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## Supplementary data

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## Research



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# Mammal survival at the Cretaceous–Palaeogene boundary: metabolic homeostasis in prolonged tropical hibernation in tenrecs

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Free-ranging common tenrecs, *Tenrec ecaudatus*, from sub-tropical Madagascar, displayed long-term (nine months) hibernation which lacked any evidence of periodic interbout arousals (IBAs). IBAs are the dominant feature of the mammalian hibernation phenotype and are thought to periodically restore long-term ischaemia damage and/or metabolic imbalances (depletions and accumulations). However, the lack of IBAs in tenrecs suggests no such pathology at hibernation  $T_{bs} > 22^{\circ}\text{C}$ . The long period of tropical hibernation that we report might explain how the ancestral placental mammal survived the global devastation that drove the dinosaurs and many other vertebrates to extinction at the Cretaceous–Palaeogene boundary following a meteorite impact. The genetics and biochemistry of IBAs are of immense interest to biomedical researchers and space exploration scientists, in the latter case, those envisioning a hibernating state in astronauts for deep space travel. Unravelling the physiological thresholds and temperature dependence of IBAs will provide new impetus to these research quests.

## 1. Introduction

At the Cretaceous–Palaeogene (K–Pg) boundary about 65.5 million years ago (Ma) the ancestor of the placental mammals (Eutheria) survived the meteorite impact at Chicxulub, Mexico [1], which killed the non-avian dinosaurs and many other animals and plants [2–4]. A small (6–245 g), insectivorous ancestor inherited a tropical Earth, along with a few egg-laying mammals (Montremata), some marsupials (Metatheria) and a few lineages (e.g. Multituberculata) which went extinct during the Cenozoic [2]. Ecological release from the vice grip which the dinosaurs held over Mesozoic mammals drove remarkably rapid evolutionary processes within several hundred thousand years of the extinction event [2]. Four new placental lineages (Xenarthra, Afrotheria, Laurasiatheria and Euarchontoglires) [2] appeared very suddenly, harbouring forms that displayed spectacular new morphological and physiological characteristics [5–8]. The long *ca.* 160 Myr stint of the nocturnal, small, insectivorous mammal was over, and gave way to the age of the mammals, the Cenozoic. Yet, no placental mammal would exist today had this ancestor not survived the global short- and long-term effects of the Chicxulub impact [3,4] and an Indian Ocean meteorite impact 40 000 years later [9]. How did this placental ancestor, as well as the monotremes and the marsupials, survive when so many other vertebrate groups did not?

There is growing debate about whether the ballistic impact ejecta that re-entered the Earth's atmosphere following the Chicxulub impact could have generated an initial infrared heat pulse sufficient to ignite wildfires globally [10–15]. If global wildfires did occur, they would undoubtedly have been responsible for the extermination of all mammals that could not seek safe refuge from the short- and long-term effects of the fires. Indeed, it is the

differential survival of vertebrates following the impact which currently provides one avenue of support for the wild-fires notion [3,11]. No large-sized, non-marine reptile, bird or mammal, that is, a vertebrate too large to seek refuge underground, in tree cavities or underwater, survived the K-Pg boundary extinction event [3]. The predominant hypothesis is that small mammals survived both the short- and long-term effects of the impact by hibernating in a safe refuge, typically, underground [3,16].

It has been estimated that the long-term effects of the impact lasted for a year or more [3,4]. However, in extant tropical placental mammals there is no known hibernation phenotype that would allow such long periods of hibernation. Long-term hibernation (more than six months) is typically associated with mammals which inhabit temperate, high-latitude and/or high-altitude, highly seasonal cold environments [17]. For example, year-long hibernation has been reported in captive mountain pygmy possums (a marsupial) [18]. Cold environments appeared in the Late Cenozoic only, and certainly did not exist at the K-Pg boundary [19,20]. Indeed, until relatively recent reports of hibernation in Malagasy primates [21,22] and tenrecs [23,24], and in the echidna (a monotreme) from semi-tropical Queensland, Australia, [25,26], it was thought that hibernation was a physiological capacity limited to high latitude, temperate mammals only [17].

