Heterothermy in Two Mole-Rat Species Subjected to Interacting Thermoregulatory Challenges

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ABSTRACT

Maintaining a high and constant body temperature ($T_b$) is often viewed as a fundamental benefit of endothermy, but variation in $T_b$ is likely the norm rather than an exception among endotherms. Thus, attempts to elucidate which factors cause $T_b$ of endotherms to deviate away from the $T_b$ that maximizes performance are becoming more common. One approach relies on an adaptive framework of thermoregulation, used for a long time to predict variation in $T_b$ of ectotherms, as a starting point to make predictions about the factors that should lead to thermoregulatory variation in endotherms. Here we test the predictions that when confronted with thermoregulatory challenges endotherms should (1) become more heterothermic, (2) lower their $T_b$ setpoint, and/or (3) increase behavioral thermoregulation (e.g., activity levels or social thermoregulation). We exposed two species of relatively homeothermic mole-rats to two such challenges: (a) ambient temperatures ($T_a$) well below the thermoneutral zone and (b) increased heat loss caused by the removal of dorsal fur. In general, our results support the adaptive framework of endothermic thermoregulation with each species conforming to some of the predictions. For example, Mashona mole-rats (Fukomys darlingi) increased heterothermy as $T_a$ decreased, highveld mole-rats (Cryptomys hottentotus pretoriae) displayed lower $T_b$’s after shaving, and both species increased behavioral thermoregulation as $T_a$ decreased. This suggests that there is some merit in extending the adaptive framework to endotherms. However, none of the three predictions we tested was supported under all experimental conditions, reiterating that attempts to determine universal factors causing variation in $T_b$ of endotherms may prove challenging.

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Therefore, deviations from a high and constant $T_b$ (i.e., heterothermy) likely represent adaptive responses to environmental or ecological pressures and should increase as the cost/benefit ratio of maintaining strict homeothermy increases (Angilletta et al., 2010).

Several recent theoretical and modeling papers make predictions about the effects of morphological, physiological, ecological, and environmental conditions on the expression of heterothermy in endotherms (Angilletta et al., 2010; Humphries et al., 2003b; Pravosudov and Lucas, 2000). To date, few of these predictions have been tested explicitly using experimental manipulation, with the possible exception of the prediction that heterothermy should increase or the $T_b$ setpoint should decrease as food availability or ambient temperature ($T_a$) decrease. Increased heterothermy under food restriction has been shown experimentally for homeothermic species (e.g., Duffy et al., 1990), daily heterotherms (e.g., Bozinovic et al., 2007; Schubert et al., 2010; Levy et al., 2011), and hibernating species (e.g., French, 2000; Humphries et al., 2003a; Munro et al., 2005; Boyles et al., 2007; Matheson et al., 2010), and a decreased $T_b$ setpoint under food restriction has also been shown several times experimentally (e.g., Hunter et al., 1999; Gutman et al., 2006). Similarly, decreasing $T_a$ leads to increased heterothermy (e.g., Németh et al., 2009) or decreased $T_b$ setpoints (e.g., Soobramoney et al., 2003). Several other factors, such as food variability (Munn et al., 2010), variability in $T_a$ (Boyles and McKechnie, 2010), sociality (Hwang et al., 2007), predation (Pravosudov and Lucas, 2000) and, of particular relevance to this study, the costs of thermoregulation, have also been suggested to interact with $T_a$ to change thermoregulatory patterns in endotherms.

One way to increase the cost of thermoregulation in mammals is by shaving some or all the fur, although the results from such experiments have been mixed. Kauffman et al. (2004) showed that removing >95% of the fur from golden-mantled ground squirrels (Spermophilus lateralis) caused no change in hibernation patterns (i.e., no apparent increase in the expression of heterothermy), but a large increase in energy intake. Similarly, several studies have reported increases in food intake (Król et al., 2007) or metabolic rate (Zhao and Cao, 2009) in laboratory mice after shaving. Conversely, Kenagy and Pearson (2000) found that shaving meadow voles (Microtus californicus), a homeothermic species, had little effect on field metabolic rate (FMR). However, in the wild, animals may not be able to increase energy expenditure because of increased foraging and predation costs associated with increased energy intake. Three possible explanations may reconcile these divergent observations. First, when faced with ecological limitations to increasing energy intake, animals may lessen thermoregulatory precision (i.e., decrease maintenance of strict homeothermy) to offset the increased energy expenditure caused by shaving instead of increasing food intake and metabolic rate to maintain homeothermy. Second, if a low cost mechanism of behavioral thermoregulation is available, animals may increase the use of behavioral thermoregulation to maintain a constant $T_b$ with little increase in energy expenditure. Third, animals may use some combination of decreased thermoregulatory precision and increased behavioral thermoregulation to balance energy intake and expenditure.

