Daily rhythms of body temperature and activity in free-living Black-tailed Tree Rats (*Thallomys nigricauda*) along an aridity gradient

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ABSTRACT

Since Black-tailed Tree Rats, *Thallomys nigricauda,* face variable thermal environments in their extensive range in southern Africa, variation in their physiological and behavioural responses to the wide range of ambient temperatures (T_as) was expected to play a role in the success and range of the species. Body temperature (T_b) and activity patterns of free-ranging Tree Rats were investigated during winter and summer at three study sites along an aridity gradient. We measured abdominal T_b using implanted iButtons®. All but three Tree Rats displayed significant 24 h T_b rhythmicity. The T_b range for Tree Rats was 32.33–40.63 °C ($n = 13$) and 32.69–40.15 °C ($n = 17$) in winter and summer respectively. Although there was variation in T_b profiles, Tree Rats generally displayed a bimodal distribution of T_b, with high and low T_b values during scotophase and photophase respectively. Site had no effect on the range of T_b in winter. Range in T_b was significantly greater in winter, when Tree Rats reduced their minimum T_b. Maximum amplitudes of daily rhythms of T_b were 259.7% of expected values. Temperatures of cavities were more stable compared with operative temperature. In winter male Tree Rats spent a significantly greater proportion of the active phase away from their home cavity compared with females. It is suggested that the energy savings in Tree Rats are a result of a combination of physiological and behavioural mechanisms allowing them to maintain nocturnal activity in winter and overall energy balance.

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1. Introduction

Terrestrial habitats represent the most complex and variable thermal environments on earth [1]. Endotherms have achieved a high degree of independence from the restrictions imposed by ambient temperature (T_a), but this advantage comes at a high energetic cost [2]. These high costs in endotherms are pronounced in small species and thus small endotherms must spend most of their daily energy budget on thermoregulation. Thus the thermal independence gained by endogenous heat production is substituted by energetic constraints as they need to replenish body fuels [2].

When challenged energetically under conditions of low T_a or decreased food supply, some small species use physiological mechanisms to minimise energy expenditure, reducing the cost of euthermy [2]. Black-tailed Prairie dogs, (*Cynomys ludovivianus*), for example, respond by allowing body temperature (T_b) to fluctuate with ambient conditions [3]. Other mammals, for example Eastern Gray Squirrels (*Sciurus carolinensis*) respond by lowering T_b [4]. Numerous small mammals decrease their T_b during the rest phase [5,6] thereby saving considerable amounts of energy [7]. This decrease results in a lowered minimum T_b and increases the amplitude or body temperature range (T_b range).

Aschoff [8] showed that, for mammals (non-primates), there is an allometric relationship between body size and the maximum amplitude of the circadian increase in T_b between an animal's daily rest and activity phase (R_t). There are typically large differences between rest and active phase T_b values in animals that are strictly diurnal or nocturnal [9], which translates into high R_t values, usually associated with energy savings through metabolic rate depression during the rest phase [10]. Moreover, high R_t values are regarded as adaptive in environments with low productivity or variable energy inputs in time and space [11,12].

In addition to endogenous thermoregulatory responses, some mammals make use of behavioural responses to T_as, suggesting that behavioural thermoregulation also plays a role in the fluctuation of T_b of an animal in its environment [13]. Behaviour is sometimes the primary means by which an animal copes with an environmental challenge [14], particularly for small mammals living in areas with wide ranges in temperature [15]. Activity periods are important components of behaviour, since they determine the length of exposure to surface conditions [16] and variability in the thermal environment could influence activity, which could have fitness consequences for animals [17].

Nocturnalism allows small mammals to avoid daytime predators and high temperature stress [18,19], but they are then limited to foraging at night. The reduced time available for energy intake presents an additional challenge since their normothermic MR is high even when resting, especially at low T_a [2]. The demands that influence how an animal allocates its time budget to different activities in the active phase

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are often conflicting, activity needed to fulfill reproductive and dietary needs (see above) while minimizing environmental costs and risks [20,21]. Moreover, individual characteristics, for example sex, may influence daily patterns of activity, possibly reflecting differences in the reproduction investment of both sexes [22].

Seasonal patterns of activity of rodents are influenced by changes in photoperiod and temperature [23–25]. The capacity for thermogenesis and energy intake is especially important for the survival of small nocturnal mammals in winter [26] when the principal thermoregulatory problem is coping with very low night-time temperatures [27] which increases the cost of both thermoregulation and foraging [26,28]. This challenge may be particularly important for non-hibernating small mammals since they lose heat rapidly and need to consume large amounts of food [21]. In such cases, in addition to physiological mechanisms discussed, additional behavioural mechanisms can be expected to occur [29,30]. Animals may make use of buffered refugia resulting in energetic benefits to the inhabitants [31,32] in addition to reducing the cost of foraging [33,34]. Moreover, animals may huddle in refugia, thereby further reducing heat loss [35].

Thallomys nigricauda, the Black-tailed Tree Rat (hereafter referred to as Tree Rat), is a relatively small (32–116 g) arboreal, nocturnal, murid rodent, occurring in mesic to xeric regions of South Africa, Botswana, Swaziland, Zimbabwe and Namibia [36]. They are folivores, feeding on young *Acacia erioloba* leaves and fine twigs and the outer green coating of seed pods, but may supplement their diets with insects and gum [36,37]. Earlier reports have suggested that Tree Rats have a promiscuous mating system [38], with young being born during the summer months [36]. While the vast majority of rodent species evade the harsh conditions by burrowing, Tree rats have adopted an arboreal lifestyle with nests situated in forks and hollows of trees (mainly *A. erioloba*) [36]. It is expected that Tree rats are exposed to greater temperature fluctuations in their arboreal nests compared to most other southern African xeric rodents which use subterranean microhabitats with stable milieux to escape daytime heat [36,37,39,40]. Moreover, since their wide distribution includes mesic, semi-xeric and xeric regions, it is also expected that sub-populations are exposed to different degrees of thermal stress. Hence we expected that Tree Rats would exhibit variation in physiological and behavioural traits in response to the thermal environment measured along an aridity gradient.

As part of a broader study of aspects of the physiology and behaviour of the Tree Rat, the aims of the current study were to (i) measure and describe T_b daily rhythms, (ii) determine whether these rhythms differed along an aridity gradient and between seasons (iii) determine and compare cavity temperatures with operative temperature (T_e), and (iv) to determine and compare activity patterns between sexes and seasons. We predicted that Tree Rats from xeric and semi-xeric sites would have a greater T_b range in winter when compared to individuals from the mesic site and that across all individuals, the T_b range would be greater in winter when compared to summer. In addition, we predicted that cavity temperatures would buffer T_e and that maintenance of T_b would influence activity patterns.

2. Materials and methods

2.1. Study sites

The study was conducted at three sites along an east–west aridity gradient [41,42]: mesic locality Weenen Game Reserve (KwaZulu-Natal Province, South Africa, 28°50′43″S; 29°59′12″E); semi-xeric site Haina Game Farm (Botswana 20°56′56″S; 23°40′40″E) and xeric site Molopo Nature Reserve (southern Kalahari savannah, North–West Province, South Africa 25°50′52″S; 22°55′37″E) [43]. Degree locations were plotted using a Magellan GPS 4000 XL. Vegetation, rainfall and temperature data for the three sites are detailed elsewhere [43]. Aridity index data for the three sites are presented elsewhere [43].