In this study, we report a plesiomorphic (ancestral) capacity for long-term hibernation that exists in an extant, phylogenetically basal, tropical placental mammal, the common tenrec, *Tenrec ecaudatus*. The Tenrecidae belong to the superorder Afrotheria, which includes elephants, dugongs and manatees, hyraxes, golden moles, elephant-shrews (sengis) and the aardvark [27]. The tenrecs colonized Madagascar from Africa ca. 47 Ma and underwent spectacular adaptive radiation on the island thereafter [28]. We measured the core body temperature ( $T_b$ ) of free-ranging animals in the dry deciduous forests of western Madagascar. We argue that the capacity for long-term tropical hibernation in basal placental mammals was the key attribute which enabled them to survive the K-Pg extinction event along with presumably heterothermic marsupial [29] and monotreme [25,26,30] ancestors.

## 2. Material and methods

### (a) Study animals

The common tenrec, *T. ecaudatus* is the largest species (1–2 kg) within Tenrecidae (Afrotheria) on Madagascar and is also one of the largest extant insectivores [31]. It has a very cosmopolitan distribution inhabiting virtually every habitat type on Madagascar, including arable land, pastureland, plantations, rural gardens and urban areas [31,32]. *Tenrec ecaudatus* is known to hibernate during the austral winter [26,33,34], but supporting data are scarce. Local hunters from Amparafara southeast of Antananarivo have reported anecdotal evidence that males hibernate earlier than females and juveniles [35,36]. Males apparently start hibernating between February and April, whereas females commence as late as May. Both sexes were reported to arouse in October and November which is the mating season [31].

Over two seasons (2010 and 2011) at Ankarafantsika (see 'Study site'), 22 tenrecs were captured; seven adult males (781–992 g), five sub-adult males (316–377 g), three adult females (661–762 g), two sub-adult females (184 and 413 g) and five

sub-adults of undetermined sex (312–467 g). All animals were caught by hand, by walking the established trails in the area at night with local guides. Individuals were located, captured and transported back to the research camp where they were housed in plastic containers lined with paper towels and provided with live insects and tinned sardines. Fifteen animals were surgically implanted with a combination of radio transmitter and body temperature data logger (see 'Procedures'), and released back into the wild within several days of capture. Animals that were not implanted were either small males (184–374 g) or were individuals in poor condition heavily infected with internal parasites. The fate of the implanted and released tenrecs varied; three were killed by feral dogs, two by unknown natural predators, three by Malagasy boas (figure 1), three disappeared from the study area either through poaching or natural movement, one hibernated for eight months in the same site, emerged and then left the study area, and three were excavated from their hibernacula after nine months of austral winter hibernation (see 'Results'). These data confirm the high rates of mortality at Ankarafantsika by feral dogs, snakes, natural predators and poachers [35], as reported also for greater hedgehog tenrecs, *Setifer setosus* [24].

