© 2018. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2018) 221, jeb185900. doi:10.1242/jeb.185900

RESEARCH ARTICLE

Extreme physiological plasticity in a hibernating basoendothermic mammal, *Tenrec ecaudatus*

Michael D. Treat[1,*], Lori Scholer[1], Brandon Barrett[1], Artur Khachatryan[1], Austin J. McKenna[1], Tabitha Reyes[1], Alhan Rezazadeh[1], Charles F. Ronkon[1], Dan Samora[1], Jeremy F. Santamaria[1], Claudia Silva Rubio[1], Evan Sutherland[1], Jeffrey Richardson[2], John R. B. Lighton[2] and Frank van Breukelen[1,*]

ABSTRACT

Physiological plasticity allows organisms to respond to diverse conditions. However, can being too plastic actually be detrimental? Malagasy common tenrecs, *Tenrec ecaudatus*, have many plesiomorphic traits and may represent a basal placental mammal. We established a laboratory population of *T. ecaudatus* and found extreme plasticity in thermoregulation and metabolism, a novel hibernation form, variable annual timing, and remarkable growth and reproductive biology. For instance, tenrec body temperature (T_b) may approximate ambient temperature to as low as 12°C even when tenrecs are fully active. Conversely, tenrecs can hibernate with T_b of 28°C. During the active season, oxygen consumption may vary 25-fold with little or no change in T_b. During the austral winter, tenrecs are consistently torpid but the depth of torpor may vary. A righting assay revealed that T_b contributes to but does not dictate activity status. Homeostatic processes are not always linked, e.g. a hibernating tenrec experienced a ~34% decrease in heart rate while maintaining constant body temperature and oxygen consumption rates. Tenrec growth rates vary but young may grow ~40-fold in the 5 weeks until weaning and may possess indeterminate growth as adults. Despite all of this profound plasticity, tenrecs are surprisingly intolerant of extremes in ambient temperature (<8 or >34°C). We contend that while plasticity may confer numerous energetic advantages in consistently moderate environments, environmental extremes may have limited the success and distribution of plastic basal mammals.

KEY WORDS: Thermoregulation, Oxygen consumption, Variable body temperature

INTRODUCTION

Tenrecs are basoendothermic placental mammals primarily from Madagascar that are phylogenetically placed in Afrotheria (Lovegrove, 2012; Everson et al., 2016). Prevailing thought is that a small tenrec species arrived in Madagascar 30–56 MYA and radiated into the remaining extant species (Poux et al., 2008; Everson et al., 2016). This tremendous adaptive radiation resulted in species that are terrestrial, fossorial, arboreal and even aquatic (Garbutt, 1999). Tenrecs have many ‘ancestral’ features that seem even more plesiomorphic than those of the reconstructed hypothetical placental ancestor *Schrëwdinger*. *Schrëwdinger* was presumed to lack a cloaca, but to have a large and gyrencephalic brain, zygomatic arches and tympanic bullae, and internal testes (O’Leary et al., 2013). In comparison, tenrecs have a cloaca and, in the case of *Tenrec ecaudatus*, have the smallest brain relative to body mass of all extant mammals (including monotremes and marsupials), are lissencephalic, lack zygomatic arches and tympanic bullae, and have internal testes that are located near the kidneys (Lillegraven and Eisenberg, 1983). These features would suggest that tenrecs may be reminiscent of basal placental mammals.

In Lovegrove’s (2012) plesiomorphic–apomorphic endothermy model, he posited that ancestral mammals were heterothermic and more rigid homeothermy is a derived condition. Lovegrove (2012) defines a basoendotherm simply as any mammal with a body temperature (T_b) in the 20th percentile of the frequency distribution of the mammalian T_b dataset, meaning they must exhibit resting T_b <35°C. Lovegrove (2012) notes that the endothermic conditions of extant basoendotherms were likely also exhibited by Cretaceous or early Cenozoic mammals. Tenrecs are considered basoendothermic because of the presumed phylogenetic placement of afrotherians and because existing data suggest their T_b is generally <35°C (Lovegrove, 2012). T_b is also moderately variable in many of the basal mammalian taxa; some monotremes, marsupials, xenarthrans and afrotherians experience active T_b that varies by as much as 8°C (Schmidt-Nielsen et al., 1966; McManus, 1969; Scholl, 1974; Gilmore et al., 2000; Oelkrug et al., 2012). The limited existing data on active tenrecs suggest a T_b always <35°C with moderate variation (T_b=31.82±0.098°C, mean±s.e.m.; Racey and Stephenson, 1996; Poppitt et al., 1994; Lovegrove et al., 2014, Levesque and Lovegrove, 2014; Levesque et al., 2014).

More pronounced heterothermy in small mammals occurs during hibernation in conjunction with metabolic depression. Importantly, metabolic depression and low T_b are linked, e.g. it is thought that the metabolic depression allows T_b to decrease and that the low T_b may allow depression of metabolic processes (e.g. van Breukelen and Martin, 2015). For instance, hibernating ground squirrels experience decreases of T_b to as low as −2.9°C (Barnes, 1989) and oxygen consumption rates to as low as 1/100th of active rates. Hibernation is also found in basal mammals including the echidna, some marsupials, and afrotherians like the elephant shrew, golden moles and tenrecs (Ruf and Geiser, 2015; Scantlebury et al., 2008). All five spiny tenrec species, including the focus of this work, *T. ecaudatus*, are known to hibernate (Stephenson and Racey, 1994). The limited data on hibernating *T. ecaudatus* demonstrate that T_b follows soil temperature for the duration of the hibernation season with no evidence of brief periods of euthermy between bouts of torpor (Lovegrove et al., 2014). The lack of interbout arousals is unique for small hibernators. Interestingly, dwarf lemurs (*Cheirogaleus medius*) will arouse from hibernation if they experience significant periods

---

[1]School of Life Sciences, University of Nevada, Las Vegas, Las Vegas, NV 89154, USA. [2]Sable Systems International, Las Vegas, NV 89032, USA.

*Authors for correspondence (michael.treat@unlv.edu; frank.vanbreukelen@unlv.edu)

M.D.T., 0000-0002-3247-4601; L.S., 0000-0002-7596-2058; T.R., 0000-0001-7128-6366; D.S., 0000-0001-7452-8922; F.v.B., 0000-0001-9653-0273

Received 6 June 2018; Accepted 20 August 2018

wherein ambient temperature (T_a) is <30°C (Dausmann et al., 2004; Dausmann et al., 2005). Soil temperature in the *T. ecaudatus* field study was as low as ~22°C for several months. An interesting question is whether *T. ecaudatus* would arouse if hibernating at an even lower T_a or whether these tenrecs simply hibernate continuously. If tenrecs are indeed plesiomorphic, perhaps a lack of interbout arousal was an ancestral hibernation characteristic. If so, what may be gleaned from characterizing the physiology of tenrec hibernation?

We established a breeding colony of *T. ecaudatus* in order to examine key parameters affecting their life history in the controlled setting of the laboratory. We found captive tenrecs to exhibit extreme physiological plasticity. Active and hibernating tenrecs may have identical T_b. Numerous other tenrec life history traits are also highly plastic. We question why such a plastic mammal is not more successful, i.e. if being plastic has selective advantages, then why do the tenrecs not have a more robust global distribution? We provide a surprising explanation that being too plastic may have limited the success and distribution of such mammals in more variable environments. Moreover, by being more precise in their thermoregulation and physiology, the more modern boreoeutherian mammals may have evolved to persist in more variable environments, leading to a wider global distribution.

MATERIALS AND METHODS

Acquisition and maintenance of the *T. ecaudatus* colony

Forty wild-caught common tenrecs, *T. ecaudatus* (Schreber 1778), were imported under federal and state permit from Mauritius in June 2014. Approval for this study was granted by the University of Nevada, Las Vegas Institutional Animal Care and Use Committee. Tenrecs were typically maintained on Mazuri insectivore diet (Saint Paul, MN, USA). Tenrecs were supplemented with Purina Puppy Chow (St Louis, MO, USA) and/or Hills A/D diet (Topeka, KS, USA). Tenrecs were weighed regularly to monitor health. All tenrecs were maintained on a 12 h:12 h light:dark cycle. For temperature-controlled experiments, tenrecs were individually housed in rat cages and/or metabolic chambers within an environmental chamber that maintained precise temperature control.

Measurement and validation of T_b

Tenrecs arrived in a torpid state during their hibernation season (austral winter), which precluded surgery to implant temperature loggers. However, we found that T_b could be reliably and accurately determined through the use of pre-calibrated iButton temperature loggers (DS1922L; Maxim Inc., San Jose, CA, USA) held against the chest by specially designed harnesses. The iButtons were typically set for high-resolution polling (~4000 samples) and sampling frequency typically ranged from 1 to 10 min depending on the desired polling duration. iButton data were downloaded at the end of each experiment period. In an unrelated study, we collected tissue samples from active and torpid tenrecs that were harnessed with chest iButtons at the time of death. We found notable regional heterothermy within the abdomen with as much as ~3°C variation in temperature depending on probe location (e.g. lower abdomen versus near the liver). In order to allow consistent T_b measurement, we measured T_b at the liver with a thermocouple. When tenrecs were housed at a T_a of 12, 20 or 28°C, liver temperature ranged from 12.5 to 30.5°C. When compared with the matching chest temperatures, liver temperature was 0.467±0.18°C (mean±s.e.m.) higher ($P<0.05$, paired *t*-test, $N=21$; $r^2>0.99$ in Fig. S1A). These results may be expected as liver temperature in other mammals is slightly higher than other indicators of core T_b (Dewasmes et al., 2003). Nevertheless, *T. ecaudatus* chest temperature reliably and accurately reflects T_b.

