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SHORT COMMUNICATION

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Was basking important in the evolution of mammalian endothermy?

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Abstract The first mammals were small, nocturnal, and presumably had low metabolic rates and were therefore probably unable to maintain a constant high body temperature throughout cool nights. How these animals, without sufficient heat production for endogenous rewarming, were able to become warm and active again before the next activity period remains unresolved. However, we discovered that, similar to reptiles, the carnivorous marsupial mammal *Pseudantechinus macdonnellensis* (body mass 30.8±5.0 g) uses the morning sun to rewarm from low (26.3±4.5°C) body temperatures during torpor. Our findings provide the first evidence of basking during rewarming from torpor in mammals and may provide an alternative explanation as to how ancestral mammals could have become nocturnal to avoid diurnal predators despite their small size and a low endogenous heat production.

Introduction

Endothermic mammals can maintain a constant high body temperature (T_b) of about 35–38°C. While a high T_b optimizes physiological processes, endothermy requires high metabolic rates (MR) and good insulation. Basal MR of endotherms are about 5–10 times (Crompton et al. 1978; Schmidt-Nielsen et al. 1980; Ruben 1995; Speakman and Thomas 2002) and field MR about 10–30 times (Nagy et al. 1999) greater than standard MR in ectothermic reptiles, and metabolic rates of the first true mammals (approx. 200 million years ago) were probably intermediate between reptiles and modern mammals (Crompton et al. 1978; Schmidt-Nielsen et al. 1980; Ruben 1995). Ancestral mammals were small (30–40 g) and, to avoid diurnal reptilian predators, nocturnal (Crompton et al. 1978). Low MR could not have prevented T_b from declining while animals were at rest and it is likely that, especially during the second, cooler, part of the night, T_b fell and animals entered some form of torpor (Lyman et al. 1982; Grigg and Beard 2000). Torpor is employed widely by small modern heterothermic mammals for energy conservation and is characterised by a substantial reduction in T_b and MR down to on average 5–30% of basal MR (Geiser and Ruf 1995). However, during endothermic arousal, MR can increase >100-fold (Riedesel and Williams 1976; Geiser and Brigham 2000). While it is likely that ancestral mammals reduced MR with T_b similarly to modern mammals, it is most improbable that their low thermal capacity would have sufficed for rewarming, especially when exposed to low ambient temperatures (T_a). Is it possible, then, that ancestral mammals employed basking for rewarming from low T_b to compensate for a low heat production, as is commonly observed in reptiles? At present, support for this hypothesis is lacking because basking during rewarming from torpor has not been observed in mammals.

To clarify this question, we investigated whether the fat-tailed antechinus (*Pseudantechinus macdonnellensis*) basks during rewarming from torpor. The species was selected because it belongs to a phylogenetically old group, and is therefore likely to provide insights into the evolution of endothermic thermoregulation, and because it belongs to a family of insectivorous marsupial mammals with a high propensity for torpor (Geiser 2002). Furthermore, although the species is supposed to be nocturnal, anecdotal reports describe that, in the past, Aborigines have captured it while sunbathing and individuals are occasionally observed sunbathing by hikers travelling along remote mountain tracks.

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Materials and methods

The study was conducted in winter (June/July) 2001 at Ormiston Gorge, MacDonnell Ranges, in central Australia. We caught six adult antechinus (two females, four males; body mass 30.8±5.0 g; females 28.3±8.3 g, males 32.1±3.5 g) using Elliott box traps along sandstone cliffs. Animals were transferred to a field laboratory, implanted intraperitoneally with calibrated (to the nearest 0.1°C) temperature-sensitive transmitters (Sirtrack, FM single stage, mass 2 g) under oxygen/forthane anaesthesia and were released at their site of capture after recovery for one night in captivity. After release, animals were tracked with manual receivers, and transmitter signals were recorded manually several times daily and at 10-min intervals with receiver/loggers (Körtner and Geiser 2000) for about 1 month. We attempted to obtain continuous data by using more than one receiver/logger for each individual and by relocating the units, but because of the short transmission range of the implanted transmitters and the movement of animals this was often not possible. The T_a was measured to the nearest 0.5°C using data loggers (Thermochron iButton; Dallas Semiconductor) and ranged from daily minima of 1.5–12.5°C to maxima of 19.5–23.5°C. The weather was sunny with the exception of a single day, which was overcast early in the morning and then intermittently for much of the day. Numeric values presented are means ±1 standard deviation for the number of individuals (‘*n*’) investigated. ‘*N*’ denotes the number of observations. Differences between means were determined using a *t*-test.