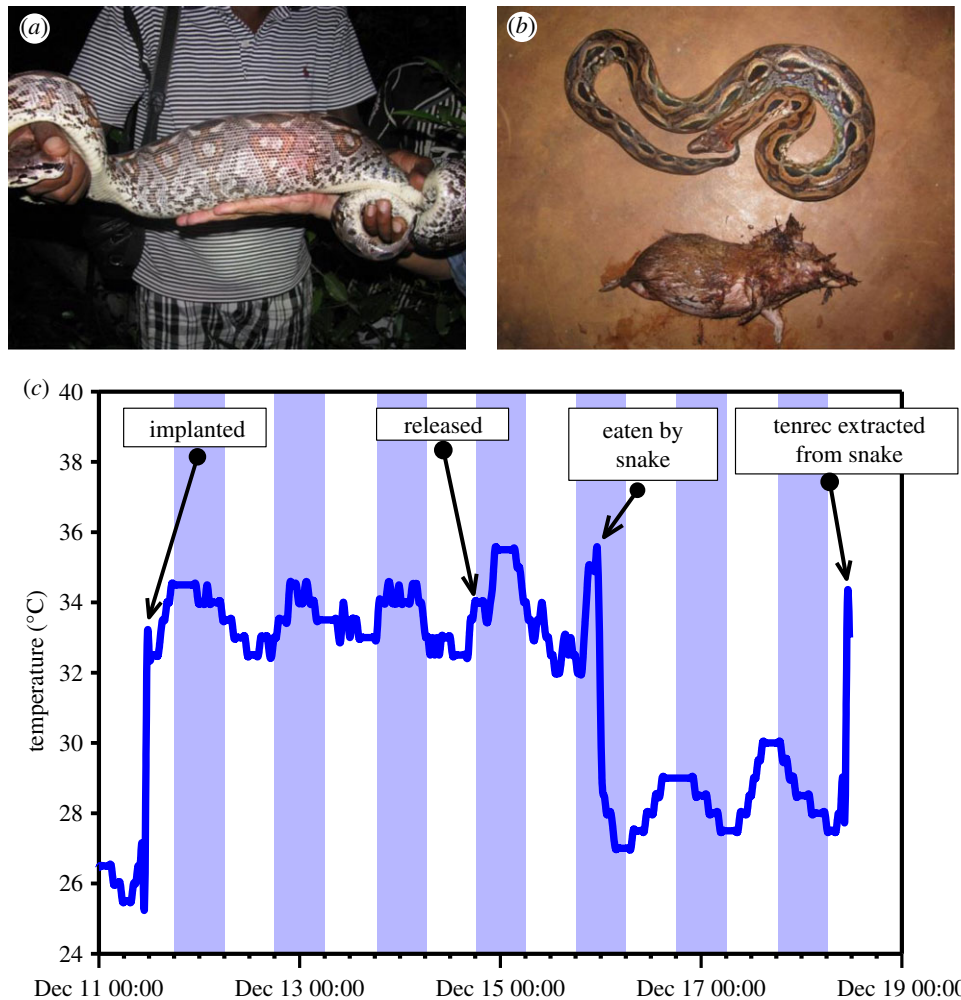
### (b) Study site

The study was conducted over two rainy seasons, from November 2009 to November 2011 in the Jardin Botanique A research area adjacent to the Ampijoroa Forestry Station in Ankarafantsika National Park (16°19' S, 46°48' E), Madagascar. The study site has been described by Levesque *et al.* [37]. Detailed ambient temperature ( $T_a$ ) data were recorded at various locations throughout the study site using DS1922L Thermochron iButtons (Dallas Semiconductor, Dallas, TX, USA) programmed to record once every 30 min at a resolution of 0.0625°C. DS1922L iButtons are inexpensive data loggers that measure and record temperature at user-defined rates which are being used increasingly in physiological and ecological research [38]. iButtons are encased in a stainless steel cap and communicate with a host computing device through a serial 1-Wire protocol. Ambient temperatures were measured by placing iButtons in black bodies (plastic cylinders spray-painted matt black) in Stevenson screens 1 m from the ground in shaded areas. Soil temperatures were recorded by burying iButtons at 0, 250 and 500 mm at various sites in the forest depending upon where animals were suspected of hibernating.

### (c) Procedures

The animals were implanted with a combination of radio transmitter and DS1922L Thermochron iButtons. Two iButtons were encapsulated in surgical wax (Paramat Extra-Merck KGaA, Darmstadt, Germany) together with a modified 2-stage collar transmitter (Merlin Systems Inc., Boise, ID, USA). The modification involved the removal of the collar and the replacement of the whip aerial with a coiled aerial. The resulting transmitter–logger packages had a total mass of around 13.0 g (mean 13.0 g, range 11.7–13.5 g). The iButtons were programmed to record body temperature at 30 or 36 min intervals with an accuracy of 0.5°C. One iButton was programmed with a delayed measurement onset that coincided with the memory limit of the other iButton. All iButtons were calibrated against a mercury thermometer prior to implantation as well as post-recovery to the nearest 0.1°C. No drift was observed.