2.2. Daily rhythms of body temperature (T_b)

Tree Rats were trapped at each study site during winter (May–July) in 2006 and 2007 and in summer (January–February 2007) using Elliot live-traps. Cavities and resting places of Tree Rats were recognised by examining the stems and bases of trees with potential cavities for faeces and the smell of excreta. Traps were also placed at sites where study animals had been previously seen and/or trapped. Traps were placed on the branches and at the base of potential trees and baited with oats and peanut butter. Traps were set in the late afternoon, checked shortly after sunrise and removed from trap sites. An average of 79 ± 3.2 traps was set per night at each study site, with a mean trap rate of 8 ± 1.0. Juvenile (<40 g) and lactating Tree rats were immediately released. Tree Rats were transported to a veterinarian within 36 h of capture. Rats were sexed, weighed, ear clipped and reproductive status was noted. Tree Rats (>40 g) were anaethesized using isoflorthane (2%, Safeline Pharmaceuticals, Johannesburg) or Anakel-V (100 mg/ml) and Chanazine (20 mg/ml).

Body temperatures were measured with surgically implanted precalibrated temperature dataloggers (DS 1922L Thermochron iButtons® (Dallas SemiConductor, Maxim, Sunnyvale, CA). These miniature dataloggers were encapsulated in stainless steel caps with a thermometer (measured to 0.5 °C), a clock and calendar, and weighed on average 3 g. iButtons® were calibrated with mercury thermometers (0.05 °C) in a water bath at temperatures from 5 to 45 °C. Buttons® were surgically implanted by the veterinarian in the peritoneal cavity of each individual animal and were programmed to record body temperature every 15 min. After the veterinarian procedure, animals were given 4–12 h to recover before being released at their point of capture. Tree rats were recaught and sacrificed 12.86 ± 3.84 days after insertion of iButtons and the iButtons® were removed.

We computed R_t according to Aschoff's [8] allometric relationship for non-primate mammals:

$$R_t = 4.762 M_b^{-0.197} \tag{1}$$

where M_b is body mass in grams.

2.3. Cavity temperatures (T_{cavity}) and environmental parameters

Temperatures of cavities (hereafter referred to as T_{cavity}) were measured using Thermochron iButtons® programmed to record temperatures every 15 min. One iButton® was implanted just inside the cavity (hereafter referred to as T_{cavity} (shallow) and a second was implanted at a depth of approximately 30 cm inside the same cavity (hereafter referred to as T_{cavity} (deep). In Weenen in summer, Tree Rats were found to be nesting within a wall of an outbuilding structure. The wall was composed of a double layer of bamboo stems positioned and secured vertically. At this site, we positioned iButtons® between the two layers of wall in an identical manner to those in tree cavities. iButtons® were positioned in two cavities at each study site during winter 2006 and summer 2007. An additional two cavities were monitored at Weenen in summer 2007. Where two cavities were monitored at a study site, T_{cavity} were measured simultaneously. Within a season, data were not collected from cavities at different study sites at the same time, although there were periods when simultaneous data were recorded. iButtons® in cavities were not removed when moving to a different study site, providing continuous data.

Ambient temperature is not the actual thermal condition experienced by the animal in its natural environment [44,45]. A useful index of the thermal potential driving heat flow between animals and their thermal environments, which takes into account radiation, air temperature, wind and humidity [46] is operative temperature (T_e) [47]. This thermal index thus gives an indication of the thermal conditions experienced by an animal in its natural surroundings [44]. Sphere thermometers may provide a reasonably accurate thermal index of

Table 1
Summary of Tree Rat deaths and numbers used for body temperature data at the three study sites in winter and summer.

Season	Site	Number implanted	Deaths			No recapture	Faulty transmitter	N
			Unknown cause	Veterinary procedure	Predation			
W	M	7		1				6
	H	6		1	1			4
	W	8	2			2	1	3
S	M	8		2	1		1	4
	H	7	1		1	1		4
	W	15	1	2	1	1	1	9

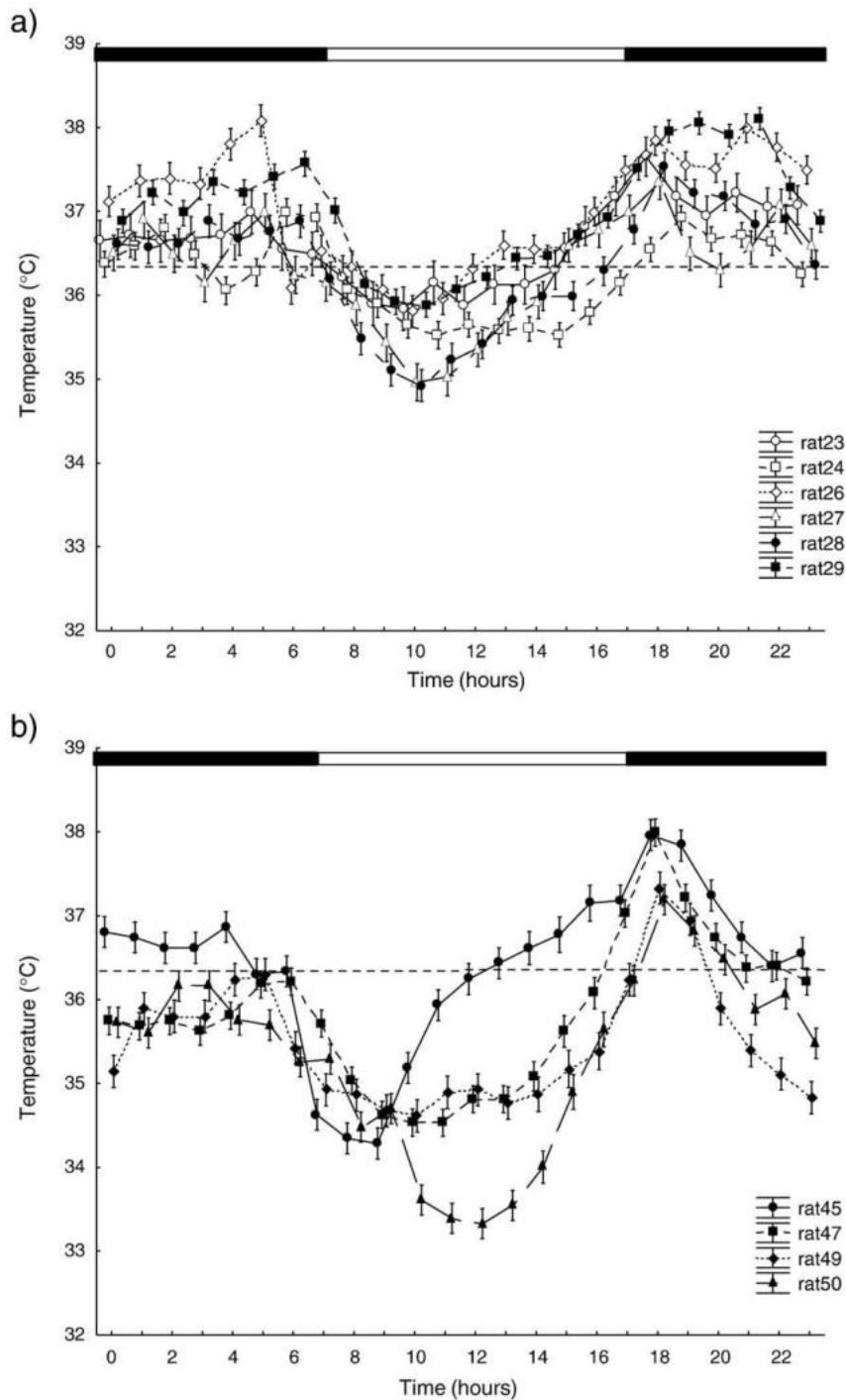W = winter; S = summer; M = Molopo; H—Haina; W = Weenen.