Respirometry

Aerobic respirometry (oxygen consumption, $\dot{V}_{O_2}$, and carbon dioxide production, $\dot{V}_{CO_2}$) was measured with the Promethion Continuous Metabolic Phenotyping System and ExpeData software (Sable Systems International, Las Vegas, NV, USA). The Promethion system auto-baselines for 30 s every 15 min with environmental air, otherwise sampling from each metabolic chamber every second. Metabolic chambers were constructed from Lettuce and Produce Keeper containers (~1.8 l; Container Store, Coppell, TX, USA). Flow rates were 500 ml min^{-1}. Preliminary analyses revealed tenrecs to display three physiological states: hibernation, facultative torpor and active. During the austral winter, tenrecs were hibernating and showed the typical signs of torpor, e.g. T_b approached T_a and tenrecs were lethargic even when disturbed. We noted that upon entry into the metabolic chamber, T_b would sometimes slowly increase by 1–6°C for various periods (taking up to 3–4 h to peak with a similar period to return to the original value) in what appeared to be a partial thermal arousal. Importantly, these tenrecs maintained a lethargic state typical of torpor and never aroused to an active state. Furthermore, at T_a <20°C, tenrecs were noted to experience 30–45 min apneic periods. To avoid sampling bias caused by the partial thermal arousals and the apneic periods, data for hibernating tenrecs represent an 8 h period of stable T_b (after ~14 h of a typical 24 h assay). During the active season (after the resumption of feeding, i.e. October to April), tenrecs were also sometimes facultatively torpid wherein T_b approached T_a and animals displayed lethargy typical of torpor. Care was taken to gently place the tenrecs into the metabolic chamber as these animals were prone to disturbance and would occasionally arouse from the facultative torpor into an active state (in contrast to hibernators, which remained consistently lethargic). Analyses were restricted to 90 min for these assays because of the lability of facultative torpor. Active-season tenrecs that demonstrated no signs of lethargy had remarkably variable resting $\dot{V}_{O_2}$ and T_b. To best illustrate this variability, the analyses comprised a 60 min period with either the highest or lowest stable $\dot{V}_{O_2}$. We defined stable as a period where there was little variability that may have indicated obvious activity or movement. The chamber was small enough to prevent the animals from exercising. Each analysis group consisted of eight tenrecs except for facultative torpor at 28°C, where only seven tenrecs were available for the analysis. All $\dot{V}_{O_2}$ data are presented as ml O_2 g^{-1} body mass h^{-1}. Box plots were generated using standard box plot parameters wherein the box identifies the first quartile (bottom line), median (middle line) and third quartile (top line) of the dataset; the whiskers represent the maximum and minimum values for each dataset. In order to best demonstrate the extreme variability in *T. ecaudatus* aerobic metabolism, we chose to omit outlier analyses and all data are included.

Electrocardiogram (ECG) measurement and heart rate analysis

ECGs were collected through use of a three-lead ECG module, iWorx Data Recorder and LabScribe (IWX-214 and LabScribe v3; IWorx Systems Inc., Dover, NH, USA). Heart rate (beats min^{-1}) was determined for a minimum of three consecutive minutes every 10 min of the analysis period.

Righting response time (RRT) assay

Tenrecs ($N=8$, except for the April assay at 28°C, wherein 7 tenrecs were used because of an unexpected mid-trial death) were housed at 12, 20 or 28°C for a minimum of 24 h prior to the righting trials. To avoid potential bias from disturbance, the order in which animals were used for each trial was randomized through use of a random number generator. We found no correlation between this order and RRT. Each trial followed strict timing protocols throughout the year, e.g. animals were placed into the apparatus within 20 s of removal from the environmental chamber and there were 3 min intervals between animals. Animals were placed on their backs in a cradle and allowed 60 s to attempt to right themselves. Righting was video recorded and the time to right was determined from the video (Movies 1 and 2).

Emergence analysis

Most hibernators experience marked changes in T_b at the cessation of the hibernation season as active behaviors resume. However, even active tenrecs have variable T_b. As a result, we used body mass changes as tenrecs resumed eating following emergence from hibernation to estimate date of emergence.

Statistics

As appropriate, data were analyzed using ANOVA with subsequent Fisher's least significant difference (LSD) *post hoc* analyses or paired and unpaired Student's *t*-test. Statistical differences were assumed when $P<0.05$. A Bonferroni adjustment in Fig. 2 was used because of the large number of comparisons. All data presented with error calculations (e.g. $\dot{V}_{\mathrm{O_2}}$, mass analysis, etc.) are given as means ±s.e.m. unless otherwise noted.

RESULTS

T_b

T_b in captive tenrecs was extremely plastic during both hibernation and the active season (Fig. 1). During the austral winter, tenrecs can seasonally hibernate at low or high T_a from at least 12 to 28°C (Fig. 1). During hibernation, tenrec T_b approximates T_a and tenrecs are consistently lethargic. Importantly, when housed at 12°C and disturbed, T_b of hibernating tenrecs was noted to increase only ∼1–6°C. Remarkably, active tenrecs may also experience T_b ranging from ∼12 to 34°C that frequently waxes and wanes throughout the day. Even with a T_b of ∼12.5°C, these animals display no lethargy or ataxia and are capable of running and swimming. Although active tenrec T_b is oftentimes quite variable throughout the day, T_b may also be relatively stable for shorter periods of time (Fig. S1B–D). Not surprisingly, the differences between T_b and T_a decreased as T_a increased, e.g. animals maintained at a T_a of 28°C had less variation in T_b than animals maintained at a T_a of 12°C. Active-season tenrecs were also capable of using torpor facultatively at a T_a of 12, 20 and 28°C (Fig. 1). Active-season tenrecs that had resumed active behaviors, e.g. eating and reproduction, were considered to be in facultative torpor when the tenrec became lethargic and T_b approximated T_a for several days. In contrast to hibernating animals, facultatively torpid tenrecs were sensitive to disturbance wherein animals would arouse into a fully active and alert state with no indication of lethargy or ataxia.

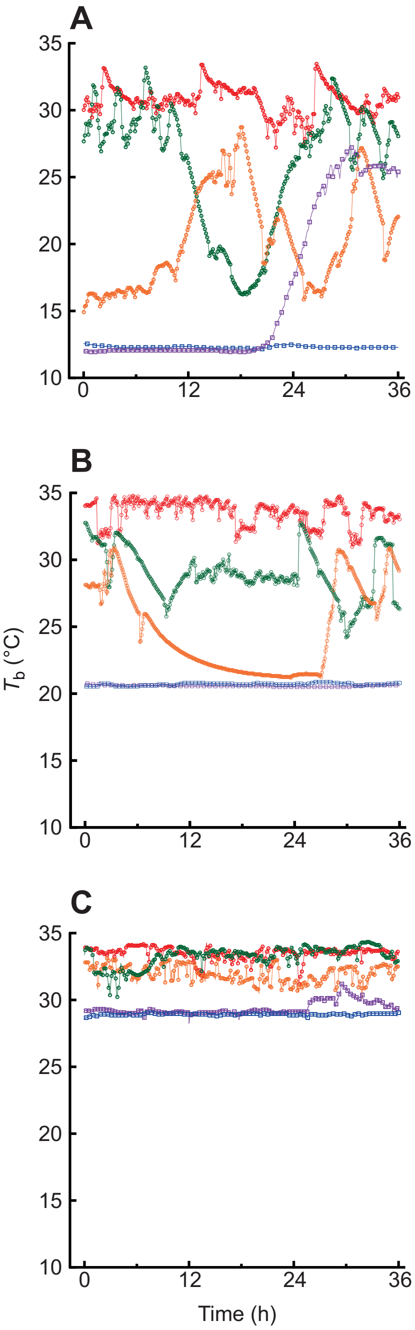

Fig. 1. Extreme variability of body temperature (T_b) of *Tenrec ecaudatus*. Tenrecs were housed at an ambient temperature (T_a) of (A) 12°C, (B) 20°C or (C) 28°C. Note the lack of homeothermy in active tenrecs (red, green and orange circles). Individual active tenrecs may have low or high T_b that can change >2.5°C h^{-1}. Alternatively, active-season tenrecs may spontaneously enter periods of facultative torpor (purple squares) where T_b approximates T_a. During the austral winter, tenrecs maintain a constant state of hibernation (blue squares).

Metabolism

Metabolism in active tenrecs may vary by 25-fold (Fig. 2). In order to best demonstrate this extreme variability, 60 min periods of the highest (active high) and lowest (active low) stable respirometry data are presented in Fig. 2. Oxygen consumption rate in active tenrecs did not simply switch between high and low levels, but rather occurred along a continuum of rates between the active high and active low levels. Tenrec $\dot{V}_{\mathrm{O_2}}$ was only partially dependent on T_b. For instance, the active low $\dot{V}_{\mathrm{O_2}}$ in Fig. 2A was not statistically different from the $\dot{V}_{\mathrm{O_2}}$ of facultative torpid or hibernating tenrecs despite these active tenrecs having higher T_b (ANOVA, $P>0.05$). Tenrecs may also have similar high $\dot{V}_{\mathrm{O_2}}$ (∼1 ml $\mathrm{O_2}$ g^{-1} h^{-1}) and T_b (∼28°C) even when there is an 8°C difference in T_a (T_a of 12 or 20°C; Fig. 2A,B). Additional examples of how metabolism may be disconnected from T_b in individual tenrecs are provided in Figs S2 and S3.

When all data were analyzed together, no differences in $\dot{V}_{\mathrm{O_2}}$ were found between the hibernating, facultative torpid or even the active

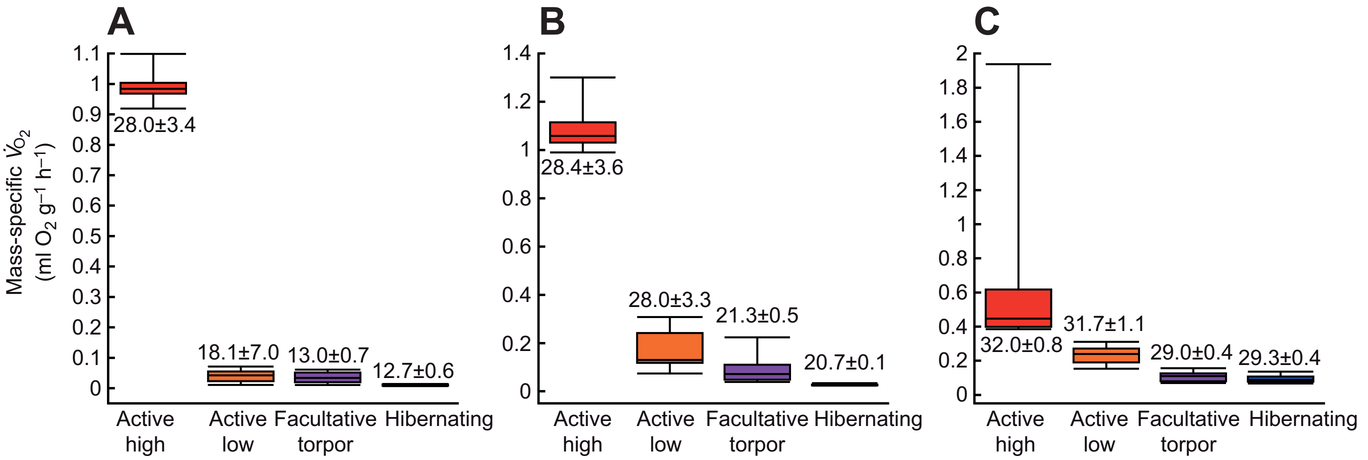

Fig. 2. Plastic oxygen consumption ($\dot{V}_{O_2}$) in tenrecs. T_a was (A) 12°C, (B) 20°C or (C) 28°C. Data represent box plots of the highest (active high) or lowest (active low) $\dot{V}_{O_2}$ in non-torpid active-season tenrecs (see Materials and Methods, N=8). For comparison, data from active-season facultatively torpid tenrecs and hibernating tenrecs are included. Note, aerobic metabolism is not necessarily related to T_b or T_b–T_a differentials, e.g. active high values for 12 and 20°C are similar. All active high groups showed significantly greater $\dot{V}_{O_2}$ than all other comparisons. No other differences were detected when all groups were analyzed together (P<0.05; ANOVA). Numbers associated with the boxes represents T_b (°C; means±s.d.).

low state at T_a of 12, 20 or 28°C (Fig. 2; ANOVA, P>0.05). Only when active animals were removed from the analyses (i.e. reducing the number of comparisons by comparing only facultative torpid and hibernating tenrecs) did statistical differences between temperatures become evident; in these comparisons, $\dot{V}_{O_2}$ decreased with decreasing temperature as expected (Q_{10}=3.7 for hibernating tenrecs and 2.0 for facultatively torpid tenrecs between 12 and 28°C; ANOVA, P<0.05).