An adaptive framework of thermoregulation (Angilletta et al., 2010) predicts that endothermic animals should increase variation in $T_a$, lower the $T_b$ setpoint, or increase behavioral thermoregulation (or some combination of the three) when faced with increased thermoregulatory challenges (Fig. 1). Here, we test these predictions under two such challenges: $T_a$ well below the thermoneutral zone (TNZ) and increased heat loss caused by shaving of the dorsal fur. These predictions assume that long-studied patterns in ectotherm thermoregulation can be extended.

Figure 1. Theoretical predictions about the effects interacting ambient temperatures ($T_a$) and shaving should have on the level of heterothermy expressed, body temperature ($T_b$) setpoint, and use of behavioral thermoregulation by endotherms. Solid lines represent control (unshaven) individuals and dashed lines represent treatment (shaven) individuals. In homeothermic endotherms, such as the mole-rat species used herein, the scope of change in the physiological variables (heterothermy and $T_b$ setpoint) should be limited relative to the scope of change in behavioral variables. The lines predicting the relationships between $T_a$ and measured variables should intersect at approximately the lower critical limit of the thermal neutral zone.

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in principle, to endotherms (Angilletta, 2009; Angilletta et al., 2010). While previous research can be interpreted in such a way as to support these predictions in endotherms (Angilletta et al., 2010), few studies have explicitly studied homeothermic endotherms in this framework, likely because of the relatively small fluctuations in \( T_b \) expressed by these species. An important step in evaluating the generality of the adaptive framework of thermoregulation is to examine the predictions in the context of species generally thought to maintain a constant \( T_b \). To this end, we conducted an experiment using two species of relatively homeothermic mole-rats (Family Bathyergidae), which have been suggested as an ideal group for the study of the evolution of endothermy (Bennett, 2009).

**MATERIALS AND METHODS**

**Study Species**

We used 10 individuals of each of the two species of mole-rats, the Mashona mole-rat (Fukomys darlingi) and the highveld mole-rat (Cryptomys hottentotus pretoriae), with different body masses, geographic ranges, and thermoregulatory patterns. The highveld mole-rat is considered homeothermic even when exposed to temperatures below the TNZ (\( T_b < 31 \)°C) (Haim and Fairall, ’86) while the Mashona mole-rat allows its \( T_b \) to decrease when exposed to temperatures below the TNZ (\( T_b < 28 \)°C) for short periods (Bennett et al., ’93). The highveld mole-rat is the larger of the two species (body mass: 70–200 g) and is found in the Highveld region of eastern South Africa (mean annual temperature 17.3°C and mean annual range 3–28°C) while the Mashona mole-rat is smaller (body mass: 45–90 g) and found in Zimbabwe (mean annual temperature 18°C and mean annual range 8–30°C). The animals used herein came from captive colonies housed for several generations at the University of Pretoria. The highveld mole-rats were collected from Tygerpoort, Pretoria (26° S, 38° E), while the Mashona mole-rats originated from populations near Goromonzzi (17° S, 31° E). In the captive colonies, animals are maintained in small groups (2–7 individuals) at 25°C (which is below the TNZ, Bennett et al., ’93) on an ad libitum diet of sweet potatoes, apples, and grapes from which they obtain all necessary nutrients and water.

