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Effects of reproductive status and high ambient temperatures on the body temperature of a free-ranging basoendotherm

Danielle L. Levesque · Kerileigh D. Lobban · Barry G. Lovegrove

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Abstract Tenrecs (Order Afrosoricida) exhibit some of the lowest body temperatures (T_b) of any eutherian mammal. They also have a high level of variability in both active and resting T_bs and, at least in cool temperatures in captivity, frequently employ both short- and long-term torpor. The use of heterothermy by captive animals is, however, generally reduced during gestation and lactation. We present data long-term T_b recordings collected from free-ranging *S. setosus* over the course of two reproductive seasons. In general, reproductive females had slightly higher (~32 °C) and less variable T_b, whereas non-reproductive females and males showed both a higher propensity for torpor as well as lower (~30.5 °C) and more variable rest-phase T_bs. Torpor expression defined using traditional means (using a threshold or cut-off T_b) was much lower than predicted based on the high degree of heterothermy in captive tenrecs. However, torpor defined in this manner is likely to be underestimated in habitats where ambient temperature is close to T_b. Our results caution against inferring metabolic states from T_b alone and lend support to the recent call to define torpor in free-ranging animals based on mechanistic and not descriptive variables. In addition, lower variability in T_b observed during gestation and lactation confirms that homeothermy is essential for reproduction in this species and probably for basoendothermic mammals in general. The relatively low costs of maintaining homeothermy in a sub-tropical environment might help shed light on how homeothermy could have evolved incrementally from an ancestral heterothermic condition.

Keywords Evolution of endothermy · Parental care · Thermoregulation · Reproduction · Heterothermy · Torpor · Madagascar · Tropics · *Setifer setosus* · Tenrec

Abbreviations

T_a	Ambient temperature measured via a black body apparatus
T_b	Core body temperature
T_{soil}	Ambient temperature measured at a depth of 250 mm below the surface
T_{tree}	Ambient temperature measured in a tree cavity
ΔT	Temperature differential ($T_b - T_a$)
T_{bmax}	Average of the 5 highest T_b data for each day
T_{bmin}	Average of the 5 lowest T_b data for each day
ΔT_b	Difference between the daily maximum and minimum T_b

Introduction

The reconstructed mammalian ancestor is postulated to have been small bodied, nocturnal and insectivorous (Crompton et al. 1978; Luo 2007; Gerkema et al. 2013; O'Leary et al. 2013), and is hypothesised to have possessed the capacity for prolonged periods of metabolic downregulation, torpor (Lovegrove 2012a). The plesiomorphy of

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D. L. Levesque (✉)
Institute of Biodiversity and Environmental Conservation,
Universiti Malaysia Sarawak, 94300 Kota Samarahan,
Sarawak, Malaysia
e-mail: lldanielle@ibec.unimas.my

D. L. Levesque · K. D. Lobban · B. G. Lovegrove
School of Life Sciences, University of KwaZulu-Natal,
P/Bag X01, Scottsville 3209, South Africa

torpor is supported by the prevalence of torpor expression in all major mammalian orders, including monotremes and marsupials (Grigg et al. 1989; Geiser 1994) and eutherian lineages with small-bodied representatives (Geiser and Ruf 1995; Lovegrove 2012b). The capacity for prolonged heterothermy, either in the form of daily torpor or hibernation (sensu Geiser and Ruf 1995), would have increased the chances of mammals surviving the harsh environments that followed the asteroid impact at the Cretaceous–Paleogene boundary (Robertson et al. 2004; Lovegrove 2012b). Furthermore, a propensity for large circadian variations in T_b, as well as the capacity for torpor are likely mid-points on the continuum between ectothermy and the highly regulated homeothermy seen in many modern mammal lineages (Crompton et al. 1978; Grigg et al. 2004; Lovegrove 2012b, a).

The study of extant mammals retaining ancestral endothermic characteristics, so-called "basoendotherms" (sensu Lovegrove 2012a), can help to understand how and why homeothermy evolved, given that it is an energetically costly form of existence. The spiny tenrecs of Madagascar (Order Afrosoricida, Subfamily Tenrecinae) are some of the best examples of extant eutherian basoendotherms (Eisentraut 1960; Crompton et al. 1978; Lovegrove and Génin 2008; Oelkrug et al. 2013). Members of this subfamily are insectivorous, primarily nocturnal, and have inhabited the sub-tropical island of Madagascar, where climates have remained fairly stable, since 55–35 mya (Eisenberg and Gould 1969; Douady et al. 2002; Olson and Goodman 2003). Well studied in captivity, the Tenrecinae have some of the lowest and most highly variable body temperatures (T_b), as well as the lowest basal metabolic rates, of any eutherian mammal (Stephenson and Racey 1995; Lovegrove 2000; Clarke and Pörtner 2010). It has recently been demonstrated that the lesser hedgehog tenrec (*Echinops telfairi*) possesses functional brown adipose tissue and has the capacity to actively rewarm from low T_bs during torpor (Oelkrug et al. 2013). However, the maintenance of a stable T_b in captivity is rare outside of gestation and lactation (Stephenson and Racey 1993a, b; Poppitt et al. 1994).

The restriction of homeothermy to periods of reproductive activity, more specifically to gestation and lactation, lends support to previous hypotheses that homeothermy evolved in mammals partially to benefit reproduction. Homeothermy could have evolved either via higher T_bs that promoted the maintenance of high and stable foetal growth rates (Parental Care Model, Farmer 2000), or by increasing the capacity for high levels of energy assimilation needed to provision the young (Assimilation Efficiency Model, Koteja 2000). To date, the only data available on the T_b patterns of free-ranging tenrecs are from the austral winter (Lovegrove and Génin 2008; Lovegrove et al. 2014), with no data available for reproductively active individuals. Thus, one of the primary aims of our study was to test the Parental Care and Assimilation Efficiency models and potential links between parental care and homeothermy using T_b data from free-ranging reproductive basoendotherms. According to the Parental Care Model (Farmer 2000, 2003), T_b would be maintained at a higher and more consistent level during gestation and lactation, whereas the Assimilation Efficiency Model (Koteja 2000, 2004) places emphasis on increases in homeothermy during the provisioning of young, particularly during the latter stages of lactation. We present the results of a 2 year study on the thermoregulation of a free-ranging population of greater hedgehog tenrecs (*Setifer setosus*, Schreber 1778) inhabiting the dry deciduous forest of western Madagascar.

