometric relationship found by McNab and Bonaccorso ($BMR=2.14BM^{0.81}$), without taking phylogeny into account, differed only slightly from ours (see McNab and Bonaccorso, 2001). Therefore in the case of pteropodid bats, ordinary least squares regression and PGLS provide similar outcomes.

RMR at the lowest measured T_a of 15°C was approximately 2-times BMR ($1.95\text{ ml O}_2\text{ g}^{-1}\text{ h}^{-1}$) indicating only moderate thermoregulatory costs during the tropical winter, as for other similar-sized pteropodids, such as *Dobsonia* spp. (McNab and Bonaccorso, 2001). Based on the measurement of the RMR– T_a relationship ($RMR=2.89-0.062T_a$, Fig. 7) and the natural daily T_a cycle during our study (Fig. 2), the energy expenditure of *N. robinsoni* during the rest phase (06:30h to 18:30h) was 20.9 kJ, which is equivalent to 21% of the predicted total energy expenditure (i.e. field metabolic rate, FMR) per day (99.2 kJ) estimated from an equation for bats (Nagy et al., 1999). However, as mentioned above, values estimated from equations that do not include the missing species in the phylogenetic tree used to derive the equation need to be used with caution. Nevertheless, in the absence of FMR data in *N. robinsoni* the value of approximately 20% of the total energy expenditure used during the rest phase seems reasonable, considering that bats did not enter torpor. However, bats expended less energy during moonlit nights, indicated by their lower T_b , which would have a decreasing effect on the total energy expenditure per day and thus an increasing effect on the relative amount of energy expended during the rest phase.

CONCLUSION

Our study presents the first continuous long-term T_b measurements in a free-ranging pteropodid bat. Our data show that *N. robinsoni* has a distinct 24 h T_b cycle with higher T_b during the active phase than during the rest phase. *Nyctimene robinsoni* exhibits signs of lunar phobia, as the T_b during brighter moon illuminations was reduced to near-resting levels. Torpor does not seem to be commonly employed by this species, but we speculate that it may occur during adverse weather conditions or at the subtropical southern end of their distribution range.

LIST OF ABBREVIATIONS

BMR	basal metabolic rate
C	thermal conductance
FMR	field metabolic rate
PGLS	phylogenetic generalized least squares
RH	relative humidity
RH _{max}	maximum relative humidity
RH _{min}	minimum relative humidity
RMR	resting metabolic rate
T_a	air temperature
$T_{a,max}$	maximum air temperature
$T_{a,min}$	minimum air temperature
T_b	body temperature
$T_{b,max}$	maximum body temperature

$T_{b,min}$	minimum body temperature
\dot{V}_{CO_2}	rate of carbon dioxide production
\dot{V}_{O_2}	rate of oxygen consumption

ACKNOWLEDGEMENTS

We would like to thank Peter Salleras and Bob Brighton for their kind permission to capture bats on their properties and Clare and Margaret Stawski for helping with fieldwork. This work was supported by a research fellowship from the Alexander von Humboldt-Foundation to A.R. and by a grant from the Australian Research Council to F.G.