Fig. 1. Mean (± SE) hourly winter body temperature of individual Tree Rats in a) Molopo, b) Haina and c) Weenen. The horizontal dashed line indicates the overall winter mean body temperature. The dark bars indicate scotophase as determined by sunset and sunrise times.
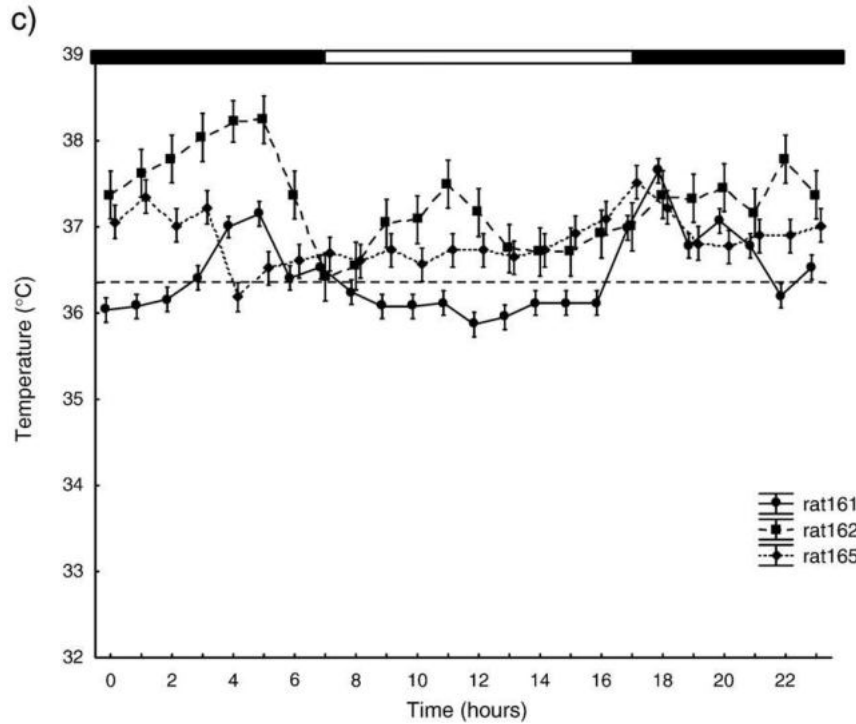
Fig. 1 (*continued*).

an animal's environment [48], with copper casts being the most accurate T_e models available [49].

Operative and T_a were recorded in the vicinity of cavity sites. Operative temperature was measured using back bulb solar radiation temperatures recorded using an iButton® placed in a black copper ball (1 mm thickness, 10 cm diameter) that was exposed to direct sunlight throughout the day at a height of 1 m. Unlike cavity iButtons®, within a season, the black bulb was moved from Molopo to Haina and replaced on the return visit, resulting in discontinuous T_e data for Molopo. Ambient temperature was measured using a calibrated DS 1921 Thermocron iButton® placed in a Stevenson's screen (temperature shield) and suspended in a tree at a height of 1.25–2 m. Temperature shields were not removed when moving between study sites, providing continuous T_a data. Minimum and maximum $T_{cavity}s$ (shallow) were compared to $T_{cavity}s$ (deep) and compared between seasons. Minimum and maximum $T_{cavity}s$ (shallow) and $T_{cavity}s$ (deep) were compared to T_e. Sunrise and sunset times for the winter and summer study periods at the three study sites were recorded.

2.4. Activity

Tree Rats were fitted with radio-transmitters (C. Dearden, Pietermaritzburg) after the surgical implanting of iButtons®. Transmitters were two-stage radio-transmitters encased in epoxy resin and attached to a cable-tie collar with a 15 cm vertical whip aerial. Radio-transmitters were powered by a single silver oxide 1.5 V watch battery and weighed 3.0 g, which was less than 5% of the average animal's body mass (2–4% of body mass). The transmitters had 60 days of battery life and an average range of 1 km. We analysed activity data for Tree Rats with T_b data. Based on this, 31 Tree Rats, 10 in winter 2006, 18 in summer 2007 and three in winter 2007 were included for the analyses. Three Tree Rats had faulty transmitters and hence no activity data were available, resulting in activity data for a total of 28 Tree Rats.

Tracking was conducted on foot with a hand-held, three-element aerial and an Alinco DJ-X10 receiver (Osaka, Japan). Fixes (the location of an animal at one point in time) were recorded by their grid co-ordinates using a handheld GPS (Magellan GPS 4000 XL). Locations of Tree Rats were obtained from direct sightings/homing in [43] and activity, where possible, was recorded with each fix. Use of homing techniques had no effect on diurnal locations. In addition, there was no evidence that nocturnal locations were affected by homing techniques since our close proximity to Tree Rats rarely appeared to affect their behaviour or movement patterns. We divided the nights from 17:00 to 07:00 into 14 hourly intervals in winter and from 19:00 to 06:00 into 11 hourly intervals in summer. Days were divided from 07:00 to 17:00 into 10 hourly intervals in winter and from 06:00 to 19:00 into 13 hourly intervals in summer.

Tree Rats were always in a "home cavity" during the day and thus assumed to be inactive. It was not possible to determine the exact nocturnal activity of Tree Rats at each fix due to their size and elusive behaviour. Moreover, it is crucial that disturbance was minimised, so as not to interfere with their routine activities. When Tree Rats were inside their cavities, permanent or temporary, during the night, it was not possible to ascertain whether they were active or not. Whereas some authors have used a fluctuating signal to determine activity [38], we found this to be an unreliable measure of activity. To determine nocturnal activity patterns, we used all fixes made at night (the hour which included sunset to the hour that included sunrise). Activity for an animal was defined as the proportion of fixes outside the cavity, expressed as a percentage.

2.5. Data analysis

iButton® data were downloaded using the DS1921 Thermochron iButton Software Download programme (Dallas SemiConductor, Maxim, Sunnyvale, CA). The periodicity and significance in the T_b cycles were analysed for individual Tree Rats using the X^2 Periodogram [50; http://www.circadian.org/periodogram.html]. This calculates ratios of variances (Q_p) for each possible circadian period and the period with the highest Q_p value is considered the true circadian pattern [50]. Statistical analyses were performed using the Statistica 7 package (Statsoft Inc., Tulsa, USA). All values are presented as mean ± SE, N is the number of animals and n is the number of measurements (or days, as indicated).