Materials and methods

Study site, capture and surgical methods

The study was conducted over two rainy seasons, from September 2010 to February 2012, in the 'Jardin Botanique A' research area adjacent to the Ampijoroa Forestry Station in Ankarafantiska National Park (16°19′S, 46°48′E), Madagascar. The site is characterised by large seasonal variations in rainfall with a distinct dry season during the austral winter (April–November) with little or no rainfall, and 1,000–1,500 mm of rain falling primarily during the remaining months (data from the Durrell Wildlife Conservation Trust, Ampijoroa 1997–2012). A detailed description of the study site, population and general methods is provided in (Levesque et al. 2012, 2013). Ambient temperature (T_a) data were recorded at various locations throughout the study site using DS1922L Thermocron iButtons (Dallas Semiconductor, Dallas, TX, USA). A variety of configurations were used: black bodies and Stevenson Screens were placed 1 m from the ground in shaded areas and soil temperature was recorded at 0, 250 and 500 mm. In 2011 and 2012, iButtons were also placed at opposing ends of the study area in two tree cavities which had previously been used as nest sites by *S. setosus*.

All animals were caught by hand, with the help of local guides, by walking the established trails in the area at night. Individuals were housed in 15–30 L plastic containers lined with paper towel and provided with live insects and tinned sardines. They were kept for a maximum of 5 days before surgery to allow for the collection of metabolic data (Levesque and Lovegrove 2014). A subset of the individuals captured with a body mass >150 g (first season: 8 males, 6 females, second season: 3 males, 4 females) was subsequently implanted with a combination of a VHF radio transmitter and body temperature data logger (DS1922L Thermocron iButtons, Levesque et al. 2012). During the first season (September 2010–August 2011), two miniaturised iButtons (Lovegrove 2009) were encapsulated in surgical wax (Paramat Extra-Merck KGaA, Darmstadt, Germany) alongside a modified two-stage collar transmitter (Merlin Systems Inc., Boise, ID, USA). The resulting packages had a total mass of around 13.0 g (mean 13.0 g, range 11.7–13.5 g). During the second season (September 2011–February 2012), a single unmodified iButton was used which increased the mass of the implant to a maximum of 14 g while not affecting the size. The iButtons were programmed to record body temperature at 30 or 36 min intervals with an accuracy of 0.5 °C. All iButtons were calibrated against a mercury thermometer to the nearest 0.1 °C prior to implantation as well as post-recovery. No drift was observed. The package was implanted via ventral midline laparotomy undertaken under sterile conditions in an enclosed laboratory site at the research camp (Levesque et al. 2012). Animals were observed for 1 day post-surgery and released at the site of capture. Implanted animals were re-captured within a week of surgery to monitor proper recovery or to conduct corrective suturing if needed.

The transmitters used in the first season of this study were highly prone to malfunction, leading to the majority of the animals being lost to the study over the hibernation period (Levesque et al. 2012). If, however, the animal was successfully recaptured the data loggers were recovered using similar surgical procedures that were used to implant the loggers. A high level of natural mortality during the second season (Levesque et al. 2013) meant that recovery surgery was unnecessary and all data loggers were collected in the field after the animal's death.

Reproductive status and sample size

The use of modified iButtons for the first season resulted in a high rate of data loss. Of the three animals recovered post-hibernation (two males, one female), T_b data from the hibernation period were recovered from the female only (Levesque et al. 2013; Lovegrove et al. 2014). Only two functional data loggers were recovered from the active period of this first season. One, covering a period of 38 days, was recovered from a male after the transmitter package was regurgitated by a boa (*Acranthophis madagascariensis*). The second was obtained from a female who died while entering a narrow tree cavity (Levesque et al. 2012) after 28 days. The reproductive status of this female throughout the study was unknown.

Switching to a single unmodified iButton for the second season resulted in an improved recovery rate of T_b data. However, a smaller number of animals were captured throughout the season and high natural mortality (Levesque et al. 2013) limited the amount of data collected. Recordings were successfully obtained from two males and three females resulting in 92 animal-days for males and 180 for females, of which 121 were during gestation and 28 during lactation. The post-hibernation data from the female from the first season (18 days) are the only data available from the period immediately preceding hibernation in either season. As this individual was not followed for the remainder of the season, her reproductive status at the time of the recordings is unclear, although she was likely in the early stages of gestation at recapture (11 November).

The female with the longest period of data available (72 days) moved out of range of the study site for an extended period of time (~40 days) during which time she was presumed to have given birth. She was heavily pregnant before disappearing and, upon recapture, appeared in the early- to mid-stages of a second pregnancy. It is not known if she was successful in suckling her first litter until weaning. She fell prey to a snake (*Boa manditra*) in the later stages of the second pregnancy (Levesque et al. 2013). Neither of the females who remained in the study area throughout the recording period successfully reared a litter. One was killed by an unknown ground predator within 11 days of giving birth, whereas the other lost a litter to unknown causes after 12 days, and was later killed by a ground predator during the early stages of second pregnancy (Levesque et al. 2013).

Data analysis

All statistics were performed using R version 3.0.2 (R Development Core Team 2011) and linear mixed modelling was implemented using the *lme* function in the R package *nlme* (Pinheiro et al. 2013). The assumptions of the models, i.e. normally distributed residuals with a mean of zero, were verified by observing qq-plots and histograms of the residuals.