Both active and torpid tenrecs experienced extended periods wherein there were unexpected relationships between T_b, $\dot{V}_{O_2}$ and heart rate. For instance, identical $\dot{V}_{O_2}$ values were accommodated by heart rates that varied by 34% (Fig. 3). Additional examples of metabolic flexibility are provided in Figs S2 and S3.

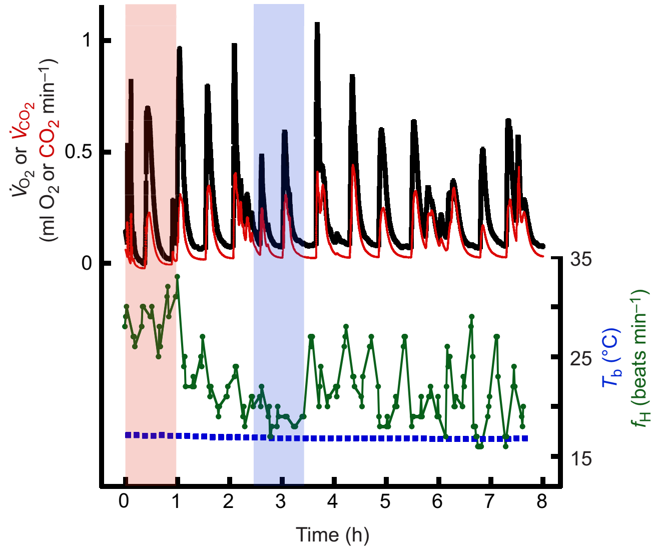

Fig. 3. Demonstration of the lack of coordination of basic homeostatic mechanisms. T_a was 16°C. Torpid $\dot{V}_{O_2}$ was the same in the two highlighted (red and blue) 60 min periods (0.171 ml O_2 min^{-1}). However, while heart rate (f_H) in the red phase averaged 28.8±2.0 beats min^{-1}, heart rate during the blue phase averaged 19.0±1.3 beats min^{-1}, representing a ∼34% decrease in heart rate despite identical $\dot{V}_{O_2}$. Note, the 30–45 min periods between breaths in this hibernating tenrec.

Righting response

As indicated above and unlike in other hibernators, we observed that T_b was a poor indicator of metabolic status. We noted that hibernating tenrecs, unlike common hibernator models such as ground squirrels, were not simply torpid or non-torpid during the hibernation season. Rather, early season hibernating tenrecs typically appeared 'less' torpid and more responsive to disturbance, mid-season hibernators were deeply torpid and resisted disturbance, and late season hibernators were less torpid. Furthermore, we found that T_b also partially predicted hibernation depth, e.g. a cold hibernating tenrec was more likely to be profoundly lethargic and a warm tenrec was more likely to be partially ambulatory and less ataxic when handled. Importantly, hibernating tenrecs were always somewhat lethargic and ataxic regardless of T_a. In order to best illustrate annual torpor use and this concept of 'more or less' torpid, we monitored lethargy in *T. ecaudatus* throughout the year through the use of a righting response assay (Fig. 4; Movies 1 and 2). In general, increased lethargy occurred when animals were housed at a lower T_a, in both active and hibernation seasons. Tenrecs housed at a T_a of 12°C were usually less likely to right themselves within the 60 s assay while tenrecs housed at a T_a of 28°C rarely spent more than a few seconds righting themselves. Hibernating tenrecs at a T_a of 28°C were very readily 'aroused' and although they were able to right quickly, we still noted some ataxia in these animals. Interestingly, some animals with T_b near T_a to as low as 12°C were able to right themselves quickly. Conversely, some warm animals took the full 60 s to right (Fig. S4). At a T_a of 12°C, a defined seasonality was present wherein *T. ecaudatus* appeared most lethargic in June–July and most active in December, consistent with our observations of the hibernation and active seasons (Fig. 4A).

Emergence from hibernation

Unlike in other hibernators, the end of the hibernation season in tenrecs was a gradual transition and occurred over a couple of weeks. As individual tenrecs transitioned out of hibernation, they slowly became less lethargic, less ataxic and more aware of their surroundings (L.S., M.D.T. and F.v.B., personal observations). Tenrecs then resumed active-season behaviors like eating, growth and reproduction. By tracking food intake and body mass, approximate dates of emergence from hibernation for each tenrec

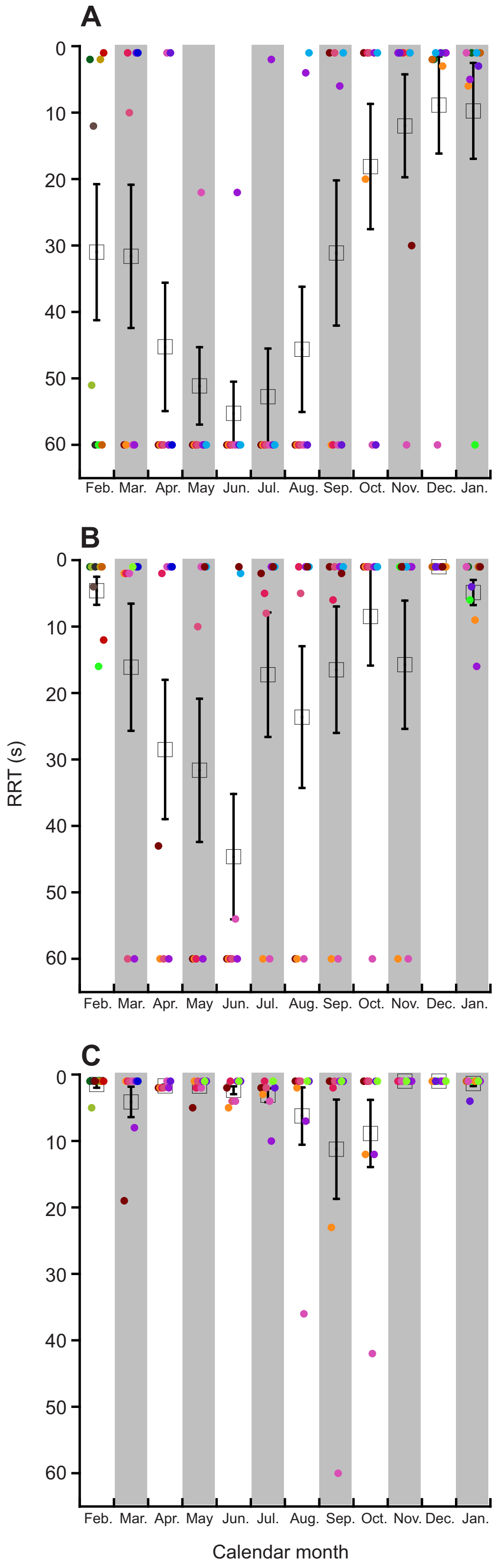

Fig. 4. Demonstration of seasonal and T_a effects on righting response time (RRT). Tenrecs were housed at a T_a of (A) 12°C, (B) 20°C or (C) 28°C. Filled circles of different colors represent individual tenrecs. Squares represent means±s.e.m. of that month's RRT. Seasonality was more evident in tenrecs housed at 12°C than at 28°C; however, even when housed at 28°C, some animals displayed a RRT of >20 s.

were determined (Fig. 5). Some tenrecs emerged as early as August or as late as January, with most tenrecs having exited hibernation by October or November (Fig. S5A).

Growth rates

To establish our colony, we obtained wild-caught juvenile and adult tenrecs that were generally small (262±15.9 g; *N*=35). Upon emergence from hibernation, these tenrecs ate copious amounts of food and grew tremendously in a short period of time (2.5- to 3-fold in ∼4 months; average maximal daily mass gain of 44.6±4.0 g day^{-1}; *N*=35; Fig. 5). This growth was not simply the result of fat accumulation as these animals also grew in scale. Furthermore, dramatic growth was not limited to juveniles as adult tenrecs also experienced similar growth (Fig. S5B).

Despite a birth mass of 12.15±0.36 g (*N*=31; four litters), captive tenrecs oftentimes weigh >400 g by the time they wean at 5 weeks. We observed juvenile tenrecs eating from their mothers' mouths and/or eating soft foods during the first week post-partum. The profound growth is not simply a function of tenrecs growing as quickly as possible as there may be surprising consistency of growth rates within a given litter (Fig. S5C,D). Further, there may be multiple growth rate trajectories represented within a given litter, e.g. some tenrecs may grow quickly while others may grow more slowly. Although most of our tenrecs grew quickly prior to the hibernation season, some juveniles entered hibernation at a body mass less than 150 g. These smaller tenrecs experienced the same profound post-hibernation growth as our wild-caught tenrecs.

T_b in pregnant and post-partum tenrecs

Prior to parturition, tenrec T_b may be variable during gestation (Fig. 6; Fig. S6). Following parturition, females experienced increased and more stable T_b (above 30°C; Fig. 6; Fig. S6). In one extraordinary case, a pregnant female housed at a T_a of 12°C experienced a >24 h period wherein T_b was 13.5±0.5°C (Fig. S6G). We estimated that she was ∼3 weeks into her pregnancy.