Results and discussion

Antechinus were resting or active for brief periods in the afternoon and the main activity period was in the first half of the night. The T_b during rest in normothermic individuals usually ranged between 33 and 36°C and increased somewhat during activity to about 35–37°C. All individuals entered torpor. Entry into torpor usually occurred around midnight (Fig. 1), and T_b fell to individual minima of 15.7–27.1°C. When sandstone cliffs were sun-exposed in the morning, torpid animals emerged to rewarm in the sun (N=24 observations with T_b<32°C), often under an overhang, with their back or side facing the sun and the head towards a crevice (Fig. 2). The time when animals were first seen basking occurred about 2 h earlier (t=7.0; P=0.0004) on sunny days (0941 hours± 36 min; n= 6; N=21; ~2:20 h after sunrise) than on the single cloudy day (1136 hours±12 min; n=3; N=3) when sun exposure of cliffs was delayed, suggesting that the animals adjust times of rewarming according to environmental conditions. Similar to hibernators, in which males terminate hibernation before females (Barnes and Ritter 1993), torpid male antechinus were seen basking earlier (0921 hours±24 min; n=4; N=12; t=4.7; P=0.018) than females (1021 hours±6 min; n=2; N=12). The T_b minima when individuals were first seen basking ranged from 19.3 to 31.3°C (26.3±4.5°C; n=6; N=6) and average basking T_b minima were 21.7±3.4°C (females, n=2; N=2) and 28.6±2.9°C (males, n=4; N=4). On one occasion, an individual that was obviously well coordinated ran up a vertical cliff towards the sun with a T_b of 22.6°C. Nevertheless, because these animals commonly basked along vertical 5–10 m deep cliffs, we probably did not always detect them at first emergence, and basking at lower T_b is therefore likely. Rewarming rates from T_b<25°C were less than half (t=2.8; P=0.048) in non-basking (0.13±0.07°C/min; n=3; N=4) than in basking (0.28±0.07°C/min; n=3; N=4) individuals.

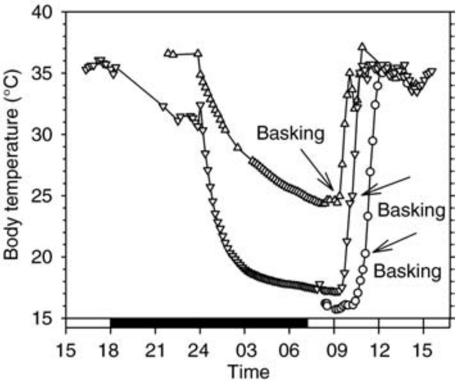

Fig. 1 Course of body temperatures of three antechinus over a 24-h period, but on different days in winter. Ambient temperatures ranged from 1.5 to 22.0°C. The *dark bar* indicates night and the *arrows* show when animals were first seen basking and rates of rewarming usually increased. Night values for one individual are missing because it was out of receiver range

Fig. 2 A basking *Pseudantechinus macdonnellensis* in the wild

Our study provides the first direct evidence that mammals may use basking to facilitate rewarming from torpor. While other studies have observed basking for thermal comfort and energy conservation in mammals (Bartholomew and Rainy 1971) and birds (Ohmart and Lasiewski 1971), these were conducted in captivity and at T_b of >33°C. The one field study (Körtner et al. 2000), which provides evidence that basking may occur during rewarming in tawny frogmouths, did not specify the T_b when basking commenced (somewhere between 30 and 36°C). Moreover, as the birds were sitting in trees, basking was to a large extent a passive process and did not involve active movement from a sleeping site in a deep crevice while torpid to a basking site for rewarming, as observed in the present study.

The likely importance of passive rewarming in ancestral mammals can be illustrated by the following calculation. The heat required for rewarming can be calculated from the temperature differential of T_b, body mass, and the specific heat of tissue (Bartholomew and Rainy 1971), and for a 30 g mammal increasing T_b from 20 to 35°C is 1545 J. If we assume that the heat production in a 30 g ancestral mammal attempting to rewarm from T_b 20°C was on average 312 J/h [50% basal MR of a 30 g marsupial (Geiser 2002); ~800% standard MR of a 30 g reptile at T_b 20°C – assuming a Q_{10} of 2 (Bennett and Dawson 1976)], the rewarming process at zero heat loss (which is unrealistic without sun or high T_a) would have required about 5 h. At a T_b–T_a differential of only 3°C, heat loss calculated from the thermal conductance for a 30 g marsupial is 360 J/h (Geiser 2002), which exceeds the above calculated heat production and would result in a decline, not rise, of T_b. If basking in the sun approximately doubled the rewarming rate of ancestral animals as in the antechinus (present study), their time of rewarming in the sun, perhaps in the afternoon before the next activity period, would have been completed within 2.5 h, which is somewhat slow but within the range of modern mammals.

Thus, we propose, in agreement with previous hypotheses (Crompton et al. 1978; Ruben 1995), that small ancestral mammals used good insulation and modest heat production to be able to forage for part of the night. However, unlike previous hypotheses (Crompton et al. 1978; Ruben 1995), which assumed homeothermy in ancestral mammals, we propose that ancestral mammals were heterothermic and, when thermally challenged or when food supply was low, became torpid. While heterothermy in ancestral mammals seems likely it is, however, improbable that the pattern of torpor was identical to that in modern mammals with thermoregulatory control of T_b during torpor. It also seems unlikely that their low MR sufficed for endothermic arousal from low T_b and they therefore required external heat, not primarily to save energy as in modern mammals (Schmid 1996; Lovegrove et al. 1999), but to speed up the rewarming process or be able to rewarm at all.

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