Ambient temperature

We compiled environmental temperatures, measured at 30–45 min intervals from the black body configuration (T_a), from those buried at a depth of 250 mm in the soil (T_{soil}) and, from the second season only, in tree cavities (T_{tree}). Exact sunrise and sunset times were obtained for each day from The United States Naval Observatory website (http://www.usno.navy.mil/USNO/). To account for the nocturnal activity pattern of the tenrecs, a day comprised of the period starting from sunrise of 1 day to the sunrise of the next. Recordings of T_a from 1 October to 10 February for each season were analysed for (a) trends in the mean daytime (rest phase) and nighttime (active phase) temperatures, (b) the maximum and minimum T_a (T_{amax}, T_{amin}, taken as an average of the five highest and five lowest, respectively), (c) the amplitude of daily temperature variability ($T_{amax} - T_{amin} = \Delta T_a$), and (d) the time of day of T_{amin} and T_{amax}. Frequency distribution tables were created with bin sizes of 0.5 °C. The proportion of time during which T_a was greater than the lower critical limit of thermoneutrality (25 °C, Levesque and Lovegrove 2014) was calculated, first for the entire day, and then for the daytime and nighttime periods separately. Differences in T_a between seasons as well as the effect of the 'day' (with 1 September as day 0) were tested with linear mixed models. T_a and T_{soil}, available from both seasons, constituted paired data which were controlled using (~1|'day/season') as the random structure. Autocorrelation between the data points was accounted for using the correlation structure corCAR1 with day as the time covariate (Pinheiro and Bates 2000).

Body temperature

A subset of the data from the three males with regards to torpor at high T_as has been previously published (Lovegrove et al. 2014), data from these individuals are included in the current analyses because of the different context. Each T_b datum was assigned the following markers, 'light' (nighttime or daytime based on sunrise and sunset times), 'day', 'sex', and, if female, 'reproductive status' (gestating, lactating, unknown). Data from the first week following the surgeries, the day of parturition ($n = 2$), as well as from the 3-to-4-day period during which the animals were housed in the laboratory for metabolic rate measurements (Levesque and Lovegrove 2014), were excluded from the analyses. In addition, a single high datum recorded for a gestating female (36.2 °C) was found to coincide with the exact moment of recapture in the field. This outlier was deemed to be the result of a stress-induced rise in T_b (Careau et al. 2011) and not representative of overall thermoregulatory patterns, and was therefore also excluded.

Using similar protocols to that of the T_a data analysis, the mean, max, min and ΔT_b as well as the time of day in which the maximum and minimum T_b occurred were calculated for each day for all individuals. Differences between seasons (using males only, $n = 3$) and reproductive status (using data collected from the second season only, 4 females and 2 males) as well as the effects of T_a and T_{tree} on T_b were performed via model selection using Akaike Information Criterion scores corrected for small sample size and Akaike weights (AICc and AICcWt, Burnham and Anderson 2002) implemented in the R package *AICcmodavg* (Mazerolle 2013). Repeated measures were controlled for using 'animal ID' as a random factor, and autocorrelation was corrected for using the correlation structure corAR1 in the form of ~1|'animal ID' (Zuur et al. 2009). All females of unknown reproductive status were excluded from this portion of the analysis. Torpor expression was quantified using the criteria determined by a concurrent study on resting metabolism (Levesque and Lovegrove 2014); a difference in T_b and T_a of <5 °C at T_as below the TNZ (<25 °C). A second analysis was performed using the lower 99 % confidence limit of a normal distribution with a standard deviation of 1 created around the mode T_b for each animal as the threshold T_b between torpor and normothermy (as per McKechnie et al. 2007). These analyses were performed three times, the first on full-day datasets, followed by a separate analysis of nighttime and daytime values.

Results

Ambient temperature

The T_a at the study site varied little, despite dramatic changes in precipitation between the dry austral winter (when *S. setosus* hibernates) and the wet summer (the reproductive season). T_{amax} remained above 30 °C throughout the year, although T_{amin} decreased during the dry season. Mean T_a collected during the active (summer) season did not differ between the two study seasons ($F_{1,129} = 0.05$, $p = 0.18$) but, after a slight increase followed by a plateau lasting from the end of October until early in December, significantly decreased over time ($F_{1,131} = 169.81$, $p < 0.001$). Similar patterns were seen in T_{amax} ($F_{1,131} = 550.43$, $p < 0.001$) which had a small (0.6 °C) but significantly higher mean in the first season ($F_{1,131} = 6.00$, $p = 0.016$). The opposite pattern was found in T_{amin} with the second season having slightly higher daily minima ($F_{1,131} = 27.5$, $p < 0.001$) and T_{amin} increasing significantly as the season progressed ($F_{1,131} = 62.86$, $p < 0.001$). T_{tree} was only available from the second season but showed similar decreases in both mean and maximum levels over time (mean: $F_{1,131} = 181.83$, $p < 0.001$, max: $F_{1,131} = 409.2$, $p < 0.001$) and an increase in minimum T_{tree} until day 100 ($F_{1,131} = 13.57$, $p < 0.001$), when it began to decrease. Patterns in T_{soil} were similar to T_{tree}, but showed oscillations with lower amplitudes and a mean (±SD) daily ΔT_{soil} of 0.65 ± 0.41 °C. All T_a values reached a peak around days 60–80 and decreased as the season progressed. Only 40 % of all recorded T_as were less than the lower critical limit of the thermoneutral zone (TNZ) of *S. setosus* (T_a ~ 25 °C) and of those only 1.2 % were below $T_a = 20$ °C. The upper critical limit of this species is unknown (but >32.5 °C, Levesque and Lovegrove 2014); however, a sizable percentage of the recorded T_a was above the highest modal T_b of 34 °C (17.3 %). Similarly, 54.9 % of all T_{tree} recordings occurred within the TNZ, with only 15.8 % above 30 °C and 29.1 % below the TNZ. The variability in T_{soil} was much less and 93.1 % of all recordings were in the TNZ with only 2.4 % falling below and 4.5 % reaching above 30 °C.

The mean time of day at which T_a reached its maximum was 13:32 (±1.2 h, range 08:43–17:02) and minimum T_a occurred at 04:45 (±1.6 h, range 20:13–09:35). Visual observations of the data indicated a large degree of overlap between seasons and an increase in variability as the season progressed, likely due to an increase in foliage and rainfall at the study site (Sato 2012). T_{tree} showed similar patterns to T_a, although with a slight delay, peaking at a mean time of 16:33 (±1.4 h, range 12:28–23:28) and reaching a minimum at 05:55 (±2.1 h, range 21:43–07:51). However, the time at min T_{tree} did not change throughout the season. T_s reached a maximum on average around 0:02 (±3.2 h, range 15:27–06:35), and a minimum at around 11:05 (±3.6 h, range 22:06–18:11). As with T_a, there did not appear to be differences between seasons but both max and min times became earlier as the season progressed.