During anaesthesia, oxygen and vapourized anaesthetic (isoflurane) were delivered to the animal through a mask at a rate of 700 ml min<sup>-1</sup>. Anaesthesia was induced at 1–2% isoflurane and maintained at 0.5%. The transmitter–logger package was inserted via an incision in the peritoneal cavity which was then sutured using 3/0 catgut and sealed with Vetbond tissue adhesive (3M, London, Ontario, Canada). An intramuscular



**Figure 1.** An illustration of predation of common tenrecs by snakes, one cause of high mortality at the Ankarafantsika site. (a) A captured Malagasy ground boa (*Acrantophis madagascariensis*) 2 days after swallowing an adult male tenrec. (b) The tenrec that was extracted from the live boa. (c) The body temperatures of the tenrec and the dead tenrec within the snake, captured by an iButton transmitter–logger package that was implanted into the tenrec. (Online version in colour.)

injection of antibiotics (1 ml/10 g of Duplocillin) was administered to prevent post-operative infection. The animals were kept for 1 day for post-surgery observations and were released at the site of capture. The locations of the animals were recorded frequently, usually daily, using either a R-1000 Telemetry Receiver (Communications Specialists, Orange, CA, USA) or a IC-R10 Communications Receiver (ICOM, Tokyo, Japan), connected to an RA-23K 'H' antenna (Telonics, Mesa, AZ, USA) or a standard 150-MHz Yagi antenna (manufactured by Cliff Dearden, Pietermaritzburg, KZN, South Africa) and a 150-MHz power booster (Merlin Systems Inc).

### 3. Results

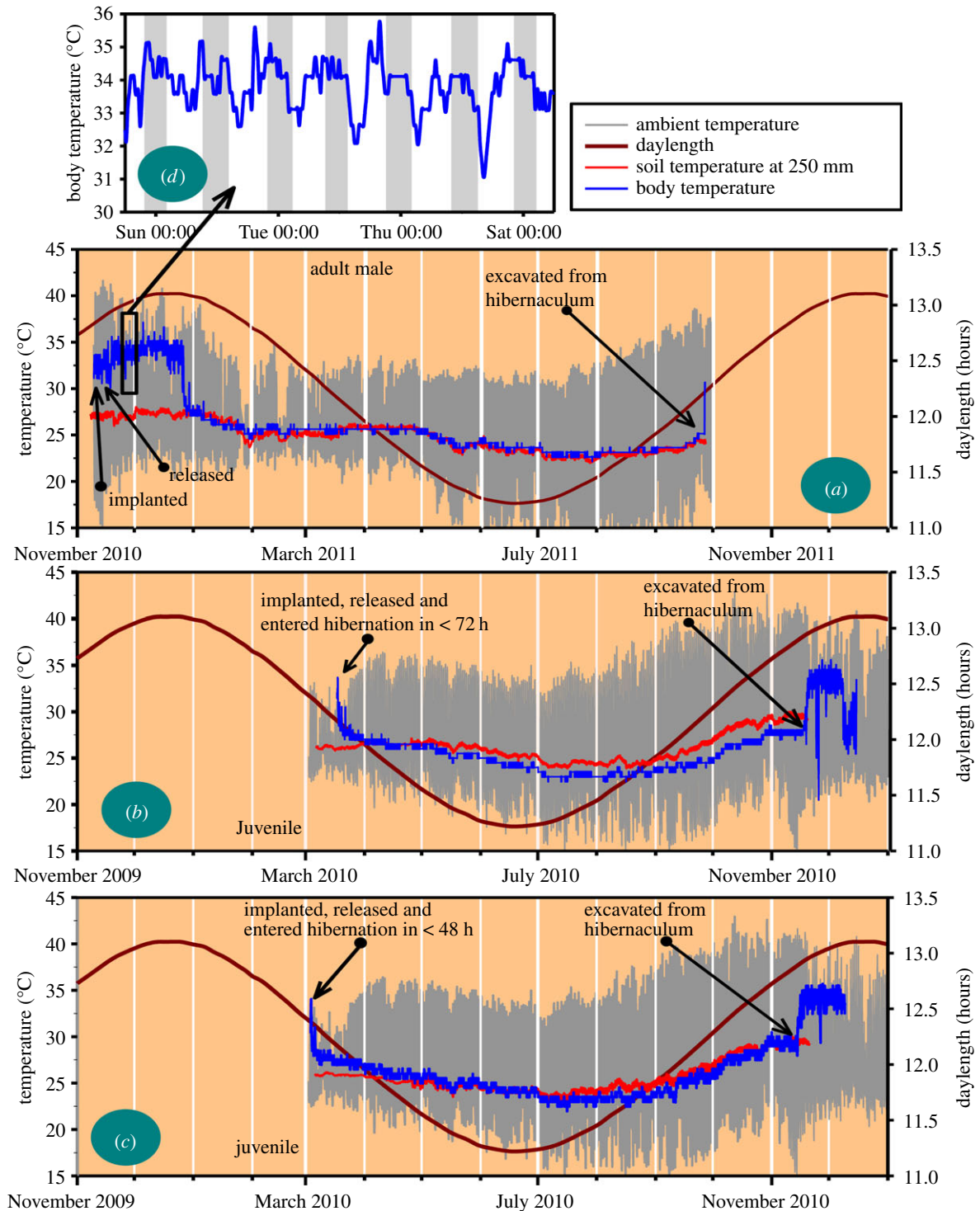
Continuous measures of  $T_b$  spanning up to nine months were obtained from three animals, two sub-adults of undetermined sex (377 and 413 g) in 2010, and one adult male (781 g) in 2011. After implantation and release, these three tenrecs avoided predation by burrowing into the sandy soil at the site at Ankarafantsika National Park. They remained in the same position until they were excavated after the transmitter signals began to weaken. We decided to excavate the animals to avoid losing the animals (and the body temperature ( $T_b$ ) data) through failed signal transmissions, and to avoid a repetition of the fate of one animal that was located daily for eight months in the same location, but which then aroused from hibernation and left the study area.