REFERENCES

- Abramsky, Z., Strauss, E., Subach, A., Kotler, B. P. and Reichman, A. (1996). The effect of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G. pyramidum*. *Oecologia* **105**, 313-319.
- Bartels, W., Law, B. S. and Geiser, F. (1998). Daily torpor and energetics in a tropical mammal, the northern blossom-bat *Macroglossus minimus* (Megachiroptera). *J. Comp. Physiol. B* **168**, 233-239.
- Bartholomew, G. A., Leitner, P. and Nelson, J. E. (1964). Body temperature, oxygen consumption, and heart rate in three species of Australian flying foxes. *Physiol. Zool.* **37**, 179-198.
- Bartholomew, G. A., Dawson, W. R. and Lasiewski, R. C. (1970). Thermoregulation and heterothermy in some of the smaller flying foxes (Megachiroptera) of New Guinea. *J. Comp. Physiol. A* **70**, 196-209.
- Bininda-Emonds, O. R. P., Cardillo, M., Jones, K. E., MacPhee, R. D., Beck, R. M., Grenyer, R., Price, S. A., Vos, R. A., Gittleman, J. L. and Purvis, A. (2007). The delayed rise of present-day mammals. *Nature* **446**, 507-512.
- Bowers, M. (1990). Exploitation of seed aggregates by Merriam's kangaroo rats: Harvesting rates and predatory risk. *Ecology* **71**, 2334-2344.
- Brigham, R. M., Gutsell, R. C. A., Wiacek, R. S. and Geiser, F. (1999). Foraging behavior in relation to the lunar cycle by Australian owl-nightjars *Aegotheles cristatus*. *Emu* **99**, 253-261.
- Butynski, T. (1984). Nocturnal ecology of the springhare, *Pedetes capensis*, in Botswana. *Afr. J. Ecol.* **22**, 7-22.
- Coburn, D. K. and Geiser, F. (1998). Seasonal changes in energetics and torpor patterns in the subtropical blossom-bat *Syconycteris australis* (Megachiroptera). *Oecologia* **113**, 467-473.
- Cryan, P. M. and Wolf, B. O. (2003). Sex differences in the thermoregulation and evaporative water loss of a heterothermic bat, *Lasiurus cinereus*, during its spring migration. *J. Exp. Biol.* **206**, 3381-3390.
- Daly, M., Behrends, P. R., Wilson, M. I. and Jacobs, L. F. (1992). Behavioral modulation of predation risk – Moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys miriamii*. *Anim. Behav.* **44**, 1-9.
- Dausmann, K. H., Glos, J., Ganzhorn, J. U. and Heldmaier, G. (2005). Hibernation in the tropics: lessons from a primate. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **175**, 147-155.
- Dietz, M. and Kalko, E. K. V. (2006). Seasonal changes in daily torpor patterns of free-ranging female and male Daubenton's bats (*Myotis daubentonii*). *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **176**, 223-231.
- Elangovan, V. and Marimuthu, G. (2001). Effect of moonlight on the foraging behaviour of a megachiropteran bat *Cynopterus sphinx*. *J. Zool.* **253**, 347-350.
- Epstein, J. H., Olival, K. J., Pulliam, J. R. C., Smith, C., Westrum, J., Hughes, T., Dobson, A. P., Akbar, Z., Sohayati, A. R., Misliah Mohamad, B., Field, H. E. and Daszak, P. (2009). *Pteropus vampyrus*, a hunted migratory species with a multinational home-range and a need for regional management. *J. Appl. Ecol.* **46**, 991-1002.
- Erkert, H. G. (1978). Sunset-related timing of flight activity in Neotropical bats. *Oecologia* **37**, 59-67.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **125**, 1-15.
- Gannon, M. R. and Willig, M. R. (1997). The effect of lunar illumination on movement and activity of the red fig-eating bat (*Stenoderma rufum*). *Biotropica* **29**, 525-529.
- Garland, T. and Ives, A. R. (2000). Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am. Nat.* **155**, 346-364.
- Garland, T., Harvey, P. H. and Ives, A. R. (1992). Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**, 18-32.
- Geiser, F. (2006). Energetics, thermal biology, and torpor in Australian bats. In *Functional and Evolutionary Ecology of Bats* (ed. A. Zubaid, G. F. McCracken and T. H. Kunz), pp. 5-22. New York: Oxford University Press.
- Geiser, F. and Coburn, D. K. (1999). Field metabolic rates and water uptake in the blossom-bat *Syconycteris australis* (Megachiroptera). *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **169**, 133-138.
- Geiser, F., Coburn, D., Körtner, G. and Law, B. S. (1996). Thermoregulation, energy metabolism, and torpor in blossom-bats, *Syconycteris australis* (Megachiroptera). *J. Zool.* **239**, 583-590.
- Geiser, F., Holloway, J. C. and Körtner, G. (2007). Thermal biology, torpor and behaviour in sugar gliders: a laboratory-field comparison. *J. Comp. Physiol. B* **177**, 495-501.
- Gilbert, B. and Boutin, S. (1991). Effect of moonlight on winter activity of snowshoe hares. *Arctic Alpine Res.* **23**, 61-65.
- Grafen, A. (1989). The phylogenetic regression. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **326**, 119-157.
- Hausler, U. and Erkert, H. (1978). Different direct effects of light intensity on entrained activity rhythm in Neotropical bats (Chiroptera, Phyllostomidae). *Behav. Proc.* **3**, 223-239.
- Hall, L. and Pettigrew, J. E. (1995). The bat with the stereo nose. *Aust. Nat. Hist.* **24**, 26-28.