Daily variations in T_b

T_b was highly variable and the difference between the daily maxima and minima (ΔT_b) ranged from 0.6 to 8.1 °C (mean: 2.6 ± 0.9 °C, $n = 312$, Table 1). Circadian rhythms were variable and while the majority of values of maximum daily T_b was recorded during the active phase and minimises during the rest phase, no overall pattern was visible either between or among individuals (Fig. 1). Active phase T_b showed slightly less variability than resting phase T_b (Fig. 2), ranging between 30 and 35 °C, compared with 26 and 36 °C during the rest phase. Daily modal T_b measured during the active phase ranged from 31.6 °C (the male from the first season) to 34 °C in a gestating female from the second season (Table 2) and was generally lower in the rest phase. 'Animal ID' was contained in all of the best ranking linear models analysing the mean, max and min T_b of males (Supplementary information Table A1). 'ID' was the only factor contained in the best-fitting model for T_{bmax} and T_{bmin}, whereas mean T_b was also influenced by T_a and 'day'. Only 'day' was contained in the best-fitting model for ΔT_b of the males (AICcWt = 0.56), although the second model containing only 'animal ID' had a large AICcWT (0.17). Insufficient data were available to make a comparison between seasons. There were, however, differences between all three males.

Comparing the data for males to those of females from the second season provided more conclusive results (Supplementary information Table A2). In all cases except for the standard deviation, T_{tree} provided a better fit to the data than T_a. However, although present in the top ranking

Table 1 Mean ± standard deviations of various parameters of T_b of *Setifer setosus* measured over two reproductive seasons

Status	Male	Female				
	Male ($N = 3$, $n = 96$)	Non-reproductive ($N = 1$, $n = 17$)	Gestating ($N = 3$, $n = 112$)	Parturition* ($N = 2$, $n = 2$)	Lactating ($N = 2$, $n = 27$)	Unknown* ($N = 2$, $n = 58$)
Mean T_b (°C)						
Mean	31.9 ± 0.7^{a}	32.5 ± 0.6^{a}	33.1 ± 0.3^{b}	32.8 ± 0.8	33.1 ± 0.7^{a}	33.2 ± 0.8
Range	30.2–33.1	30.5–33.2	32.5–34.1	32.2–33.3	31.8–33.8	30.6–34.1
SD T_b (°C)						
Mean	0.9 ± 0.3^{a}	1.0 ± 0.5^{a}	0.7 ± 0.2^{b}	1.4 ± 0.2	0.8 ± 0.2^{a}	0.9 ± 0.4
Range	0.4–2.3	0.5–2.5	0.3–1.3	1.3–1.5	0.4–1.0	0.3–3.1
Modal T_b (°C)						
Mean	31.6 ± 1.0^{a}	32.7 ± 0.6^{a}	32.9 ± 0.6^{b}	33.1 ± 1.6	33.0 ± 0.9^{b}	33.0 ± 0.9
Range	29.6–35.1	31.5–34.0	31.5–34.5	31.9–34.2	31.0–34.7	29.1–35.0
Min T_b (°C)						
Mean	30.6 ± 1.0^{a}	30.9 ± 1.3^{a}	32.1 ± 0.5^{b}	30.4 ± 0.6	31.8 ± 0.7^{b}	32.0 ± 1.3
Range	27.4–32.6	26.5–32.5	30.7–33.3	30.0–30.8	30.2–32.8	25.9–33.4
Max T_b (°C)						
Mean	31.9 ± 0.7^{a}	32.5 ± 0.6^{a}	33.1 ± 0.3^{a}	32.8 ± 0.8	33.1 ± 0.7^{a}	33.2 ± 0.8
Range	30.2–35.1	30.5–33.2	32.5–34.1	32.2–33.3	31.8–3.8	30.6–34.1
ΔT_b (°C)						
Mean	2.8 ± 0.9^{a}	3.0 ± 1.3^{a}	2.2 ± 0.6^{b}	4.4 ± 0.3	2.5 ± 0.5^{a}	2.5 ± 1.1
Range	1.1–7.1	1.5–6.8	1.0–3.9	4.2–4.6	1.3–3.4	0.6–8.1

Different lowercase letters indicate significant differences according to reproductive status

* Day of parturition was excluded from the statistical analysis due to a small sample size. Unknown refers to two females from different seasons, one which left the study site for an extended period of time during mid-late gestation, returning midway through a second pregnancy. Sample sizes are provided for the number of individuals (*N*) as well as the number of recording days (*n*)