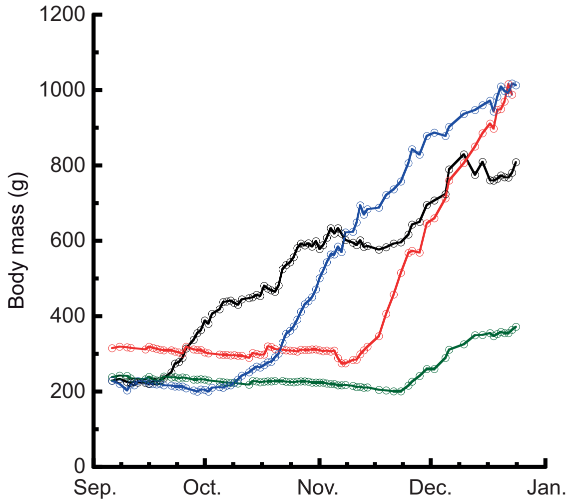

Fig. 5. Tenrecs may experience extreme growth following exit from hibernation. Tenrecs were observed to gradually increase in activity for as much as 2 weeks prior to the onset of very rapid growth and mass gain. Different colors represent individual tenrecs. Average daily maximum mass gain was 44.6±4 g day^{-1}, *N*=35.

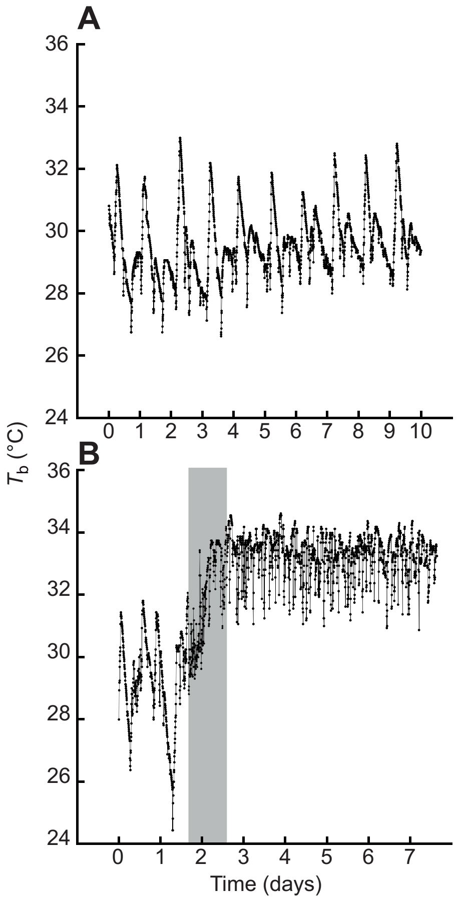

Fig. 6. Tenrecs can invoke periods of higher endothermy/homeothermy. (A) A non-pregnant tenrec shows typical variation in T_b. (B) Tenrecs that give birth (shaded area indicates day of parturition) maintain a higher and less variable T_b post-partum. These tenrecs were housed at room temperature.

DISCUSSION

Common tenrecs have highly variable T_b and rates of oxygen consumption (Figs 1–3 and 6; Figs S1–S4 and S6). This variability is not restricted to the hibernation season in tenrecs. Moderately variable active-season T_b is prevalent in many of the basal mammalian taxa. In monotremes like the echidna *Tachyglossus aculeatus*, active T_b was 30.7±1.03°C with a range of as much as 4.1°C when held at a T_a between 0 and 25°C (Schmidt-Nielsen et al., 1966). In a marsupial, the opossum *Didelphis viginiana*, T_b was typically 33–35°C, with the lowest recorded T_b reaching 30.8°C when held at a T_a from −10 to 32°C (McManus, 1969). In a xenarthran, the brown-throated three-toed sloth, *Bradypus variegatus*, active T_b ranged from 28 to 35°C with the circadian cycle (Gilmore et al., 2000). Of note is that these ranges for T_b are relatively moderate, with few animals experiencing variations of more than 8°C. Even in other afrotherians like elephant shrews, T_b varied by only a few degrees during the active season (Mzilikazi and Lovegrove, 2004; Mzilikazi and Lovegrove, 2005; Oelkrug et al., 2012). We found ∼20°C variation in T_b in both active and hibernating tenrecs.

In *T. ecaudatus*, active-season aerobic metabolism (active low) may be statistically comparable to that of even torpid tenrecs and independent of a reduction in T_b (Fig. 2). Conversely, oxygen consumption in active tenrecs may also be ∼25-fold higher (active high). For instance, at a T_a of 12°C, stable $\dot{V}_{O_2}$ across a 60 min period in active tenrecs was as low as 0.0405±0.021 ml O_2 g^{-1} h^{-1} (active low) or as high as 0.9916±0.052 ml O_2 g^{-1} h^{-1} (Fig. 2). Surprisingly, T_b did not dictate metabolism. Tenrecs housed at 12 and 20°C maintained similar $\dot{V}_{O_2}$ and T_b, e.g. active high $\dot{V}_{O_2}$ across a 60 min period for animals maintained at a T_a of 20°C was 1.0856±0.097 ml O_2 g^{-1} h^{-1} despite these animals having the same T_b (∼28°C) as the active high animals that were maintained at 12°C. Remarkably, T_b of the active low animals housed at 20°C was also ∼28°C, despite these tenrecs having a ∼6.4-fold lower $\dot{V}_{O_2}$ than that of the active high animals. We note that active low metabolism is not simply torpor use. T_b was higher than T_a in active low tenrecs. Furthermore, active low tenrecs did not exhibit the lethargy and ataxia of facultatively torpid tenrecs found during the active season. Although the data presented here do not offer a mechanistic basis, it appears tenrecs may be able to modulate heat retention and conductance independent of other physiological parameters like $\dot{V}_{O_2}$. An alternative explanation for the lack of a relationship between $\dot{V}_{O_2}$ and T_b is that there could be a significant anaerobic component to metabolism. The data for $\dot{V}_{CO_2}$ generally coincide with those for $\dot{V}_{O_2}$ and do not support the use of anaerobic metabolism. Further, identical T_b and $\dot{V}_{O_2}$ values could be accommodated by heart rates that vary by 34% (Fig. 3). These data support a notion that metabolism in tenrecs may simply be plastic in comparison to T_b. In common tenrecs, the large variation in metabolism is not associated with the use of torpor or hibernation.

In most mammalian species, such profound changes in T_b and metabolism would be associated with the use of torpor or hibernation (Ruf and Geiser, 2015; van Breukelen and Martin, 2015). Torpor is traditionally defined as a reduction in metabolism to levels below what is required to maintain normal metabolic activities. In many cases, torpid T_b may approach T_a and is associated with extreme metabolic depression. In other cases, a more moderate depression of metabolism results in torpid T_b being higher than T_a. The depressed metabolism serves as a mechanism to conserve energy during times of limited resource availability or environmental stress. Active suppression of metabolism has been previously demonstrated in hibernating black bears (Tøien et al., 2011). Upon exit from hibernation, bear T_b increases by ∼2°C. However, $\dot{V}_{O_2}$ slowly increases over the ensuing 2–3 weeks. In tenrecs, remarkable metabolic suppression is seen during facultative torpor and hibernation. For instance, hibernating tenrec $\dot{V}_{O_2}$ at 12°C is 0.0115±0.023 ml O_2 g^{-1} h^{-1}. For comparison, hibernating Arctic ground squirrel $\dot{V}_{O_2}$ at 4°C is 0.012 ml O_2 g^{-1} h^{-1} (Buck and Barnes, 2000). Interestingly, euthermic (T_b ∼36°C) Arctic ground squirrel $\dot{V}_{O_2}$ at a T_a of 2°C approximates our active high $\dot{V}_{O_2}$ at a T_a of 12 and 20°C (Karpovich et al., 2009), indicating that tenrecs are not simply hypometabolic. It appears that tenrecs are able to suppress aerobic metabolism to a degree equal to that of the most competent hibernators despite being at least 8°C warmer.

In all described mammalian hibernators to date, the hibernation phenotype consists of bouts of torpor interrupted by brief periodic returns to euthermy wherein critical homeostatic processes are restored (van Breukelen and Martin, 2015). Lovegrove et al. (2014) found that wild *T. ecaudatus* did not experience these interbout arousals. Common tenrecs hibernate in small, underground burrows ∼1 m deep that are sealed to the outside with soil for the 8–9 month hibernation season (Lovegrove et al., 2014; Rand, 1935). Recent video evidence showed 13 torpid tenrecs were removed from a single hibernaculum by hunters, suggesting tenrecs may hibernate socially (https://youtu.be/w8OAm_eeNd8). Soil temperatures in the Lovegrove et al. (2014) field study were never <22°C, which precluded colder tenrec T_b. Data for fat-tailed dwarf lemurs, *Cheirogaleus medius*, demonstrate that periodic interbout arousals occur only if the tree hole is <30°C during its hibernation season (Dausmann et al., 2004). An important question is whether lower T_b (i.e. T_b <22°C) during hibernation would elicit the use of periodic arousals in common tenrecs (van Breukelen and Martin, 2015). When held at a T_a between 12 and 28°C during the hibernation season, we found captive tenrecs had a core T_b that closely approximated T_a (Fig. 1; Figs S1B–D, S2) and found no evidence of natural periodic interbout arousals even at a T_b as low as ∼12°C. Upon disturbance, some tenrecs experienced ∼1–6°C increases in T_b that may last from <1 h to 14 h. We noticed these partial thermal arousals occurred in close proximity to the daily checks or weighings. Tenrec thermal arousals are highly variable and lack predictability, features inherent to canonical interbout arousals. If the function of an interbout arousal is to allow re-establishment of homeostatic processes with high T_b (van Breukelen and Martin, 2001), it is difficult to see how a modest increase in T_b, e.g. 12.5–15°C, would accomplish those functions. Further, these same partial thermal arousals occurred at a T_a of 28°C where no similar need could be rationalized. As a result, we contend that the periods of increased T_b in captive tenrecs do not represent a natural feature of tenrec hibernation and should not be considered canonical interbout arousals. Instead, we liken these partial thermal arousals to unsuccessful alarm arousals. In ground squirrels, handling of torpid animals prematurely induces an interbout arousal where T_b fully returns to euthermic levels for the prescribed 12–20 h period before continuing the next torpor bout (alarm arousal; Utz and van Breukelen, 2013). Importantly, not all manipulations cause alarm arousals. In some squirrels, T_b may increase ∼1–2°C before returning to the pre-handling T_b. In our experience with ground squirrels, we have never seen a partial arousal where the increase in T_b was greater than 2°C. Tenrecs never fully arouse from torpor during the hibernation season and there is always some indication of lethargy and ataxia. This continuous lethargy/torpor may be demonstrated by examination of heart rates. During the active season, heart rate was 151.3±10.8 beats min^{-1} at room temperature (data not shown; N=7). We handled tenrecs while they were hibernating at room temperature. Heart rate increased during handling to as high as 87 beats min^{-1} (71.2±5.15 beats min^{-1}; N=5 tenrecs) but quickly returned to values of 32.6 ±2.04 beats min^{-1} within 94.4±35.7 s. Even with the reduced heart rate, some tenrecs were able to ambulate (albeit these tenrecs were ataxic).