3. Results

3.1. Ambient conditions (T_a)

During the study, the mean T_a was 14.10 ± 0.26 °C (range 4.60–27.66 °C) and 22.03 ± 0.29 °C (range 11.13–36.65 °C) in winter and summer respectively at Weenen. At Molopo, the mean T_a was 11.50 ± 0.22 °C (range −4.94–28.12 °C) and 28.34 ± 0.19 °C (range 12.14–42.12 °C) in winter and summer respectively. The T_a was 15.55 ± 0.43 °C (range 3.13–30.68 °C) and 25.47 ± 0.26 °C (range 16.61–38.10 °C) in winter and summer respectively at Haina.

3.2. Daily rhythms of body temperature (T_b)

No T_b data were recorded for Weenen in winter 2006 due to malfunctioning iButtons®. We experienced Tree Rat deaths, mainly due to predation (Table 1). In addition, a number of iButtons® could not be retrieved due to faulty transmitters. Consequently, we obtained continuous T_b measurements for a total of 13 and 17 Tree Rats in winter and summer respectively (Table 1). Mean body mass was 67.52 ± 3.15 g (range 42.3–102.10 g). Body temperature was measured for a mean period of 8.39 ± 1.59 days in winter and 8.53 ± 1.59 days in summer. The T_b range for Tree Rats was 27.65–40.63 °C ($n = 13$) and 32.69–40.15 °C
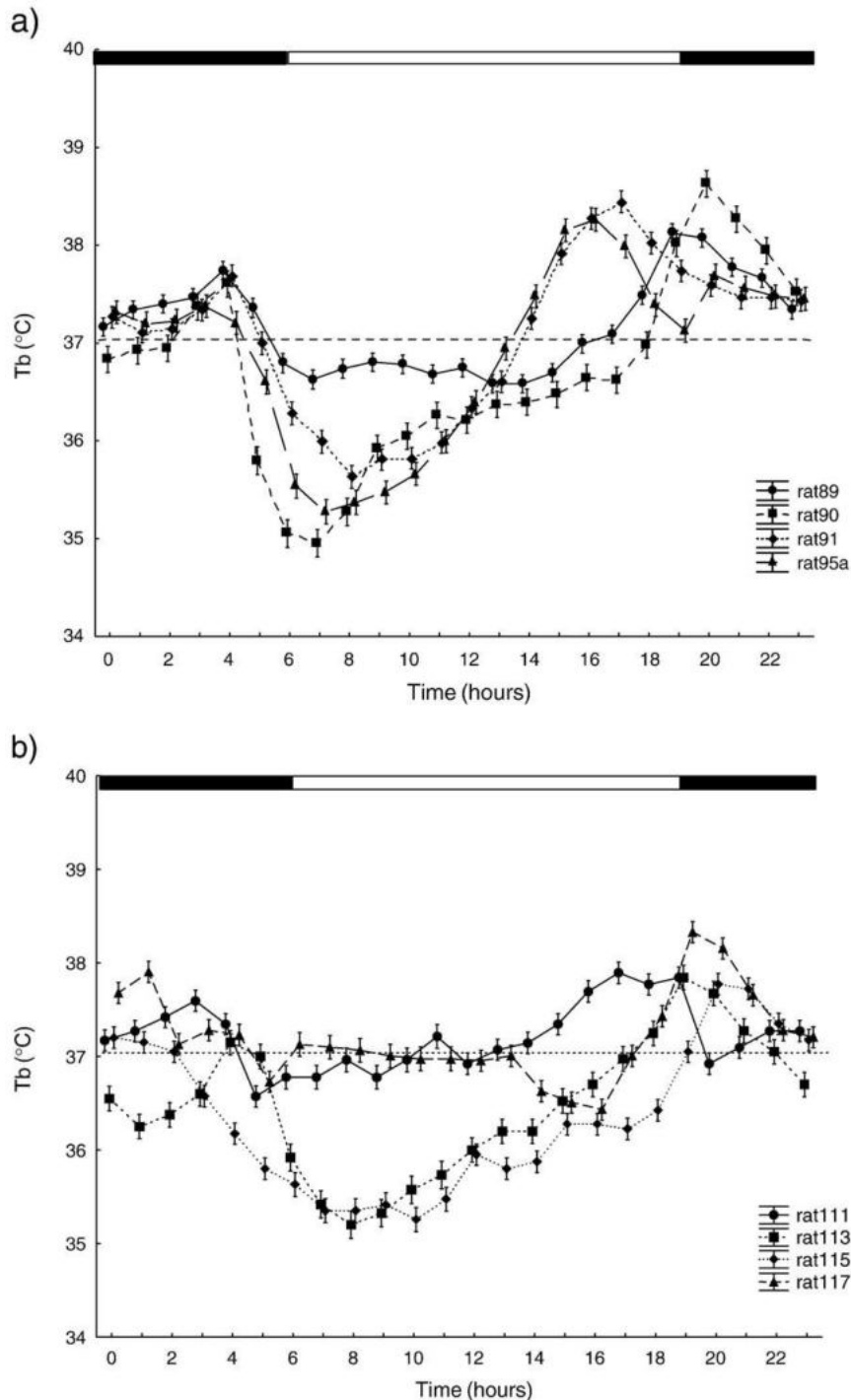

Fig. 2. Mean (± SE) hourly summer body temperature of individual Tree Rats in a) Molopo, b) Haina and c) Weenen. The horizontal dashed line indicates the overall summer mean body temperature. The dark bars indicate scotophase as determined by sunset and sunrise times.
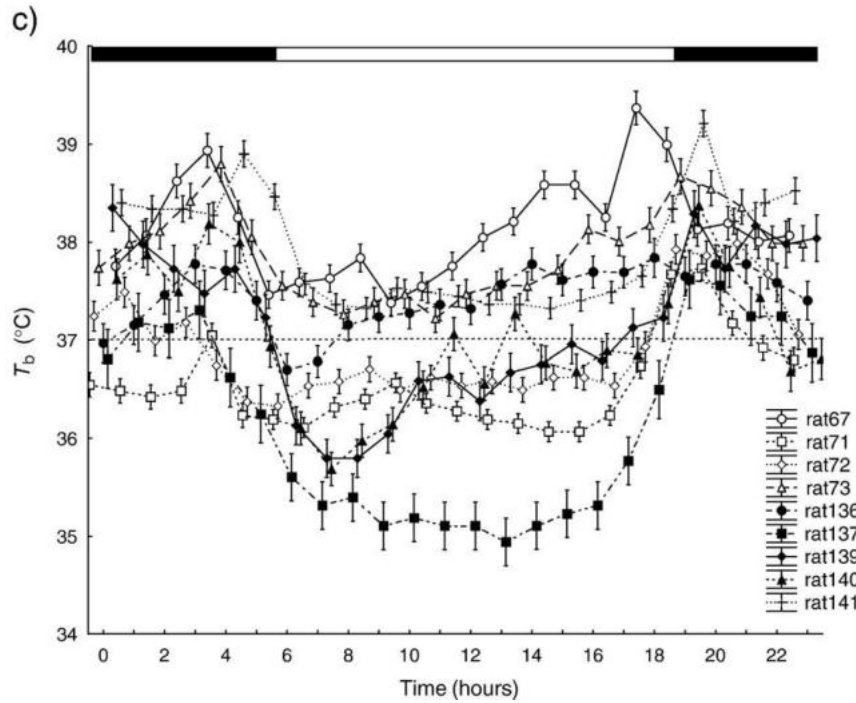
Fig. 2 (*continued*).