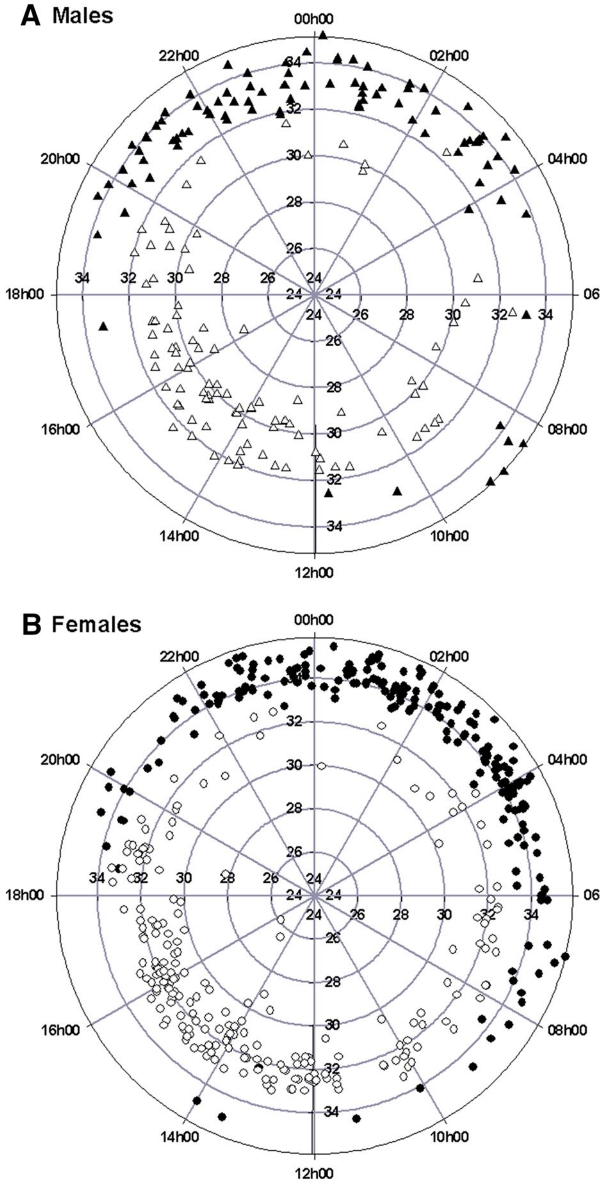

Fig. 1 Time of day (radians) at which maximum (*black*) and minimum (*hollow*) T_b (°C, distance from the centre) were measured in free-ranging. **a** Male (*triangles*) and, **b** female (*circles*) *Setifer setosus* in the dry deciduous forest of western Madagascar

models, neither T_{tree} nor T_a influenced T_b by more than ±0.08 °C. Gestating females had higher mean and modal T_b than males and the non-reproductive female (Table 1; Fig. 2) and mean T_b was influenced by T_{tree} (Supplementary information Table A2). 'Reproductive status' was not contained in the top ranking model describing T_{bmax} but was similarly influenced by T_{tree}. In contrast, neither of the environmental temperatures was included in the best model for T_{bmin}, and both gestating and lactating females had higher minimum T_bs (by 0.8–1.1 °C). Interestingly, only gestating, and not lactating females, had less variable T_bs than the non-reproductive individuals, supported by the analysis of both of the standard deviations and the ΔT_b (Table 1).

Torpor during the reproductive season

Using the criteria we established in a previous study on the thermoregulation of *S. setosus* (Levesque and Lovegrove 2014), torpor, outside of hibernation, was observed only on 11 out of 272 animal-days. Torpor bouts defined in this manner were observed in males, six by the first season male lasting 0.5–3 h with an average torpid T_b of 29.4 °C. In addition, torpor was expressed by the first season female on a single day with T_b decreasing as low as 25.6 °C, and by the non-reproductive female from the second season on the first 2 days following emergence from hibernation. A single torpor bout was also observed in a male in the second season (visible in Fig. 3a) which lasted 3 h before T_a increased above the 25 °C T_a threshold limit for torpor. A single bout lasting for a single recording point (30 min or less) was observed in one of the second season females on the day of parturition.

Torpor expression, evaluated using the threshold T_b obtained from the normal distributions around the modal T_b, provided slightly different results (Table 2). Using this definition, all but one of the bouts by the first season male mentioned above (with a threshold T_b of 28 °C) would be classed as rest phase decreases in T_b and not torpor. Higher incidences of torpor were reported in all other animals, all of which, with higher modal T_bs, had higher torpor threshold T_bs (30.0–31.2 °C). Torpor was more common during the daytime than at night. Both the lone female from the first season and the non-reproductive female from the second season expressed torpor on over 10 % of all recording days. The percentage of time spent in torpor was low (<1 %) for most of the remaining individuals. However, the total percentage of daytime T_as that fell below 28 °C (the lowest threshold T_b) over the entirety of two study seasons was only 34 % (another 31 % of which were above 34 °C, the highest modal T_b) and the mean T_a recorded at the time of each daily T_b minima was 28.1 ± 5.0 °C (range 19.2–39.1 °C) and T_{tree} was 25.8 ± 2.1 °C (range 20.9–32.1 °C).

A re-analysis of the respirometry data from torpid individuals presented in Levesque and Lovegrove (2014) indicated that it took anywhere from 1.75 to 7.74 h for animals to reach a steady-state T_b once exposed to an experimental temperature. The time to a steady state was dependent on T_a ($F_{1,32} = 6.20$, $p = 0.018$, $n = 33$) and the interaction between T_a and T_b ($F_{1,32} = 6.23$, $p = 0.018$, $n = 33$), but not body mass, which was not included in the best-fitting model. A subset of these data from 21 to 24 °C, matching the average minimum full-day T_a for the study site (~22 °C), showed that, regardless of T_b or mass, it took a mean time of approximately 3.77 ± 1.46 h ($n = 14$, range 1.75–6.99 h) for the animals to reach a steady state.