The animals were located at a depth between 250 and 500 mm in sandy soil. No discernable hibernaculum cavity or tunnel could be found during excavation. All three tenrecs were found to be torpid, and aroused fully within 1 h (figure 2).

The unique and most salient characteristic of the hibernation bouts which all three animals displayed was that they did not arouse once in a continuous period of hibernation lasting for eight to nine months. The  $T_b$  during hibernation never decreased below 22°C (figures 2 and 3). The hibernation  $T_b$  tracked soil temperature which also did not decrease below 22°C throughout the austral winter (figures 2 and 3). Unfortunately, we do not know how long the hibernation bouts might have lasted had we not excavated the animals.

### 4. Discussion

The lack of interbout arousals (IBAs) in tenrecs is particularly noteworthy because all temperate hibernators arouse periodically to normal  $T_b$ s for 12–24 h and then re-enter hibernation [39,40]. The mammalian hibernation phenotype sustains cardiovascular, biochemical and neuronal functions at low hibernation  $T_b$ s that are not expressed in non-hibernators [41–43]. For example, whereas the heart continues to function at a dramatically reduced rate during hibernation, in non-hibernators the onset of arrhythmia occurs at 32°C, atrial

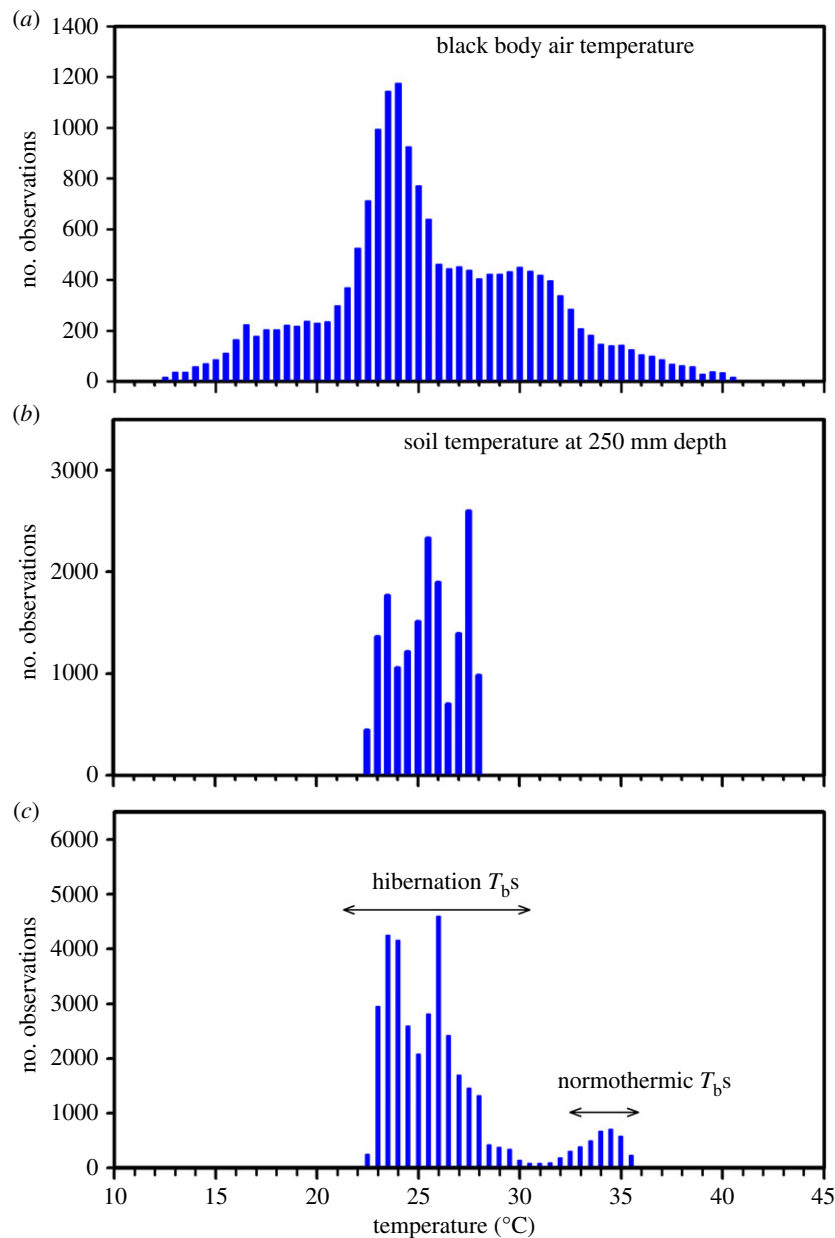


**Figure 2.** Hibernation bouts of eight to nine months in three common tenrecs (*Tenrec ecaudatus*) measured in the dry deciduous forest of western Madagascar. Note the complete lack of IBAs. The measures of soil temperature in (a) were obtained less than 3 m from the hibernaculum, whereas those in (b,c) were measured about 200 m from the hibernaculum, accounting for the lack of precise fit of the soil temperatures to the corresponding  $T_b$ s in (b,c). The torpor bouts in (b,c) in the period following excavation were induced in the laboratory when the animals were exposed to an ambient temperature of 18°C. The data in (d) illustrate the daily rhythms of  $T_b$  in a normothermic adult male tenrec prior to entry into hibernation. (Online version in colour.)