$(n = 17)$ in winter and summer respectively. All, with the exception of three Tree Rats, from different study sites, had a significant 24 h T_b rhythmicity ($P < 0.05$; 15 min resolution) using the X^2 Periodogram analysis (Q_p range 156–1316, $df = 94$–98). Non-significant 24h T_b rhythmicity was the result of insufficient data points.

Thermal profiles of the T_b of Tree Rats revealed several trends in winter (Fig. 1a–c) and summer (Fig. 2a–c). Although thermal profiles varied between individuals, there was little variation in T_b within individuals as indicated by low SE (Table 2, Figs 1 and 2). Tree rats had a distinct nychthermeral T_b pattern, being lower during the day and higher at night (Figs 1 and 2). In winter and summer, generally, T_b peaked in early scotophase. Some individuals reached a second T_b peak in late scotophase. Mean core T_b declined from the onset of light and reached minimum T_b ($T_b$min) generally in the first half of photophase,

Table 2
Mean, minimum and maximum body temperature of Tree rats at the three study sites in winter and summer respectively where $n = $ the number of measurements.

	Site	Individual	n	Mean (°C)	Minimum (°C)	Maximum (°C)	Range (°C)
Winter	Molopo	23	434	36.65 ± 0.05	32.66	39.15	6.49
		24	1432	36.31 ± 0.03	34.15	40.13	5.98
		26	1516	37.04 ± 0.03	33.15	40.63	7.48
		27	1516	36.48 ± 0.03	32.66	40.63	7.97
		28	1468	36.05 ± 0.04	27.65	39.13	11.48
		29	1432	36.91 ± 0.03	33.64	39.13	5.49
	Haina	45	376	36.39 ± 0.06	33.16	39.14	5.98
		47	374	35.83 ± 0.06	33.13	39.11	5.98
		49	376	35.48 ± 0.05	33.05	38.55	5.50
		50	376	35.31 ± 0.07	32.11	38.59	6.48
	Weenen	161	440	36.46 ± 0.03	34.66	38.65	3.99
		162	440	37.15 ± 0.05	34.18	40.15	5.97
		165	292	36.85 ± 0.04	34.57	39.06	4.49
Summer	Molopo	89	1432	37.24 ± 0.02	34.17	40.14	5.97
		90	1391	36.85 ± 0.03	32.69	39.67	6.98
		91	943	37.08 ± 0.03	34.16	39.64	5.48
		95a	1437	36.96 ± 0.03	34.15	40.13	5.98
	Haina	111	464	37.22 ± 0.03	35.13	39.12	3.99
		113	456	36.53 ± 0.04	34.20	38.69	4.49
		115	464	36.37 ± 0.04	34.61	39.09	4.48
		117	464	37.19 ± 0.03	35.14	39.62	4.48
	Weenen	67	328	38.15 ± 0.04	36.63	40.12	3.49
		71	1220	36.55 ± 0.02	34.62	39.61	4.99
		72	2680	37.02 ± 0.02	34.12	39.11	4.99
		73	372	37.93 ± 0.03	36.68	39.67	2.99
		136	433	37.39 ± 0.03	35.66	39.15	3.49
		137	434	35.82 ± 0.07	33.69	38.68	4.99
		139	488	37.05 ± 0.04	35.17	39.66	4.49
		140	432	36.86 ± 0.05	33.57	39.06	5.49
		141	488	37.87 ± 0.03	36.66	40.15	3.49

after which it steadily increased. The T_b rhythms of individual Tree Rats were not highly synchronized, with increases and decreases in T_b between rest and activity often several hours apart (Figs 1 and 2). Using frequency distributions of the time at which maximum T_b ($T_b$max) and
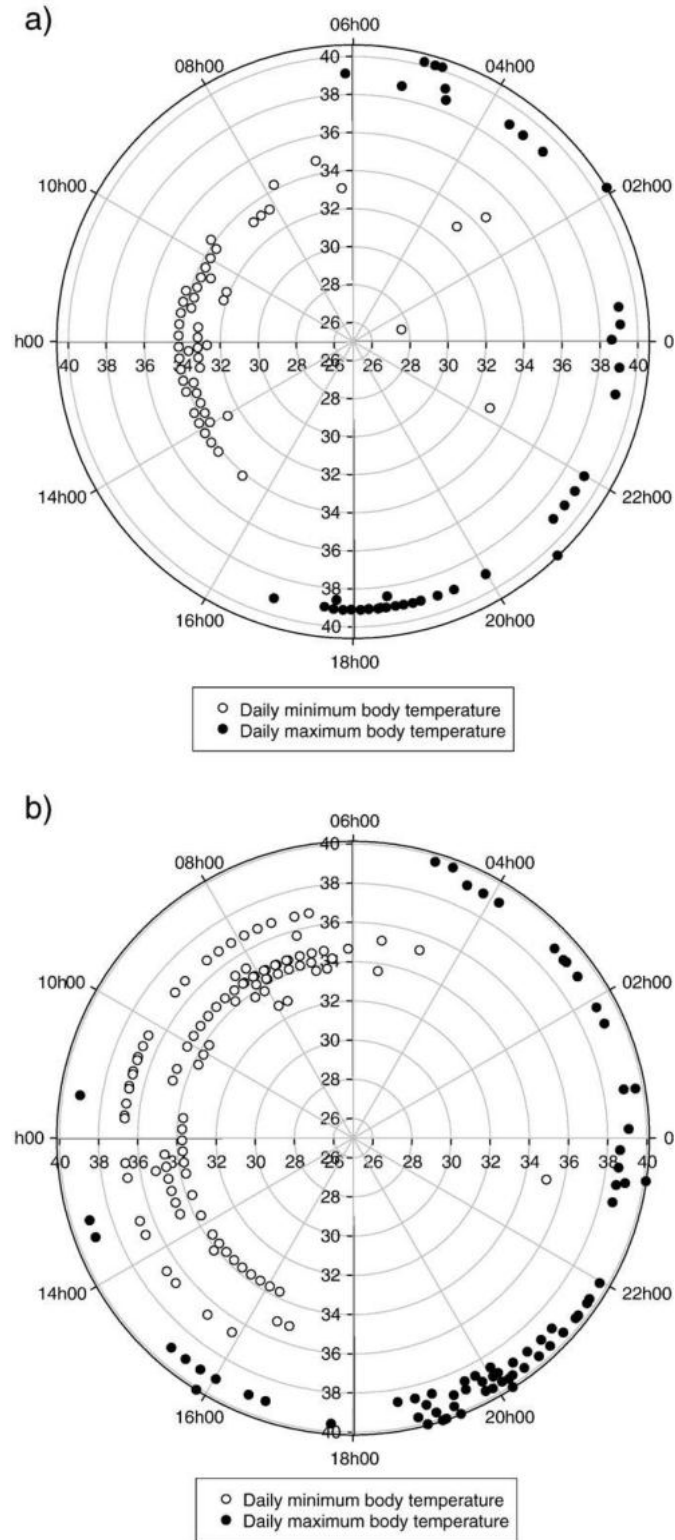

Fig. 3. Circular distributions of the time of day (degrees) of the daily minimum body temperature (unfilled circles) and daily maximum body temperature (filled circles) of Tree Rats at the three study sites in a) winter and b) summer.