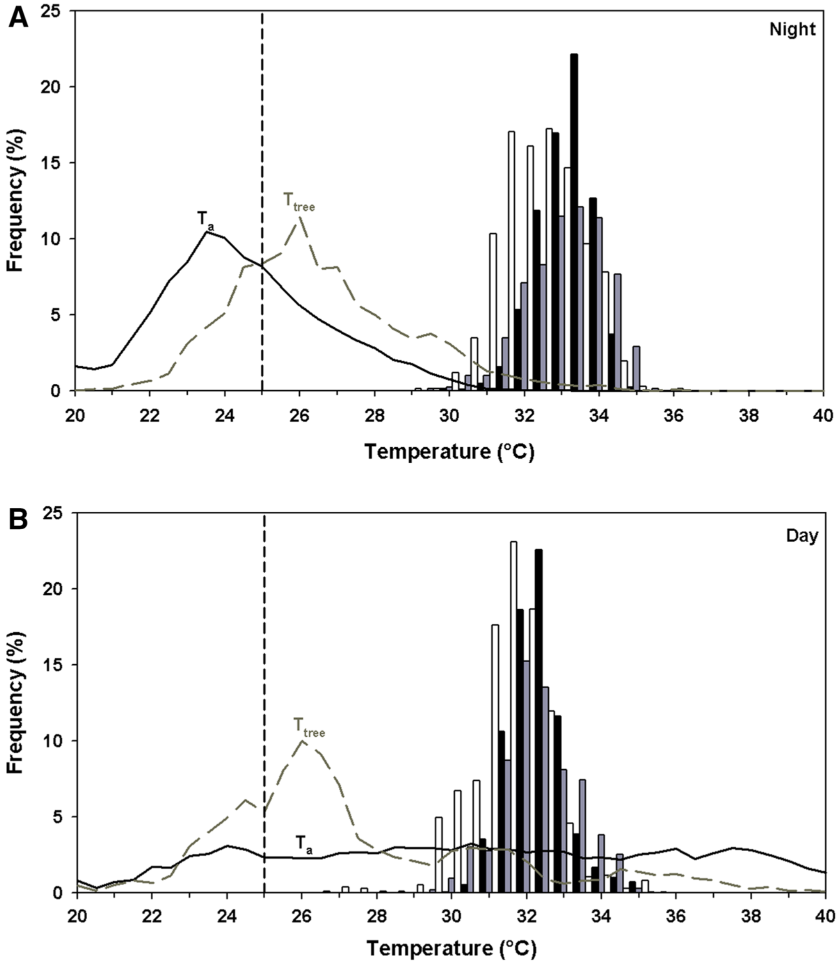

Fig. 2 Distribution of nighttime (active phase, **a**) and daytime (rest phase, **b**) body temperatures of male (*hollow bars*) and gestating (*black bars*) and lactating (*grey bars*) female *Setifer setosus*. Environmental temperature distributions are indicated by the *black lines* (T_a) and the *dashed grey lines* (T_{tree}) and the lower critical limit of the thermoneutral zone is marked via a *dashed vertical line*

Table 2 Modal T_b for each individual *Setifer setosus* during the active season

	First season		Second season					
	SF11	SF17	SF07	SF22	SF23	SF24	SF25	SF26
Number of days	$n = 27$	$n = 36$	$n = 17$	$n = 68$	$n = 31$	$n = 73$	$n = 42$	$n = 18$
Sex	Female	Male	Female	Female	Female	Female	Male	Male
Modal T_b (°C)								
Full 24 h	32.6	30.6	33	33	33.8	33.4	32.6	32
Night	33.6	31.6	33.5	34	33.8	33.4	33.1	32
Day	32.6	30.6	32.5	33	32.8	32.4	32.1	31.5
Threshold T_b (°C)								
Full 24 h	30.0	28.0	30.4	30.4	31.2	30.8	30.0	29.4
Night	31.0	29.0	30.9	31.4	31.2	30.8	30.5	29.4
Day	30.0	28.0	29.9	30.4	30.2	29.8	29.5	28.9
Time $T_b <$ threshold T_b (%)								
Full 24 h	4.0	0.0	4.9	0.0	0.7	0.8	0.5	1.1
Night	3.3	0.0	1.5	0.1	0.3	0.8	0.0	0.0
Day	12.2	0.9	11.8	0.1	1.0	0.8	1.6	2.0

Values are provided for night time (active phase) and daytime (rest phase) and full day. The threshold T_b for torpor expression was calculated using the 99 % confidence limit of a normal distribution around the modal T_b with a standard deviation of 1

Assuming that nighttime activity ceased between 04:30 and 05:30 (Levesque et al. 2013), T_b would reach equilibrium with T_a anywhere between 08:00 and 09:40, by which time the mean T_a at the site was already 27.3 ± 2.3 °C ($n = 132$, range 22.4–32.5 °C) and T_{tree} was 26.6 ± 2.4 °C ($n = 132$, range 22.5–29.7 °C); both of these ambient temperatures

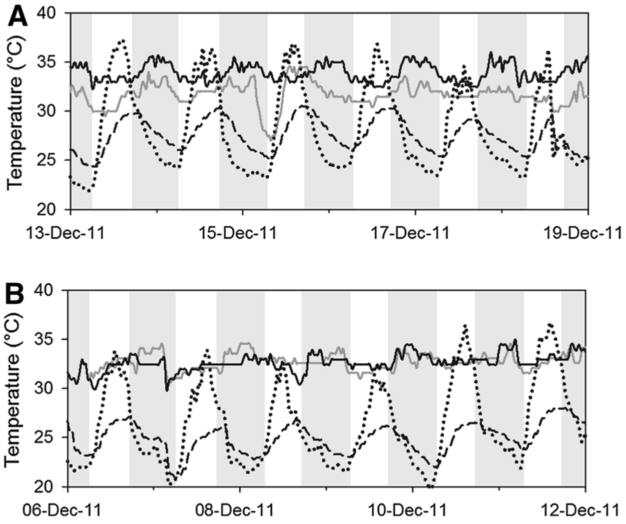

Fig. 3 Sample traces of T_b of free-ranging *Setifer setosus*. Females (*black lines*) had generally higher, less variable, T_b than males (*grey lines*), more so during gestation (**a**) than during lactation (**b**). Torpor expression was highly limited by high environmental temperatures, both air (*dotted line*) and from a former nest site in a tree cavity (*dashed line*)

fall within the TNZ. Similarly, the temperature 250 mm below the ground surface (at a similar depth to 7.4 % of all nest sites occupied during the second season, Levesque et al. 2012) rarely fell below 25 °C, the lower limit of the thermoneutral zone, at any time. T_a increased throughout the day, leading to a corresponding increase in T_b (Fig. 3).

In terms of potential torpor use, increases in T_a prevented T_b decreasing far below 27 °C, making it almost impossible to detect torpor accurately unless, as was likely the case with the male (Fig. 3a), activity ceased early in the night (before 03:00). In addition, on a number of occasions, mainly in the early-to-middle parts of the season (before the decrease in T_a seen around day 100), multiple instances of putative "hyperthermic daily torpor" were observed. This hypothetical form of torpor (see Lovegrove et al. 2014) occurs when torpor bouts initiated at the end of the nocturnal activity period continues beyond the point where T_a increases above T_b leading to greater T_bs during the rest phase. In fact, on 13.3 % of all recording days, the max rest-phase T_b of an animal was higher than its individual modal T_b for the active phase (~34 °C). These instances are clearly visible in Fig. 1 and fall mostly between noon and 18:00. On many of these days, T_b decreased with the commencement of activity as can be seen around 15 December in the trace from the male in Fig. 3a.