fibrillation at 30°C and cardiac arrest at 15°C [41]. These hypothermic influences do not occur in hibernators. In the most extreme case, Arctic ground squirrels (*Urocyon parryi*) maintain  $T_b$  at  $-2^{\circ}\text{C}$  to  $-3^{\circ}\text{C}$  during three-week hibernation bouts [44].

There is much debate surrounding the fitness benefits of IBAs in temperate hibernators given the very high energetic costs that are involved in arousals [40,41,45]. IBAs may be associated with the restoration of neuronal function

and metabolic imbalances (depletion and accumulation of metabolites) as well as gluconeogenesis [41,45–47]. It is becoming increasingly apparent that hibernation is a plesiomorphic trait in mammals [7,25,48] (although see [49]) so IBAs could be a derived trait in the temperate hibernation phenotype which evolved following the onset of global cooling *ca.* 50 Ma [7]. However, lesser hedgehog tenrecs (*Echinops telfairi*) display IBAs when held at a constantly low temperature in the laboratory [50,51], and early laboratory data



**Figure 3.** Frequency distributions of black body air temperatures (a), soil temperatures at a depth of 250 mm (b) and body temperatures (c) of an adult male tenrecs (data from figure 2a). Note that, throughout the austral winter, neither the soil nor the body temperature decreased below 22°C. (Online version in colour.)

suggest that *T. ecaudatus* can self-arouse from hibernation at  $T_b$ s below 20°C [52]. IBAs cannot be discerned, though, from data from free-ranging *E. telfairi* or *S. setosus* during the austral winter [23,53]. The lack of IBAs that we report here may therefore represent a temperature-dependent response and may not necessarily constitute a characteristic of the plesiomorphic hibernation phenotype.