$T_b$min occurred each day, although Tree Rats varied in the time of day when $T_b$max and $T_b$min were reached, there was a clear bimodal distribution of T_b data, with $T_b$max values during the night and $T_b$min values during the day (but see below) (Fig. 3a, b).

The variation in the T_b range between sites in winter was not significant (ANOVA, $F_{2,10} = 2.93$, $P = 0.10$). In summer, this variation was significant (ANOVA, $F_{2,14} = 8.83$, $P = 0.003$) (Table 2), with the T_b range in Molopo greater than in Weenen and Haina (Post-hoc, Tukey, $P = 0.003$ and 0.014 respectively). There was a significant effect of season on $T_b$min and $T_b$max (RMANOVA, $F_{2,27} = 5.42$, $P = 0.01$) and on T_b range (ANOVA, $F_{1,28} = 9.89$, $P = 0.004$). The mean range in winter was 6.41 ± 0.51 °C while 4.72 ± 0.26 °C in summer. In winter, lower mean $T_b$min's were recorded than in summer, although this was not significant.

Despite the low winter night-time ambient temperatures, there was little evidence of torpor in Tree Rats. A single individual, Tree rat 28, dropped T_b from 36.14 °C to 27.65 °C in 30 min at 00:52 on a morning in winter in Molopo. Besides this, $T_b$min for Rat 28 occurred during the day (rest phase).

The mean R_t was 5.42 ± 0.30 (range 2.99–11.48) which is 259.7% (137 to 557.4%) of the predicted maximum circadian amplitude in body temperature for non-primate mammals. R_t was significantly higher in winter than summer (independent t-test: $t = 2.95$, $df = 29$, $P = 0.03$).

3.3. Cavity temperatures (T_{cavity}) and environmental parameters

No T_{cavity}s were recorded for Weenen in winter 2006 due to malfunctioning iButtons®. A deep iButton® was removed from a single cavity in Haina in winter 2006 and summer 2007 presumably by Tree Rats, and hence temperatures from these cavities could not be used. Temperatures of three cavities were thus recorded in winter and for seven cavities in summer (Table 3). Cavities used by Tree Rats varied greatly in position and structure including cavities in live trees or in dead tree stumps lying horizontally on the ground. Only one male Tree rat in Molopo used a typical bird "nest".

There were significant differences between minimum T_{cavity} (shallow) when compared to T_e (RMANOVA, $F_{1,8} = 13.82$, $P = 0.006$, Fig. 4)

Table 3
Mean, minimum and maximum cavity temperature, operative temperature and ambient temperature at the two study sites in winter and summer respectively (see text for abbreviations and explanations).

| Site	Parameter	n	Mean (°C)	Minimum (°C)	Maximum (°C)	Range (°C)
Winter						
Molopo	Cavity (shallow)	1487	13.11 ± 0.12	1.58	23.67	22.09
	Cavity (deep)	1328	12.72 ± 0.14	0.04	25.10	25.06
	T_e	373	12.78 ± 0.55	−5.39	33.68	39.07
	T_a	1427	11.73 ± 0.22	−4.47	28.66	33.13
Haina	Cavity (shallow)	376	20.12 ± 0.35	9.09	32.61	23.52
	Cavity (deep)	376	20.02 ± 0.35	9.11	32.14	23.03
	T_e	376	17.76 ± 0.66	2.06	42.08	40.02
	T_a	376	15.55 ± 0.41	3.57	28.62	25.05
Summer						
Molopo	Cavity (shallow)	1432	27.72 ± 0.14	13.59	39.58	25.99
	Cavity (deep)	334	25.94 ± 0.23	19.62	37.11	17.49
	T_e	498	29.26 ± 0.33	19.16	49.10	29.94
	T_a	1432	28.06 ± 0.16	13.67	39.17	25.50
Haina	Cavity (shallow)	438	26.16 ± 0.13	20.62	32.11	11.49
	Cavity (deep)	343	26.33 ± 0.15	21.15	34.64	13.49
	T_e	441	26.36 ± 0.29	16.61	42.58	25.97
	T_a	438	25.47 ± 0.26	16.61	38.10	21.49
Weenen	Wall (shallow)	488	22.82 ± 0.26	12.69	37.20	24.51
	Wall (deep)	488	22.11 ± 0.27	11.13	36.64	25.51
	T_e	488	23.13 ± 0.30	11.63	41.13	29.50
	T_a	488	22.34 ± 0.28	11.63	36.64	25.01
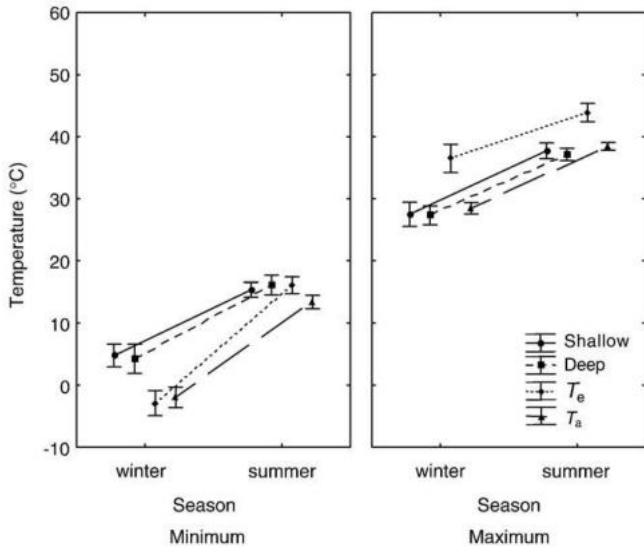
Fig. 4. Mean (± SE) minimum and maximum operative temperature, ambient temperature and cavity temperature (shallow and deep) in summer and winter (see text for abbreviations and explanations).

Table 4
Cavity temperature range, operative temperature range and ratio of cavity temperature range to operative temperature range for three and seven cavities in winter (w) 2006 and summer (s) 2007 respectively (see text for abbreviations and explanations).