To better understand this more or less torpid concept, we employed a RRT assay (Fig. 4). Our assay data confirmed our observations that hibernation in tenrecs represents a continuum, with animals being most torpid in June during the austral winter (Fig. 4A). We found T_b to be a less than reliable indicator of metabolic status. T_b partially predicts activity status, with warmer tenrecs being able to right themselves more quickly. However, not all tenrecs were predictable, e.g. one tenrec with a T_b of 29.5°C experienced a 30 s RRT despite being housed at 12°C (Fig. S4).

Torpid tenrecs (T_b <20°C) experienced repeated cycles of relatively short, single-peak bursts followed by as much as 45 min of waning oxygen consumption (Fig. 3; Fig. S2). The ventilation pattern was reminiscent of insect discontinuous gas exchange (Lighton, 1998). This mechanism is proposed to allow efficient gas exchange in subterranean environments that become hypoxic and hypercapnic. However, our experiments did not involve exposure to hypoxia or hypercapnia. One possible function of these brief bursts of metabolic activity may be that they serve the same role as a canonical interbout arousal. For instance, one might envisage periodic increases in heart rate as in Fig. 3 that may lead to higher blood pressure and pulses in kidney function without increases in T_b. We found that tenrecs hibernating at a T_a of 12°C are able to urinate (M.D.T., L.S. and F.v.B., personal observations). In ground squirrels, kidney function is restricted to the interbout arousal (Jani et al., 2013). Our laboratory is currently investigating these ideas.

In common models of hibernation like arctic ground squirrels, the timing of immergence and emergence from hibernation is generally synchronized and highly predictable to within a few days (Sheriff et al., 2011). In *T. ecaudatus*, the timing seems much more plastic. We noted that tenrecs slowly exited hibernation and became more aware of their surroundings and less lethargic over the course of ∼2 weeks. Tenrecs then resumed active-season behaviors, e.g. rapid and coordinated movement, eating, voiding of waste products, and reproduction. The timing of emergence of our captive tenrec population varied by ∼5 months (Fig. 5; Fig. S5A). We have maintained the colony since 2014 and have observed no indications that the annual cycle is shifting from a southern towards a northern hemisphere cycle. Tenrecs immerged into hibernation as early as January and in some exceptional cases as late as July (data not shown). Most tenrecs were hibernating by May.

Plastic growth rate trajectories were evident in neonatal, juvenile and adult tenrecs. While the profound mass gain in neonatal tenrecs is not as extreme as the ∼25% daily mass gain in neonatal hooded seals, *Cystophora cristata*, which wean at ∼3–5 days of age, the mass gain in these seals is mostly fat (Bowen et al., 1985), whereas in tenrecs the mass gain reflected changes in skeletal dimension. Interestingly, profound growth even occurred in adult tenrecs. Indeterminate growth is considered the ancestral condition in amniotes (Hariharan et al., 2016); during indeterminate growth, increases in the length of the major body axis occur after the animal is thought to have reached a mature size. That our wild-caught adult tenrecs grew 2.5±0.37-fold suggests a degree of indeterminate growth that appears unique in the mammalian world (Hariharan et al., 2016).

Tenrecs mated upon emergence from hibernation (∼September to November). Little is known of the reproductive biology of tenrecs other than that it seems to be plastic. In the lesser hedgehog tenrec, *Echinops telfairi*, gestation is reported to vary between 50 and 79 days (Künzle et al., 2007). Gestation length in *T. ecaudatus* is suggested to be 58–64 days (Eisenberg, 1975). We have observed tenrecs giving birth as early as November and as late as February; however, we are not familiar with any studies indicating how factors like lowered and variable T_b and/or use of facultative torpor might affect gestation length. Interestingly, pregnant tenrecs were found to display extremely variable T_b (as low as 13.5±0.5°C) with little apparent effect on their reproductive success (Fig. S6G; Nicoll, 1982).

Common tenrec litter size may be enormous (as many as 32 babies), although litter sizes of 16–20 are more typical (Nicoll and Racey, 1985). Our colony's litter sizes were generally smaller, with a maximum of 19. Superfetation has been suggested in tenrecs (Poduschka, 1996). This ability to simultaneously support multiple litters at different developmental stages in the uterus is well documented in European hares (Roellig et al., 2011). In our limited experience, one tenrec was determined to be pregnant, isolated from further interactions with males, gave birth in isolation and was subsequently maintained in isolation for 40 days before giving birth to another litter. This occurrence suggests that, although rare, tenrecs may avail themselves of superfetation. A combination of large litter size and superfetation would suggest tremendous reproductive output is available to these tenrecs.

Endothermy in modern placental mammals is widespread. Although there are several tenable models for why endothermy may have evolved, all predict selective advantages to animals that maintain warmer and more stable T_b (Lovegrove, 2016). Are tenrecs simply not able to maintain a warmer and more stable T_b? We found female tenrecs became increasingly endothermic and homeothermic on the day of parturition (Fig. 6; Fig. S6). These data suggest that while tenrecs are normally very plastic and display highly variable T_b, they may experience periods wherein increased endothermy/homeothermy is possible. While *T. ecaudatus* display this increased endothermy/homeothermy post-parturition, work with other species of tenrec (*E. telfairi* and *Setifer setosus*) suggests increased homeothermy while tenrecs are pregnant or across the breeding season in males (Oelkrug et al., 2013; Levesque and Lovegrove, 2014).

If increased endothermy/homeothermy were advantageous and given these tenrecs are capable of increased endothermy/homeothermy, then why not be more consistently homeothermic? The answer may lie in the advantages of being plastic. Many consider canonical mammalian hibernation as a means of passing the winter when resources are low. Tenrecs may simply be exploiting hibernation-like strategies in their active-season physiology. Varying metabolism and T_b would presumably allow for the conservation of energetic stores. One can then flip this argument around and ask why a placental mammal would be less plastic. That answer may lie in the limits to plasticity. Despite being considered a hypervariable environment, much of Madagascar is rather warm (Ohba et al., 2016). In fact, Madagascar's climate is thought to have changed very little since tenrecs first colonized the island 30–56 MYA (Everson et al., 2016; Ohba et al., 2016). We found tenrecs appear highly stressed when T_a or T_b is <8°C or >34°C as cold animals may cease ventilating and hot animals pant and breathe irregularly (Kayser, 1961; Oelkrug et al., 2013; Scholl, 1974; M.D.T., L.S., B.B. and F.v.B., personal observations). In the wild, the likelihood of tenrecs being exposed to a T_a outside of their tolerated range is rare. Thus, the highly plastic T_b exhibited by tenrecs may have worked well on an isolated island with moderate environmental temperatures and few homeothermic competitors. In more thermally variable environments, however, the plasticity seen in *T. ecaudatus* may not have allowed basoendothermic mammals to persist. Interestingly, the ranges of extant mammals like monotremes, marsupials, afrotherians and xenarthrans favor more moderate climates (Johansen, 1962).

Acknowledgements

We thank Barry Lovegrove and Owen Griffith for assistance acquiring our tenrec colony. We also thank the numerous undergraduates and volunteers from the van Breukelen laboratory for assistance with animal husbandry and maintenance.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: M.D.T., F.v.B.; Methodology: M.D.T., J.R., J.R.B.L., F.v.B.; Software: J.R., J.R.B.L.; Formal analysis: M.D.T.; Investigation: M.D.T., L.S., B.B., A.K., A.J.M., T.R., A.R., C.F.R., D.S., J.F.S., C.S.R., E.S., J.R., J.R.B.L.; Data curation: M.D.T., D.S., J.F.S., C.S.R.; Writing - original draft: M.D.T., F.v.B.; Writing - review & editing: M.D.T., F.v.B.; Visualization: M.D.T., F.v.B.; Supervision: M.D.T., F.v.B.; Project administration: M.D.T., F.v.B.; Funding acquisition: F.v.B.

Funding

This study was funded by National Science Foundation grants IOB 0448396 and IOS 1655091.

Supplementary information

Supplementary information available online at http://jeb.biologists.org/lookup/doi/10.1242/jeb.185900.supplemental

References

Barnes, B. M. (1989). Freeze avoidance in a mammal: body temperatures below 0°C in an Arctic hibernator. *Science* **244**, 1593-1595.

Bowen, W. D., Oftedal, O. T. and Boness, D. J. (1985). Birth to weaning in 4 days: remarkable growth in the hooded seal, *Cystophora cristata*. *Can. J. Zool.* **63**, 2841-2846.

Buck, C. L. and Barnes, B. M. (2000). Effects of ambient temperature on metabolic rate, respiratory quotient, and torpor in an arctic hibernator. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **279**, R255-R262.

Dausmann, K. H., Glos, J., Ganzhorn, J. U. and Heldmaier, G. (2004). Physiology: hibernation in a tropical primate. *Nature* **429**, 825-826.

Dausmann, K. H., Glos, J., Ganzhorn, J. U. and Heldmaier, G. (2005). Hibernation in the tropics: lessons from a primate. *J. Comp. Physiol. B.* **175**, 147-155.

Dewasmes, G., Loos, N., Delanaud, S., Ramadan, W. and Dewasmes, D. (2003). Liver temperature during sleep. *Sleep* **26**, 948-950.

Eisenberg, J. F. (1975). Tenrecs and solenodons in captivity. *Int. Zoo Yearb.* **15**, 6-12.

Everson, K. M., Soarimalala, V., Goodman, S. M. and Olson, L. E. (2016). Multiple loci and complete taxonomic sampling resolve the phylogeny and biogeographic history of tenrecs (mammalia: tenrecidae) and reveal higher speciation rates in Madagascar's humid forests. *Syst. Biol.* **65**, 890-909.

Garbutt, N. (1999). *Mammals of Madagascar*. Yale University Press.

Gilmore, D. P., Da-Costa, C. P. and Duarte, D. P. F. (2000). An update on the physiology of two-and three-toed sloths. *Braz. J. Med. Biol. Res.* **33**, 129-146.

Hariharan, I. K., Wake, D. B. and Wake, M. H (2016). Indeterminate growth: could it represent the ancestral condition? *Cold Spring Harb. Perspect. Biol.* **8**, a019174.

Jani, A., Martin, S. L., Jain, S., Keys, D. and Edelstein, C. L. (2013). Renal adaptation during hibernation. *Am. J. Physiol. Renal Physiol.* **305**, F1521.