The lack of IBAs in free-ranging *T. ecaudatus* may point to a critical threshold  $T_b$  only below which accumulated metabolic imbalances are sufficient to necessitate periodic restorative euthermia. Data from free-ranging *Cheirogaleus* dwarf lemurs from Madagascar illustrate and support this threshold concept well [54]. During hibernation, dwarf lemurs lacked IBAs when  $T_b$  passively tracked large daily fluctuations in hibernaculum temperatures (daily  $T_b$  minima 15.5–19.3°C, maxima 28.5–31.2°C). However, in well-insulated hibernacula, IBAs did occur because daily minima were 18.4–20.3°C but maxima only 23.1–25.0°C, i.e. never exceeding 30°C. These data suggest that, in poorly insulated hibernacula, daily increases in  $T_b$  to approximately 30°C through passive heating

may be sufficient to restore accumulated metabolic imbalances that occurred when daily  $T_b$  decreased below 20°C, whereas the  $T_b$  maxima in well-insulated hibernacula were too low for restorative metabolic homeostasis.

The identification of putative  $T_b$  thresholds for metabolic imbalance, as well as the minimum  $T_b$  threshold for restorative metabolic homeostasis, has important implications for biomedical research and future space travel. It should provide new impetus in understanding the limits of induced metabolic suppression and hypothermia for prolonged medical treatments, such as trauma, strokes, asphyxiated neonates, or for hibernation induction in astronauts.

It has been predicted that manned space flights to Mars will occur within 20–30 years and that the astronauts will travel in a hibernating state for the six to nine months that it will take to get there [55–57]. This prediction assumes, of course, that ischaemic damage, for example to the heart, will be avoided at  $T_b$ s that currently compromise function. Our tenrec data suggest that periodic arousals from hibernation will not be necessary if the  $T_b$  of hibernating astronauts is maintained

above a certain threshold  $T_b$  which, in the case of tenrecs, was approximately 22°C. Reductions of  $T_b$  below this threshold, though, are likely to induce metabolic imbalances and ischaemic damage. Pinpointing the lowest safe limits of a human hibernating  $T_b$  is important because it will have profound logistical and cost implications for deep space travel.

Hibernation lowers the risk of extinction [58], increases winter survival rates [59], and facilitates reproductive and life-history flexibility [24,60]. Indeed, *T. ecaudatus* display some of the most unique mammalian life-history traits, such as the largest litter sizes (as many as 30), of all mammals [61]. Our study also revealed an exceptionally high mortality rate during the non-hibernating season at the site from predation [24]. Thus, selective factors involved in long-term tropical hibernation seem to be different from those which drove derived seasonal hibernation in temperate hibernators. Our hibernation data show some affinities to the 'pro-toendothermy' first noted in echidnas [25,26], suggesting retention of plesiomorphic characteristics of hibernation on Madagascar through phylogenetic inertia.

In tropical hibernators, there is arguably no fitness benefit to remaining active above ground and exposed to predators when not directly involved in reproduction [25]. Thus, we support the argument that, in addition to the seasonal reduction in food availability and the prohibitive costs of normothermy which make hibernation essential in temperate hibernators, the minimization of predation risk and hence the increase in longevity also confers huge fitness benefits to tropical hibernators. Predation-avoidance hibernation may be an ancient plesiomorphic characteristic in mammals

and is a legacy, perhaps, of the 163 Myr of ecological suppression by the dinosaurs. It enabled the ancestral placentals, as well as the marsupials and monotremes also known to hibernate [30,39], to endure the short- and long-term devastations of the K-Pg asteroid impact, a capacity which is possibly the sole explanation for the existence of mammals today. Although the lack of IBAs would undoubtedly have conserved energy during sustained hibernation, they probably represent a temperature-dependent physiological response which was not necessarily a critical component of the plesiomorphic hibernation phenotype.

**Ethics statement.** All procedures involving the use of animals were approved by Madagascar National Parks (Permit 218/09/MEF/SG/DGF/DCB.SAP/SLRSE and 158/10/MEF/SG/DGF/DCB.SAP/SCBSE) and comply with all national Malagasy laws.

**Data accessibility.** All data reported in this study can be accessed from the electronic supplementary file.

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