Discussion

T_b datasets from free-ranging animals in warm climates are valuable but rare. This study presents a long-term dataset of core T_b collected from a species of free-ranging basoendotherm during reproduction, in an environment where T_a routinely increases above T_b. We report a number of novel findings. First, data obtained from reproductive females confirmed the results of laboratory studies on similar species and demonstrated an increase in the degree of homeothermy during both gestation and lactation (Stephenson and Racey 1993b; Poppitt et al. 1994). Second, the level of torpor use by free-ranging *S. setosus* during the active (reproductive season) was much lower than expected based on previous studies in the laboratory.

Circadian rhythms in T_b are a characteristic of all endotherms, with T_b decreasing during the rest phase and usually increasing at the onset of activity. The level of T_b variability during the rest phase is often dependent on T_a (Aschoff 1981; Refinetti and Menaker 1992), although this is amplified in some species compared to others (Refinetti 1998). One of the characteristics of basoendotherms (Lovegrove 2012a) is that T_b is highly variable and that the distinction between normothermy and rest-phase decreases in T_b is often indistinct (Kuchel 2003; Grigg et al. 2004; Canale et al. 2012a). For example, *E. telfairi* held in captivity over a range of T_as showed rest-phase decreases in T_b that ranged from slight transient decreases (to ~28 °C from 31 °C) at a T_a of 27 °C, to larger more profound decreases (clear incidences of torpor) at lower T_as. The patterns we observed in *S. setosus* more closely mirrored that of *E. telfairi* housed at 27 °C, despite a wider range of T_a present at the study site. Interestingly, the time of day at which T_b reached either a maximum or a minimum was unrelated to the peaks in T_a, and all the parameters of environmental temperature showed very little influence on the extreme T_bs. However, thermal inertia and the large daily changes in amplitude in both T_a and T_{tree} can explain these patterns. These large increases in environmental temperatures occasionally led to rest-phase T_b increasing above the active phase T_b. Although this pattern is fairly novel, it has now been observed in a number of species (Lovegrove et al. 2014) and is likely to become more common as T_b data are collected from more species of nocturnal, tree-nesting mammals inhabiting warm climates.

In addition to smaller daily variations in T_b, torpor expression in *S. setosus* was much lower than expected based on previous studies of captive animals. Despite the fact that torpor expression is often underestimated in the laboratory (see Geiser et al. 2000 for a review), our data represent one of the few cases where the opposite pattern was observed. This is primarily due to the interactions with environmental temperatures, however, and not the physiological characteristics of this species per se. The results clearly demonstrate that the T_a at the study site was not conducive to low T_b during torpor. Even during hibernation, T_b closely tracked T_a throughout hibernation and increased to above 30 °C every day (see Fig. 1.A in Lovegrove et al. 2014). Interestingly, the highest T_bs measured in *S. setosus* (>36 °C) occurred on two occasions during hibernation, both immediately preceding a change in T_b amplitude which in a hibernating lemur (*Cheirogaleus medius*) was indicative of a change in nest site (Dausmann et al. 2005). However, high T_b measured during torpor does not necessarily negate metabolic downregulation, and significant energy savings from torpor at high T_as (32–35 °C) have been demonstrated in a species of spiny mouse (*Acomys russatus*, Grimpo et al. 2013).

The use of heterothermy in warm climates comes at a relatively low cost as high temperatures facilitate passive rewarming compared with the more energetically costly active rewarming necessary in colder climates (Lovegrove et al. 1999; Canale et al. 2012a). Nevertheless, despite a reliance on exogenous passive heating, functional brown adipose tissue has been recorded in *E. telfairi* (Oelkrug et al. 2013) and earlier studies indicate that *S. setosus* also possess the ability to actively rewarm from torpor (Kayser 1960; Hildwein 1964). However, the need for active rewarming from torpor was completely unnecessary in this study, even during hibernation (see Lovegrove et al. 2014), passive rewarming was employed. *S. setosus* can be active at T_bs as low as 28 °C (Eisenberg and Gould 1969; Crompton et al. 1978), after which point activity itself may be used as a means of heat production (see Lovegrove and Génin 2008; Humphries and Careau 2011). Thus, arousal from torpor in this species occurs at a comparatively lower cost than it does in typical daily heterotherms. It should be noted, however, that the body mass of the animals in the Crompton study was suspiciously low (~120 g), indicating the use of either juveniles or *E. telfairi*.

Difficulties in distinguishing resting T_bs from active T_bs and torpor from normothermy also occurred in another basoendothermic mammal, the echidna (*Tachyglossus aceulatus*, Order: Monotremata) in semi-tropical Queensland (Kuchel 2003). Echidnas are characterised by their low and highly variable T_b (Grigg and Beard 2000; Nicol and Andersen 2006; Brice 2009) and during the warmer summer months, the distinction between normal rest-phase decreases in T_b and short torpor bouts is difficult to discern. The T_as reported were lower than those measured here, and echidnas shelter underground, where T_as remain below normothermic T_bs year-round allowing for larger decreases in T_b than we recorded in *S. setosus*. The substantial variability in echidna T_b led Kuchel (2003) to suggest caution in defining torpor based on T_b patterns (i.e. T_b above or below a certain threshold) and suggested the use of mechanistic properties, such as metabolic rate or heart rate, instead of T_b. A greater push for mechanism-based definitions of torpor has received more attention as T_b patterns of free-ranging individuals from a wider range of environments become available (Boyles et al. 2011; Canale et al. 2012a). A single value for T_b can occur during many different metabolic states (Brice et al. 2002; Canale et al. 2012a) and activity can occur at surprisingly low T_b (Kuchel 2003; Rojas et al. 2012; Turner et al. 2012). It has been suggested that more studies should attempt to measure field metabolic rate or employ other more accurate proxies for metabolism such as heart rate (Anderson and Jetz 2005; Speakman and Krol 2010; Canale et al. 2012a; Boyles et al. 2013).

Even while torpid, it appears that individual *S. setosus* have some control over rest-phase T_b, as the choice of nest site has a large impact on their thermal environment (Dausmann et al. 2005, 2009). Behavioural means of avoiding torpor have been reported for a primate from mainland Africa, *Galago moholi* (Nowack et al. 2013), as well as from a number of temperate heterotherms whose choice of hibernacula can vary according to sex or reproductive condition (Buck and Barnes 1999; Willis and Brigham 2005). Interestingly, only a small percentage (7.4 %) of nest sites observed during the first season was below ground (Levesque et al. 2012). A large number of nest sites were fully or partially exposed such that T_bs were equal to the T_{tree} measurements or somewhere between T_{tree} and T_a. Thus, on the majority of days, the animals chose a thermal environment that would actively prevent the opportunity for low T_b during torpor. The increased costs of low T_b—high costs of rewarming and potentially lower vigilance due to increased lethargy—presumably outweigh the minimal benefits of a slightly lower T_b during torpor (Bieber et al. 2014).