Cavity	Season	Position	Range (°C)	T_e range (°C)	Ratio	%
1	w	Shallow	22.09	39.07	0.57	56.54
		Deep	25.06	39.07	0.64	64.14
2	w	Shallow	22.55	39.07	0.58	57.72
		Deep	21.07	39.07	0.54	53.93
3	w	Shallow	23.52	40.02	0.59	58.77
		Deep	23.03	40.02	0.58	57.55
4	s	Shallow	24.00	24.98	0.96	96.08
		Deep	23.99	24.98	0.96	96.04
5	s	Shallow	25.48	24.98	1.02	102.00
		Deep	25.98	24.98	1.04	104.00
6	s	Shallow	25.99	29.94	0.87	86.81
		Deep	17.49	29.94	0.58	58.42
7	s	Shallow	20.98	29.94	0.70	70.07
		Deep	16.49	29.94	0.55	55.08
8	s	Shallow	11.49	25.97	0.44	44.24
		Deep	13.49	25.97	0.52	51.94
9	s	Shallow	24.51	29.50	0.83	83.08
		Deep	25.51	29.50	0.86	86.47
10	s	Shallow	24.01	29.50	0.81	81.39
		Deep	24.01	29.50	0.81	81.39

and maximum temperatures (RMANOVA, $F_{1,8} = 41.33$, $P = 0.0002$, Fig. 4) and between minimum T_{cavity} (deep) when compared to T_e (RMANOVA, $F_{1,8} = 19.91$, $P = 0.002$, Fig. 4) and maximum temperatures (RMANOVA, $F_{1,8} = 37.42$, $P = 0.0003$, Fig. 4). There was no significant difference between minimum T_{cavity} (shallow) when compared with T_{cavity} (deep) (RMANOVA, $F_{1,8} = 0.03$, $P = 0.88$, Fig. 4) or between maximum temperatures (RMANOVA, $F_{1,8} = 0.46$, $P = 0.52$, Fig. 4). There was a significant difference between minimum T_{cavity} (shallow) and T_{cavity} (deep) in winter and summer (RMANOVA, $F_{1,8} = 21.76$, $P = 0.002$, Fig. 4) and between maximum temperatures in the cavity in winter and summer (RMANOVA, $F_{1,8} = 24.56$, $P = 0.001$, Fig. 4). When considering day and night, deep cavity temperatures generally displayed a slight delay response (lag) when compared to shallow temperatures. The magnitude of this temperature lag between shallow and deep regions varied between cavities.

We calculated the T_e range and range of T_{cavity} (T_{cavity}range) for each cavity over each study period and computed the ratio of the two values (T_{cavity}range divided by T_e range) and expressed as a percentage. The ratios reflect the degree to which the cavities were buffered against T_e changes and allow comparison of the buffering effects of cavities when data are recorded on different days at different T_e [51]. Cavities in winter provided significantly greater buffering than in summer (ANOVA, $F_{1,18} = 6.27$, $P = 0.022$, Table 4).

3.4. Activity

Although there was variation in the times in which female Tree rats were out of their home cavities, more time was spent out of cavities during the first half of the scotophase than in the second half of the scotophase during both winter and summer. In contrast, male Tree Rat activity was more evenly distributed over the night in both seasons (Fig. 5). Male Tree Rats spent a significantly greater mean proportion of time out of their cavities when compared to females in winter (independent t-test: $t = 2.62$, $df = 26$, $P = 0.01$). Season had no effect on the mean proportion of time spent outside their home cavity in either males (independent t-test: $t = -0.27$, $df = 23$, $P = 0.79$) or females (independent t-test: $t = -0.42$, $df = 23$, $P = 0.68$). Males only differed significantly from females in the cavities between 4 and 5 am in winter (Kruskal–Wallis, $H_{(1,11)} = 6.29$, $P = 0.01$) and between 3 and 4 am in summer (Kruskal–Wallis, $H_{(1,12)} = 4.88$, $P = 0.03$).

4. Discussion

Our study, which provides the first continuous T_b measurements for a free-living Tree Rat, shows that *T. nigricauda* has a 24 h T_b rhythm typical of that for other endothermic animals [13] with two distinct temperature levels, the lower corresponding to resting and the higher to activity. Circadian patterns of T_b and activity patterns confirmed their nocturnalism [36]. Lack of individual variation within hourly T_b measurements is supported by highly significant circadian rhythm patterns which supports the concept of internal circadian clock control of T_b [13]. Individual Tree Rats usually displayed a fairly constant T_b throughout the study, although every individual in winter had some T_bs < 35 °C and > 38 °C and in summer < 37 °C and > 38 °C. The lability of T_b differed between different individuals, and reasons for this variation in thermal profiles are not known, but could be a consequence of variation in activity [52] as a result of foraging success, reproductive drive and predator–prey interactions [53], or an energy saving mechanism [10].

Minimum T_bs were recorded during periods of rest, while $T_b$max corresponded to periods of activity (except rat 28). Low T_bs are usually associated with rest phase and high T_bs with the active phase [8] and although T_b rhythms are not generated by activity cycles, they are affected by them and usually correlated [54]. Thus the nychthemeral T_b rhythm of Tree Rats may be influenced by both the circadian rhythm and increased heat production due to activity. As above, variation in the time and number of peak T_bs may be a consequence of variation in activity [51]. The peak T_b in the evening is consistent with the findings of Lovegrove and Heldmaier [10] and lack of further peaks in his study (except for one rat) could be attributed to the fact that movement of captive Tree Rats in cages was restrained and at the same level of intensity throughout the active phase. Thus differences would presumably reflect some aspect of captivity, since captivity has an effect on movement and behaviour and thus possibly thermoregulatory patterns of Tree Rats.