Johansen, K. (1962). Responses to heat and cold in lower mammals. *Int. J. Biometeorol.* **6**, 3-28.

Karpovich, S. A., Tøien, Ø., Buck, C. L. and Barnes, B. M. (2009). Energetics of arousal episodes in hibernating arctic ground squirrels. *J. Comp. Physiol. B* **179**, 691-700.

Kayser, C. (1961). *The Physiology of Natural Hibernation*. Oxford, New York: Pergamon Press.

Künzle, H., Nautrup, C. P. and Schwarzenberger, F. (2007). High inter-individual variation in the gestation length of the hedgehog tenrec, *Echinops telfairi* (Afrotheria). *Anim. Reprod. Sci.* **97**, 364-374.

Levesque, D. L. and Lovegrove, B. G. (2014). Increased homeothermy during reproduction in a basal placental mammal. *J. Exp. Biol.* **217**, 1535-1542.

Levesque, D. L., Lobban, K. D. and Lovegrove, B. G. (2014). Effects of reproductive status and high ambient temperatures on the body temperature of a free-ranging basoendotherm. *J. Comp. Physiol. B* **184**, 1041-1053.

Lighton, J. R. B. (1998). Notes from underground: towards ultimate hypotheses of cyclic, discontinuous gas-exchange in tracheate arthropods. *Integr. Comp. Biol.* **38**, 483-491.

Lillegraven, J. A. and Eisenberg, J. F. (1983). Eisenberg, J. F. The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior. The University of Chicago Press, Chicago and London 1981. *J. Mammal.* **64**, 188-190.

Lovegrove, B. G. (2012). The evolution of endothermy in Cenozoic mammals: a plesiomorphic-apomorphic continuum. *Biol. Rev.* **87**, 128-162.

Lovegrove, B. G. (2016). A phenology of the evolution of endothermy in birds and mammals. *Biol. Rev.* **92**, 1213-1240.

Lovegrove, B. G., Lobban, K. D. and Levesque, D. L. (2014). Mammal survival at the Cretaceous– Palaeogene boundary: metabolic homeostasis in prolonged tropical hibernation in tenrecs. *Proc. R. Soc. B* **281**, 20141304.

Mcmanus, J. J. (1969). Temperature regulation in the opossum, *Didelphis marsupialis virginiana*. *J. Mammal.* **50**, 550-558.

Mzilikazi, N. and Lovegrove, B. G. (2004). Daily torpor in free-ranging rock elephant shrews, *Elephantulus myurus*: a year-long study. *Physiol. Biochem. Zool.* **77**, 285-296.

Mzilikazi, N. and Lovegrove, B. G. (2005). Daily torpor during the active phase in free-ranging rock elephant shrews (*Elephantulus myurus*). *J. Zool.* **267**, 103-111.

Nicoll, M. E. (1982). Reproductive ecology of Tenrec ecaudatus (Insectivora: Tenrecidae) in the Seychelles. *Doctoral dissertation, University of Aberdeen.*

Nicoll, M. E. and Racey, P. A. (1985). Follicular development, ovulation, fertilization and fetal development in tenrecs (*Tenrec ecaudatus*). *J. Reprod. Fertil.* **74**, 47-55.

Oelkrug, R., Meyer, C. W., Heldmaier, G. and Mzilikazi, N. (2012). Seasonal changes in thermogenesis of a free-ranging afrotherian small mammal, the western rock elephant shrew (*Elephantulus rupestris*). *J. Comp. Physiol. B* **182**, 715-727.

Oelkrug, R., Goetze, N., Exner, C., Lee, Y., Ganjam, G. K., Kutschke, M., Müller, S., Stöhr, S., Tschöp, M. H., Crichton, P. G. et al. (2013). Brown fat in a protoendothermic mammal fuels eutherian evolution. *Nat. Commun.* **4**, (2140).

Ohba, M., Samonds, K. E., Lafleur, M., Ali, J. R. and Godfrey, L. R. (2016). Madagascar's climate at the K/P boundary and its impact on the island's biotic suite. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **441**, 688-695.

O'Leary, M. A., Bloch, J. I., Flynn, J. J., Gaudin, T. J., Giallombardo, A., Giannini, N. P., Goldberg, S. L., Kraatz, B. P., Luo, Z.-X., Meng, J. et al. (2013).

The placental mammal ancestor and the post–K-Pg radiation of placentals. *Science* **339**, 662-667.

Poduschka, W. (1996). Hyperthelie, Wurfgröße und trächtigkeitsdauer bei der unterfamilie Tenrecinae Cabrera, 1925. (Mammalia: Insectivora: Tenrecidae), nebst Bemerkungen zur Längsstreifung der Gattung Hemicentetes. *Contrib. Zool.* **66**, 119-128.

Poppitt, S. D., Speakman, J. R. and Racey, P. A. (1994). Energetics of reproduction in the lesser hedgehog tenrec, *Echinops telfairi* (Martin). *Physiol. Zool.* **67**, 976-994.

Poux, C., Madsen, O., Glos, J., De Jong, W. W. and Vences, M. (2008). Molecular phylogeny and divergence times of Malagasy tenrecs: influence of data partitioning and taxon sampling on dating analyses. *BMC Evol. Biol.* **8**, 102.

Racey, P. A. and Stephenson, P. J. (1996). Reproductive and energetic differentiation of the Tenrecidae of Madagascar. In *Biogéographie de Madagascar* (ed. W. R. Lourenço), pp. 307-319. Paris: ORSTOM.

Rand, A. L. (1935). On the habits of some madagascar mammals. *J. Mammal.* **16**, 89-104.

Roellig, K., Menzies, B. R., Hildebrandt, T. B. and Goeritz, F. (2011). The concept of superfetation: a critical review on a 'myth' in mammalian reproduction. *Biol. Rev.* **86**, 77-95.

Ruf, T. and Geiser, F. (2015). Daily torpor and hibernation in birds and mammals. *Biol. Rev.* **90**, 891-926.

Scantlebury, M., Lovegrove, B. G., Jackson, C. R., Bennett, N. C. and Lutermann, H. (2008). Hibernation and non-shivering thermogenesis in the Hottentot golden mole (*Amblysomus hottentottus longiceps*). *J. Comp. Physiol. B.* **178**, 887.

Schmidt-Nielsen, K., Dawson, T. J. and Crawford, E. C. (1966). Temperature regulation in the echidna (*Tachyglossus aculeatus*). *J. Cell. Physiol.* **67**, 63-71.

Scholl, P. (1974). Temperaturregulation beim madegassischen Igeltanrek *Echinops telfairi* (Martin, 1838). *J. Comp. Physiol. A* **89**, 175-195.

Sheriff, M. J., Kenagy, G. J., Richter, M., Lee, T., Tøien, Ø., Kohl, F., Buck, C. L. and Barnes, B. M. (2011). Phenological variation in annual timing of hibernation and breeding in nearby populations of Arctic ground squirrels. *Proc. R. Soc. Lond. B Biol. Sci.* **278**, 2369-2375.

Stephenson, P. J. and Racey, P. A. (1994). Seasonal variation in resting metabolic rate and body temperature of streaked tenrecs, *Hemicentetes nigriceps* and *H. Semispinosus* (insectivora: tenrecidae). *J. Zool.* **232**, 285-294.

Tøien, Ø., Blake, J., Edgar, D. M., Grahn, D. A., Heller, H. C. and Barnes, B. M. (2011). Hibernation in black bears: independence of metabolic suppression from body temperature. *Science* **331**, 906-909.

Utz, J. C. and van Breukelen, F. (2013). Prematurely induced arousal from hibernation alters key aspects of warming in golden-mantled ground squirrels, *Callospermophilus lateralis*. *J. Therm. Biol.* **38**, 570-575.

van Breukelen, F. and Martin, S. L. (2001). Translational initiation is uncoupled from elongation at 18 C during mammalian hibernation. *Am. J. Physiol.* **281**, R1374-R1379.

van Breukelen, F. and Martin, S. L. (2015). The hibernation continuum: physiological and molecular aspects of metabolic plasticity in mammals. *Physiology* **30**, 273-281.