- Hayssen, V. and Lacy, R. C. (1985). Basal metabolic rates in mammals-taxonomic differences in the allometry of BMR and body mass. *Comp. Biochem. Physiol. A Physiol.* **81**, 741-754.
- Jacobs, D. S., Kelly, E. J., Mason, M. and Stoffberg, S. (2007). Thermoregulation in two free-ranging subtropical insectivorous bat species: *Scotophilus* species (Vespertilionidae). *Can. J. Zool.* **85**, 883-890.
- Körtner, G. and Geiser, F. (1995). Body temperature rhythms and activity in reproductive Antechinus (Marsupialia). *Physiol. Behav.* **58**, 31-36.
- Körtner, G. and Geiser, F. (1998). Ecology of natural hibernation in the marsupial mountain pygmy-possum (*Burramys parvus*). *Oecologia* **113**, 170-178.
- Körtner, G. and Geiser, F. (2000). Torpor and activity patterns in free-ranging sugar gliders *Petaurus breviceps* (Marsupialia). *Oecologia* **123**, 350-357.
- Körtner, G., Song, X. and Geiser, F. (1998). Rhythmicity of torpor in a marsupial hibernator, the mountain pygmy-possum (*Burramys parvus*), under natural and laboratory conditions. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **168**, 631-638.
- Lang, A. B., Kalko, E. K. V., Romer, H., Bockholdt, C. and Dechmann, D. K. N. (2006). Activity levels of bats and katydidids in relation to the lunar cycle. *Oecologia* **146**, 659-666.
- Law, B. S. (1996). Residency and site fidelity of marked populations of the common blossom bat *Syconycteris australis* in relation to the availability of Banksia inflorescences in New South Wales, Australia. *Oikos* **77**, 447-458.
- Law, B. S. (1997). The lunar cycle influences time of roost departure in the common blossom bat, *Syconycteris australis*. *Aust. Mammal.* **20**, 21-24.
- Lockard, R. and Owings, D. (1974). Seasonal variation in moonlight avoidance by bannertail kangaroo rats. *J. Mammal.* **55**, 189-193.
- Lovegrove, B. G. and Raman, J. (1998). Torpor patterns in the pouched mouse (*Saccostomus campestris*; Rodentia): a model animal for unpredictable environments. *J. Comp. Physiol. B* **168**, 303-312.
- Maloney, S. K., Bronner, G. N. and Buffenstein, R. (1999). Thermoregulation in the Angolan free-tailed bat *Mops condylurus*: A small mammal that uses hot roosts. *Physiol. Biochem. Zool.* **72**, 385-396.
- Martins, E. P. and Hansen, T. F. (1996). The statistical analysis of interspecific data: a review and evaluation of phylogenetic comparative methods. In *Phylogenies and the Comparative Method in Animal Behaviour* (ed. E. P. Martins), pp. 22-75. New York: Oxford University Press.
- McNab, B. K. (1989). Temperature regulation and rate of metabolism in three Bornean bats. *J. Mammal.* **70**, 153-161.
- McNab, B. K. and Bonaccorso, F. J. (2001). The metabolism of New Guinean pteropodid bats. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **171**, 201-214.
- Morrison, D. W. (1978). Lunar phobia in a Neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera Phyllostomidae). *Anim. Behav.* **26**, 852-855.
- Morrison, D. W. (1980). Foraging and day-roosting dynamics of canopy fruit bats in Panama. *J. Mammal.* **61**, 20-29.
- Morrison, P. (1959). Body temperatures in some Australian mammals. I. Chiroptera. *Biol. Bull.* **116**, 484-497.