In contrast to our predictions, there was no effect of site on T_b range in winter, which may be interpreted as a response to similar degrees of thermal stress along the aridity gradient. However, similarity in response may be the result of a combination of energy saving mechanisms, including the thermal benefits of huddling and buffered cavities. In accordance with our predictions, there was an effect of season on T_b range. The larger winter T_b range, a result of
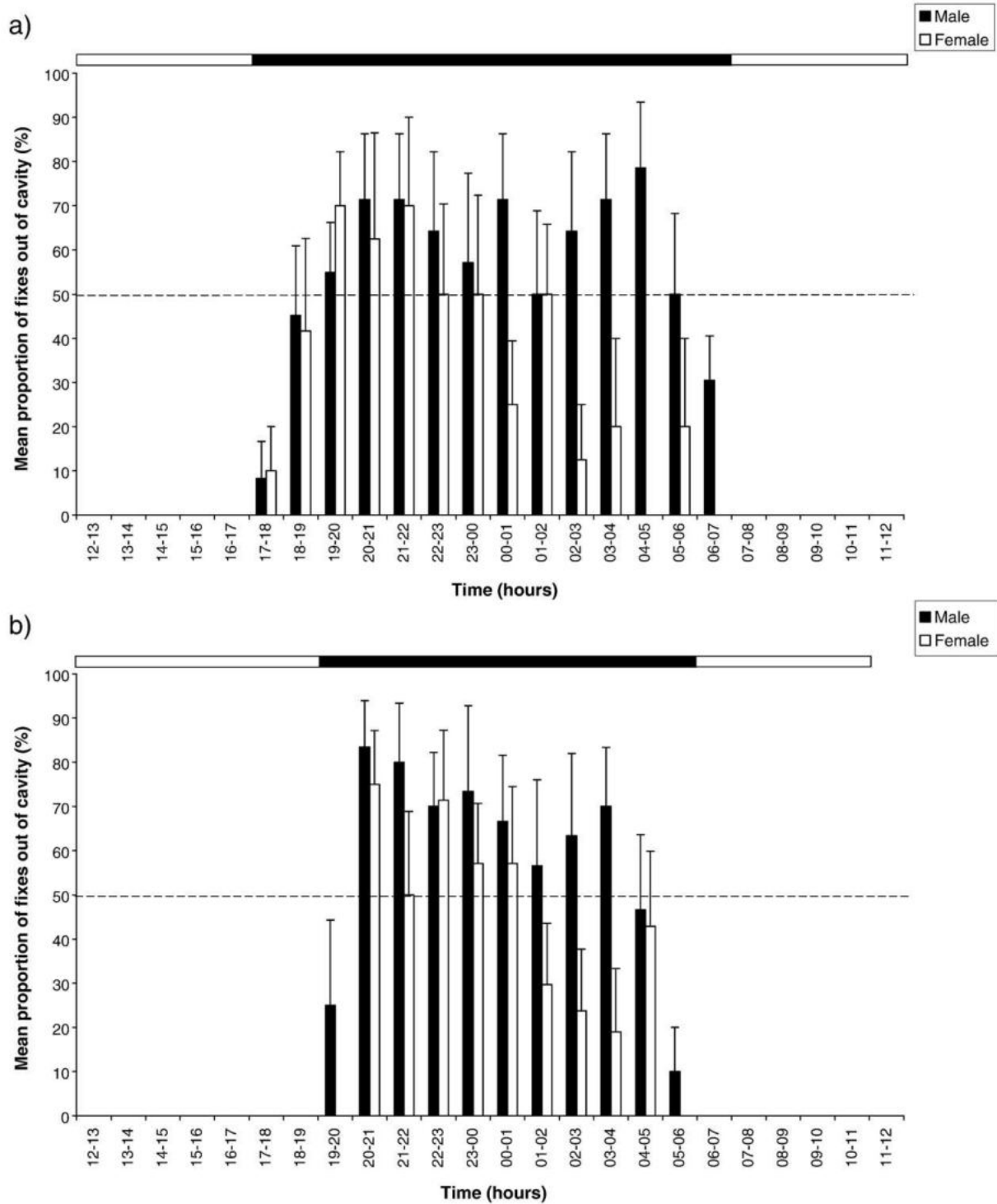
Fig. 5. Nocturnal activity profiles of male and female Tree Rats in a) winter and b) summer. Bars show the mean ± SE of the percentages of fixes where animals were located out of their home cavity in 1 h intervals. The horizontal dashed line indicates a mean of 50% of fixes out of the home cavity. The dark bar indicates scotophase as determined by sunset and sunrise times.

allowing T_b to fluctuate with low T_as, results from typical mean maximum T_b values (38.5–40.63 °C), but low mean minimum T_b values (27.65–34.66 °C). This shallow hypothermia in winter when Tree Rats lowered their minimum T_bs is presumably an energy saving device in response to lower T_a during the day (but see below) when compared to summer, allowing Tree Rats to spend less energy on thermoregulation. Similar variation in T_b, caused by reduced minimum T_b rather than increased maximum T_b has been found in Numbats (*Myrmecobius fasciatus*), when not entering torpor [6] and in Antelope Ground Squirrels (*Ammospermophilus leucurus*) [55].

It is difficult to define the drop in T_b of Tree Rat 28 on the single occasion in winter. Although possibly not a typical energy saving mechanism employed, it does suggest that this species is capable of tolerating and making use of the mechanism. A drop in T_b during periods of activity particularly in winter would incur a similar energetic advantage to the drop during periods of inactivity and has been shown in elephant shrews [56], providing an energetic benefit by reducing the T_b–T_a gradient during the coldest part of the night [57].

We expected the R_t to be greater than the value predicted by Ashoff's [8] allometric equation since some mammals may lower their

T_b during their rest phase when exposed to low T_as [4] as a mechanism of conserving energy, resulting in increased amplitudes of T_b. The mean R_t in the present study was greater than that of six captive *T. paedulcus* individuals (152.5%), expressed as a percentage [10]. However, this was expected and is in accordance with their observations. The rodents in their study may not have maintained minimum conductances as they were kept at a constant T_a higher than the lower critical limits of thermoneutrality, resulting in underestimated R_t values [10]. In addition, movement in the wild would increase T_b through muscular thermogenesis [58] and hence result in lower maximum $T_b$max's recorded in captive animals.

In agreement with our predictions, cavity temperatures buffered T_e, albeit minor buffering when compared to the buffering of temperatures within burrows beneath the soil [59]. This is indicated by significantly lower maximum and higher minimum T_{cavity}s, resulting in smaller temperature fluctuations and lower temperature ranges over 24 h within the cavities when compared to T_e. However, Tree Rats in cavities in winter were still exposed to low T_{cavity}s and to sub-zero T_es at night. Variation in the magnitude of buffering in shallow and deep regions of cavities was similar between seasons and in both regions of cavities, as indicated by similar ratios. This trend concurs with the findings of Lovegrove et al. [60]. Variation in the magnitude of the temperature lag between shallow and deep cavity regions and between T_{cavity}, T_e and T_a in different cavities, was possibly due to the influence of cavity structure on the rate of heat exchange [32].

When taking both sexes into account, Tree Rats did not curtail their activity during winter as expected. This could possibly be the result of the greater activity of males in winter, when compared to females, which could be explained by the reproductive flexibility of Tree Rats. In this study, male Tree Rats had larger home ranges than females [43], which support the promiscuous mating system as suggested by Eccard et al. [38]. Although Tree Rats are reported to have a summer breeding season [36], a lactating female with new-born offspring was found in July 2006 in Molopo (pers. obs.). This observation implies that males were reproductively active during winter months and thus we would expect them to spend more time away from their cavities when compared to females. On the other hand, our methodology may have overestimated male activity. Several male Tree Rats had more than one cavity tree and alternated between these trees on different nights (pers. obs.). In addition, some had "temporary shelters" which they used to varying degrees during the night (pers. obs.). When Tree Rats occupied these alternative and temporary sites, activity was noted as "active" since they were away from their home cavity. Male and female activity in summer and female activity in winter concur with the findings of a previous study [38], and the greater proportion of time spent outside cavities by males in winter, when compared to the previous study can be attributed to the methods employed.

In summary, nocturnal Tree rats face thermoregulatory challenges in winter, particularly in xeric and semi-xeric regions, and mechanisms to conserve energy would be selected for. Our study showed that Tree Rats did maintain T_b at the three aridity sites but allowed T_b to fluctuate with T_a more than expected, by lowering $T_b$min during the rest phase as a mechanism to conserve energy. In addition, cavities provide a buffered microclimate which may result in further energy savings by reducing the T_b–T_a gradient. These energy savings, a result of a combination of physiological and behavioural mechanisms in response to the thermal environment, are sufficient to negate the need to reduce their activity in winter and thus they are presumably able to meet their foraging and reproductive needs.

Acknowledgements

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