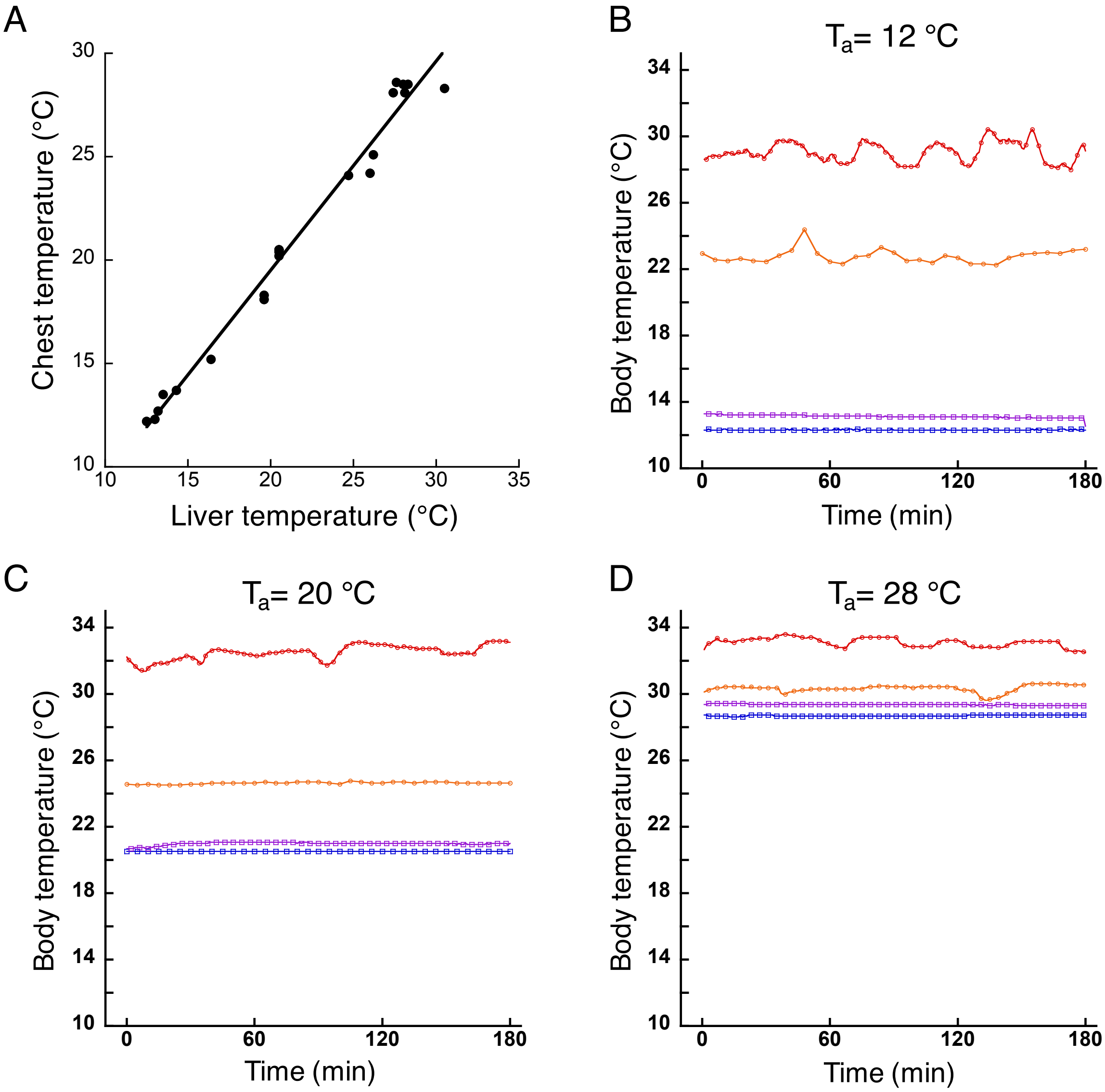

Fig. S1. Body temperature at the chest in *Tenrec ecaudatus* approximates liver temperature and can be relatively stable. A) Data obtained via an iButton against the chest were compared to data collected using a thermocouple during tissue sampling. Animals represented all states (N=21; r^2=0.99). Chest temperature provided an appropriate estimate of body temperature. B-D) Although the patterns seen in Fig. 1 of the main body are most common, body temperature can be relatively stable in active tenrecs. Tenrecs were housed at T_a of B) 12°C, C) 20°C, or D) 28°C. Different colors represent individual tenrecs. All animals except hibernating tenrecs (blue squares) were sampled during the active season. Purple squares represent tenrecs that spontaneously entered brief periods of torpor during the active season (facultative torpor).

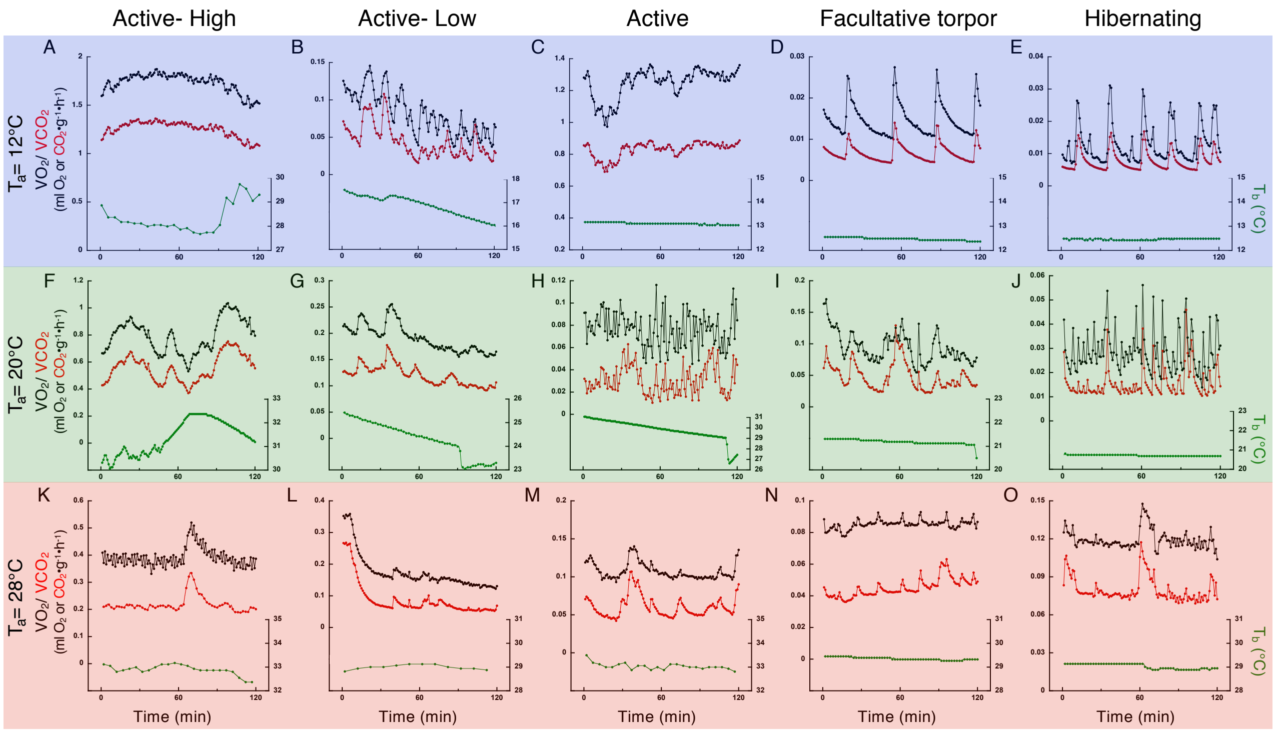

Fig. S2. Representative respirometry and T_b data for active, facultatively torpid, and torpid tenrecs housed at 12°C (blue shaded: A-E), 20°C (green shaded: F-J), and 28°C (red shaded: K-O). In A, F, and K, data are presented for animals having relatively high VO_2. In B, G, and L, data are presented for animals having relatively low VO_2. In C, H, and M, data are presented for animals showing marked disconnects between VO_2 and T_b e.g. in C, this tenrec had a very high metabolism despite having a very low and stable T_b. In D, I, and N, data for facultatively torpid tenrecs during the active season are displayed while E, J, and O show data for hibernating tenrecs.

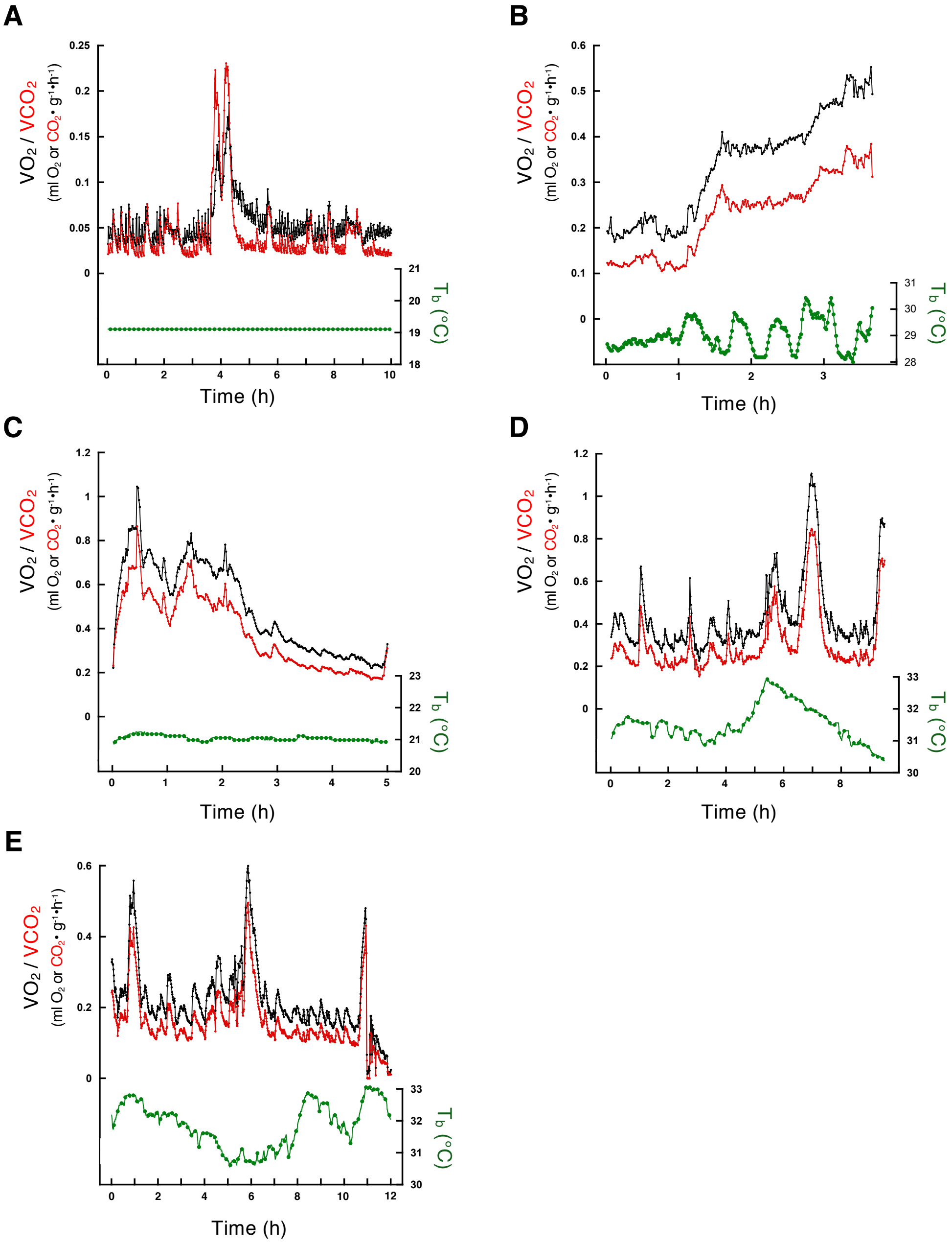

Fig. S3. Additional examples of physiological disconnects in tenrecs. Note the numerous instances where VO_2/VCO_2 is changing without a concomitant change to T_b (A, B, C), or where T_b is changing without the expected change in VO_2/VCO_2 (D and E). Additionally, these physiological disconnects are sustained over the course of hours in most instances.