- Nagy, K. A., Girard, I. A. and Brown, T. K. (1999). Energetics of free-ranging mammals, reptiles, and birds. *Annu. Rev. Nutr.* **19**, 247-277.
- Palmer, C. and Woinarski, J. C. Z. (1999). Seasonal roosts and foraging movements of the black flying fox (*Pteropus alecto*) in the Northern Territory: resource tracking in a landscape mosaic. *Wildl. Res.* **26**, 823-838.
- Paradis, E., Claude, J. and Strimmer, K. (2004). APE: Analysis of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289-290.
- Parsons, J. G., Cairns, A., Johnson, C. N., Robson, S. K. A., Shilton, L. A. and Westcott, D. A. (2006). Dietary variation in spectacled flying foxes (*Pteropus conspicillatus*) of the Australian Wet Tropics. *Aust. J. Zool.* **54**, 417-428.
- Presley, S. J., Willig, M. R., Castro-Arellano, I. and Weaver, S. C. (2009). Effects of habitat conversion on temporal activity patterns of phyllostomid bats in lowland Amazonian rain forest. *J. Mammal.* **90**, 210-221.
- Refinetti, R. (1999). Relationship between the daily rhythms of locomotor activity and body temperature in eight mammalian species. *Am. J. Physiol.* **277**, R1493-R1500.
- Rohlf, F. (2001). Comparative methods for the analysis of continuous variables: Geometric interpretations. *Evolution* **55**, 2143-2160.
- Schmid, J. and Speakman, J. R. (2000). Daily energy expenditure of the grey mouse lemur (*Microcebus murinus*): a small primate that uses torpor. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **170**, 633-641.
- Scholander, P. F., Hock, R., Walters, V. and Irving, L. (1950). Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *Biol. Bull.* **99**, 259-271.
- Speakman, J. R. and Racey, P. A. (1991). No cost of echolocation for bats in flight. *Nature* **350**, 421-423.
- Spencer, H. J. and Fleming, T. H. (1989). Roosting and foraging behavior of the Queensland tube-nosed bat, *Nyctimene robinsoni* (Pteropodidae)-preliminary radio tracking observations. *Aust. Wildl. Res.* **16**, 413-420.
- Stawski, C., Turbill, C. and Geiser, F. (2009). Hibernation by a free-ranging subtropical bat (*Nyctophilus bifax*). *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **179**, 433-441.
- Teeling, E. C. (2009). Hear, hear: the convergent evolution of echolocation in bats? *Trends. Ecol. Evol.* **24**, 351-354.
- Turbill, C. (2009). Temperature effects on metabolic rate and torpor in southern forest bats (*Vespertilio regulus*). *Aust. J. Zool.* **57**, 125-127.
- Turbill, C., Law, B. S. and Geiser, F. (2003). Summer torpor in a free-ranging bat from subtropical Australia. *J. Therm. Biol.* **28**, 223-226.
- Turbill, C., Körtner, G. and Geiser, F. (2008). Timing of the daily temperature cycle affects the critical arousal temperature and energy expenditure of lesser long-eared bats. *J. Exp. Biol.* **21**, 3871-3878.
- White, C. R. and Seymour, R. S. (2003). Mammalian basal metabolic rate is proportional to body mass^{2/3}. *Proc. Natl. Acad. Sci. USA* **100**, 4046-4049.
- White, C. R., Blackburn, T. M. and Seymour, R. S. (2009). Phylogenetically informed analysis of the allometry of mammalian basal metabolic rate supports neither geometric nor quarter-power scaling. *Evolution* **63**, 2688-2667.
- Wolfe, J. and Summerlin, C. (1989). The influence of lunar light on nocturnal activity of the old field mouse. *Anim. Behav.* **37**, 410-414.