The respirometry measurements we obtained demonstrated that gestation and lactation resulted in a decrease in heterothermy, both in terms of an overall decrease in T_b variability (during gestation), as well as a decrease in torpor use (during both stages of reproduction), in female *S. setosus* (Levesque and Lovegrove 2014). Torpor has been recorded in pregnant tenrecs in captivity, but its usage is rare compared with heterotherms from more temperate climates (Nicoll and Thompson 1987; Stephenson and Racey 1995; Willis et al. 2006). Temperate heterotherms have been shown to use torpor to extend gestation so that lactation, the most energetically costly stage in the life history of female mammals (Clutton-Brock et al. 1989), coincides with peak food availability (Richard et al. 2002; Willis et al. 2006) or with more favourable environmental conditions (Morrow and Nicol 2009). Torpor during reproduction has also been found in response artificially induced caloric restriction (Canale et al. 2012b). In the current study, torpor was only observed on two occasions during reproduction, both in the same female during the early stages of gestation during the second season 46–49 days prior to parturition (Levesque and Lovegrove 2014) and at T_as much lower than those commonly observed at the study site (14 and 21 °C).

Torpor in lactating females, however, cannot conclusively be ruled out. Two of the females in the second season showed a pronounced decrease of around 1–2 °C below normal rest-phase T_bs on the estimated date of parturition. T_b recordings from these individuals during lactation were only available for short periods of the time as both mothers were killed by predators before their litters were weaned. Interestingly, two females during the first season spent very little time active during lactation. One female did not leave the nest site at night for an entire month (discussed in Levesque et al. 2013). Although no T_b data are available to confirm the use of torpor over this time period, given the environmental conditions and the fact that both females maintained a relatively steady body mass throughout lactation, it seems likely. More data are necessary to conclude whether or not torpor is common during lactation in tenrecs.

The effects of reproduction on thermoregulation by males were more difficult to determine, as it is not possible to measure the reproductive status of males due to the lack of external testes (Petter and Petter-Rousseaux 1963; Kleisner et al. 2010). Elevated levels of testosterone in reproductively active males have been shown to reduce torpor expression (Mzilikazi and Lovegrove 2002; Fietz et al. 2010). Likewise, warm temperatures are necessary for spermatogenesis (Barnes et al. 1986; Kleisner et al. 2010). However, only short periods at normothermic temperatures are necessary for adequate sperm production (Fowler and Racey 1987) and the high rest-phase T_as experienced by this population would negate any potential negative effects of torpor on spermatogenesis. Therefore, torpor avoidance for these reasons is not likely. Brown adipose tissue deposits have been found surrounding the reproductive organs of *E. telfairi,* which indicates the potential utility of warming this area in habitats with colder T_as (Oelkrug et al. 2013) but the high T_as to which tenrecs were exposed in our study offsets the necessity of physiological means of maintaining high T_bs.

Conclusion

This study confirmed that *S. setosus* show a large degree of heterothermy, in terms of both torpor and in daily T_b variations. The thermoregulatory patterns of this species, a tropical basoendotherm, stand in sharp contrast with those of most high-latitude species. Whereas the latter group (meso- and supraendotherms sensu Lovegrove 2012a) maintains elevated T_bs over a wide range of T_a, primarily through physiological mechanisms, and homeothermy is the norm, *S. setosus* rather rely on T_a to regulate T_b, and thermolability is the norm. Similar to what we have reported from previous respirometry experiments (Levesque and Lovegrove 2014), reproduction and high T_a were causes for an increased level of homeothermy in this species. Increases in homeothermy during reproduction have been observed in other species with basoendothermic characteristics, such as echidnas (Beard and Grigg 2000; Nicol and Andersen 2006) and sloths (*Bradypus griseus*, Morrison 1945). Our findings provide support, albeit limited, for the Parental Care Hypothesis (Farmer 2000) in that gestating, and to a lesser extent lactating, females had higher and less variable body temperatures than the other animals. The lack of data from the latter stages of lactation, as well as the lack of information on changes in metabolism during that time, precludes discussion of the Assimilation Efficiency Model. It is worth noting, however, that neither hypothesis is mutually exclusive (Koteja 2004; Kemp 2006), nor and more comprehensive studies are necessary. In addition, our data along with a small sample of skin temperatures from tarsiers (*Tarsius syrichta*) presented in Lovegrove et al. (2014) are the only studies, to our knowledge, to observe how T_as at or near T_b affect thermoregulation in basoendotherms. Both of these datasets show that high T_a can reduce the opportunities for low T_b during torpor and potentially mask the physiological state of the animal (Canale et al. 2012a; Lovegrove et al. 2014).

Interestingly, females in the population we studied hibernate for at least 5 months and can give birth to up to three litters in a single season, while simultaneously accumulating sufficient fat reserves (>100 g) for the subsequent hibernation period (Levesque et al. 2012; 2013). Low thermoregulatory costs, combined with high levels of food availability, likely contribute to the high energetic outputs observed. Our findings show that the increase in homeothermy observed in captive tenrecs during reproduction does indeed occur in the wild, where, although food availability is not likely to be equal to ad libitum food, T_a can be much more favourable. Along with data collected from incubating echidnas (Beard and Grigg 2000; Nicol and Andersen 2006) as well as gestating sloths (Morrison 1945), our data provide further support for the hypotheses which link reproduction to the evolution of endothermy in mammals. The thermal environment of the study site was conducive to the maintenance of a high and stable T_b, with little additional energetic cost of thermoregulation. Slight increases in homeothermy during reproduction in similarly warm habitats were therefore a probable first step along the progressive evolution from heterothermic to homeothermic endothermy (Kemp 2006; Lovegrove 2012a).

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