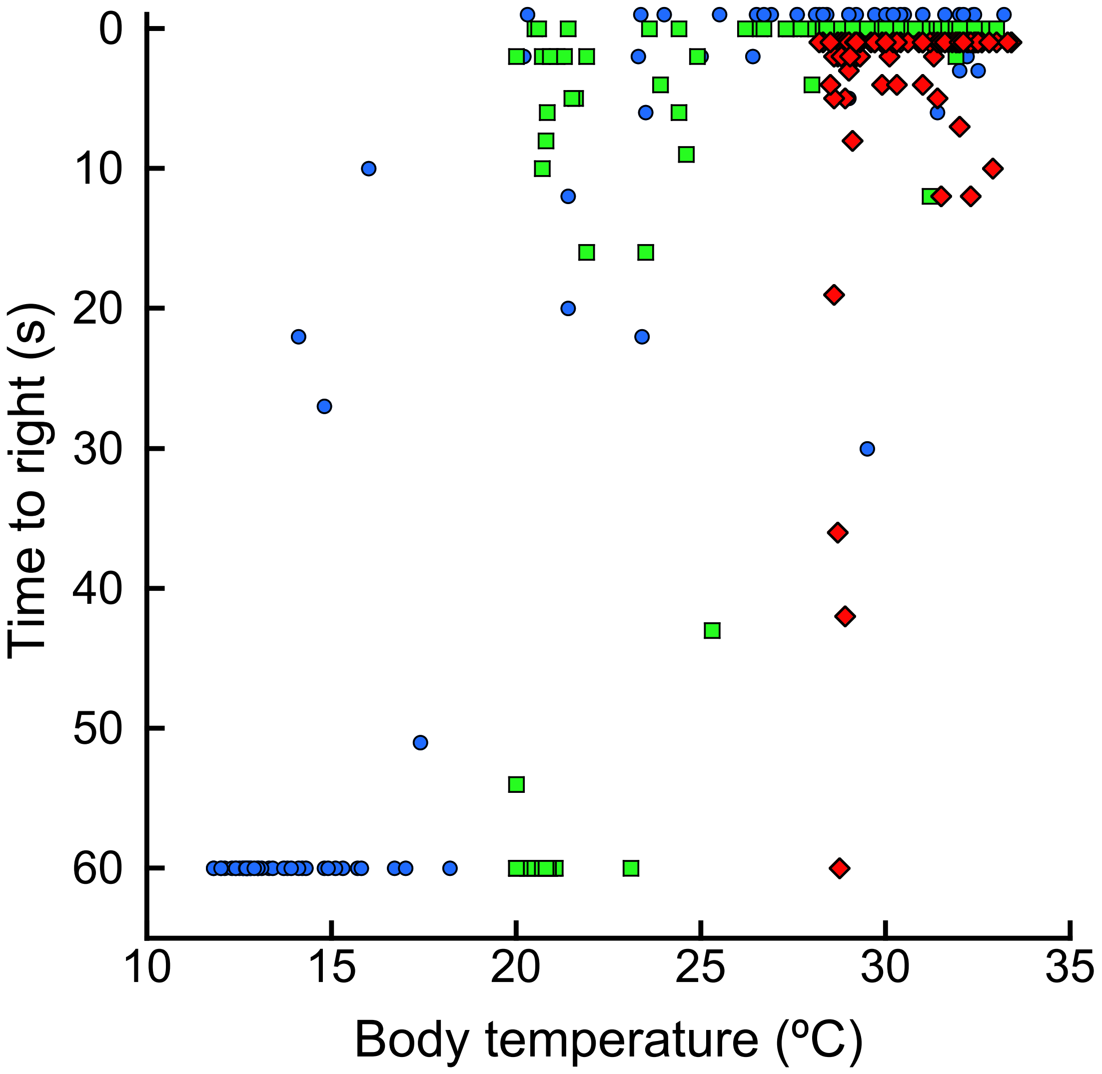

Fig. S4. Righting response time as a function of T_b. Tenrecs were housed at T_a of 12°C (blue circles), 20°C (green squares), or 28°C (red diamonds) for at least 24 h prior to assay. Tenrecs were placed into a cradle and time to right was determined. Note that while righting time is *generally* dependent on T_b, examples of warm tenrecs with long righting times and cold tenrecs with short righting times can be found. For instance, one animal housed at T_a=12°C took 30 s to right despite having a T_b of 29.5°C.

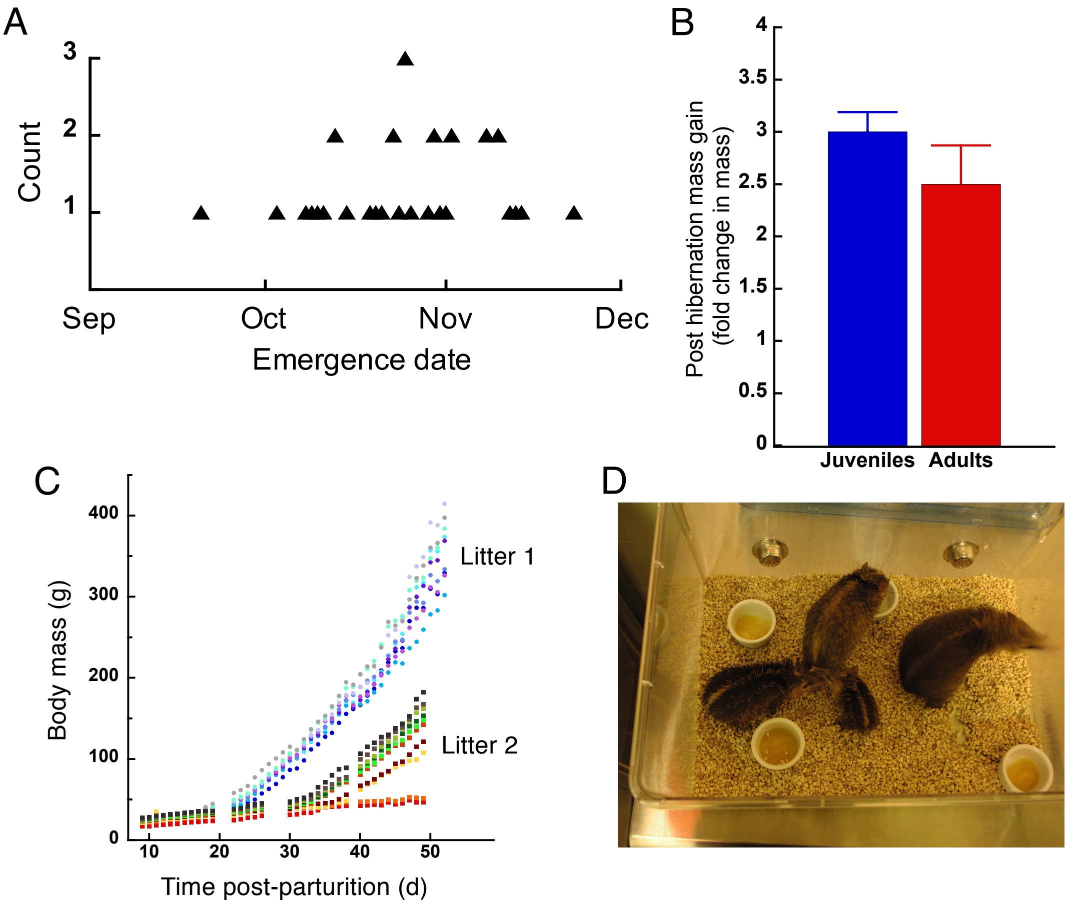

Fig. S5. Date of hibernation emergence is plastic and growth is dramatic in tenrecs. A) Data represent the Fall 2014 active season (N=34 individual tenrecs). As many as 3 tenrecs emerged from hibernation on a given date. Emergence date in other years has ranged from as early as August to as late as January. B) Juveniles (blue bar; N=29) and adults (red bar; N=7) experience similar growth post-hibernation (mean ± s.e.m; P>0.05; unpaired t-test). Mean maximum weight gain was 44.6 ± 4.0 g • d^{-1} and represents both increases in lean and fat mass. C) At birth, tenrecs weigh 12.15 ± 0.36 g (N=31; 4 litters) but *may* experience profound postnatal growth. Different colors represent individuals. Gaps represent days of no mass data. Litter 1 (circles; N=9; two larger individuals in D) is 13 days older than litter 2 (squares; N=11; two smaller individuals in D).

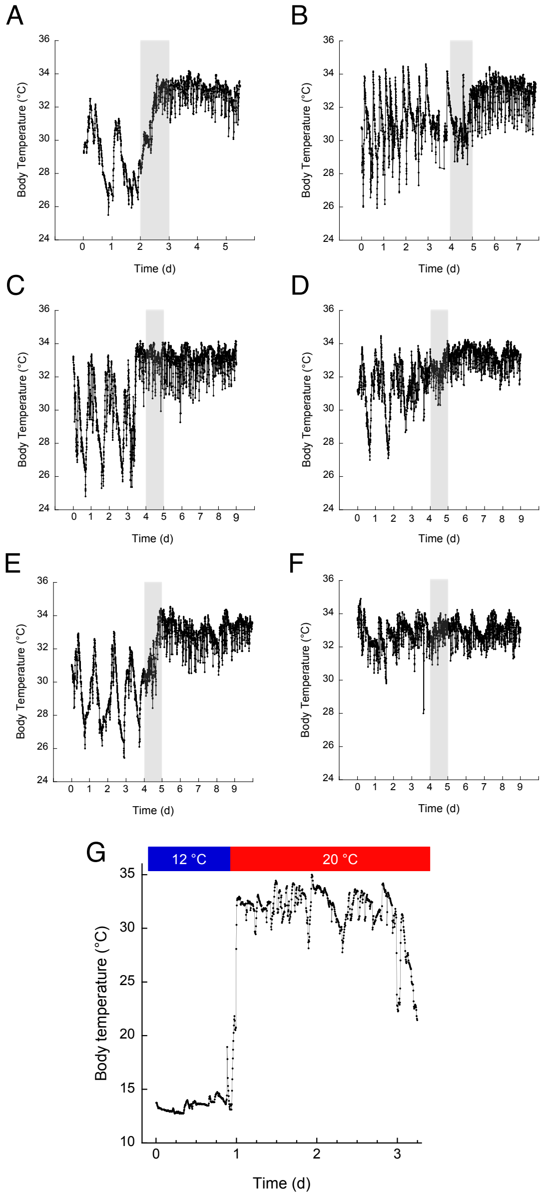

Fig. S6. Tenrecs can invoke periods of higher endothermy/homeothermy following parturition and may experience relatively low T_b during pregnancy. In A-F, Tenrecs were maintained at room temperature. Six additional tenrecs that gave birth (shaded area= date of parturition). Note the relative variable T_b prior to parturition followed by more stable and warmer T_b. G) In the course of our studies, we exposed a tenrec to 12°C wherein she maintained T_b of 13.5 ± 0.5°C. The tenrec was then shifted to T_a of 20°C where T_b was maintained well above T_a. The exposure to 12°C occurred on October 25, 2015 and she gave birth on November 30, 2015. We estimate she was ~3 weeks pregnant at the time of 12°C exposure. Common tenrec gestation is typically 58-64 d (Künzle et al., 2007).

Movie S1. Demonstration of active tenrec in the righting response assay. Tenrecs were placed into a cradle and time to right was determined.

Movie S2. Demonstration of torpid tenrec in the righting response assay. Tenrecs were placed into a cradle and time to right was determined.