**Preparation of Animals**

We used temperature-sensitive dataloggers (iButtons, Model DS1922, Maxim Semiconductor, Dallas, TX) with a resolution of 0.0625°C to measure \( T_b \) at 12-min intervals. The iButtons weighed approximately 3.1 g, so they were less than 7% of body mass for all individuals. We calibrated iButtons and coated them with biologically inert wax before a registered veterinarian implanted them intraperitoneally. The animals were fully anesthetized during the procedure by being induced with a facial mask using 5% isoflurane, and maintained on 2.5% isoflurane. The mole-rats were given meloxicam (Mobic, Ingelheim Pharmaceutics) for analgesia and enrofloxacin (Baytril 5%, Bayer Animal Health) for prophylactic antibiotic cover during the surgery. The abdominal wall and skin were closed in two layers with 5/0 monocryl. The surgical site was covered (Opsite, Smith and Nephew) to prevent the mole-rats from interfering with the sutures and the mole-rats were observed until each had fully recovered from the anesthetic. We allowed the animals three weeks to recover from surgery before beginning the experiment. During this period, animals were maintained on ad libitum food at 25°C. Seven days before the start of the experiment, we shaved a patch of dorsal fur from half of the individuals of each species. Standardization of the area shaved was not possible, so we instead shaved from approximately the front shoulders to within 1 cm of the base of the tail and laterally from the midline on each side of the body. The dorsal fur of mole-rats is denser than the ventral fur and is the area where the lowest heat loss occurs (Sumbera et al., 2007); thus, shaving the dorsal fur should have the largest effect on heat loss in these species. The area was intended to be large enough to open a significant thermal window but to avoid any areas where growing hair could be uncomfortable (e.g., in joints or on the head). The goal of this experiment was to explicitly test predictions about variation in \( T_b \), not energetic benefit of fur to mammals. Thus, we did not measure metabolic rates in these individuals and cannot estimate the increase in heat loss experienced after shaving. However, two other species (Elephantulus myurus and Micaelamys namaquensis) were subjected to a similar shaving procedure for another experiment (importantly, the shaved areas were considerably smaller in that experiment) and experienced increases in thermal conductance of 10–30% (JG Boyles, unpublished data).

**Experimental Design**

We conducted the experiment in a climate-controlled room on the University of Pretoria campus from March 13 to April 7, 2010. During the experiment, we maintained animals individually in 380 \( \times \) 540 \( \times \) 440 cm plastic tubs with a 300 \( \times \) 80 \( \times \) 80 cm PVC nest box affixed in the corner of each box. We did not give the animals materials specifically for nesting, but most individuals carried wood shavings from the larger tub into the nest box. Each nest box contained a hinged trelade that depressed a micro-switch when animals entered the box (Fig. 2). The micro-switches were connected to a digital converter, which was interfaced to a computer to record visits to the nest box. We exposed the mole-rats to four \( T_b \) treatments (30, 24, 18, and 12°C) in descending order, although actual temperatures during the treatments were 29.56°C ± 0.27 SD, 24.51 ± 0.52, 18.48 ± 0.77, and 13.2 ± 0.91, respectively. Animals were maintained on a constant diet of sweet potatoes during treatments. Any uneaten food was removed and weighed daily at approximately 11:00 and the mass of food was adjusted as necessary to ensure animals had sufficient food to survive but were still slightly food restricted.
(i.e., we did not want animals to simply increase food intake to offset the increased cost of thermoregulation). Therefore, each Mashona mole-rat received 30, 30, 35, and 45 g (wet mass) of food during each temperature treatment, respectively, and each highveld mole-rat received 40, 40, 40, and 50 g of food during each treatment, respectively. The mole-rats consumed essentially all of the food given each day with the exception of small scraps. Each treatment $T_a$ and the experimental diet was maintained for five consecutive days after which the $T_a$ was changed back to 25°C (maintenance $T_a$) for two days and the animals were provided food ad libitum. This period was intended to restore body mass lost during treatments (which it did, see results), which might affect $T_b$ during subsequent treatments. Beginning at the 18°C treatment, some individual Mashona mole-rats began losing control of $T_b$ and were occasionally found cold and lethargic in the mornings even though they, without exception, had substantial amounts of uneaten food on those days (this was the only time food was left). This suggests that these animals were pathologically hypothermic and no longer controlling fluctuations in $T_b$ (i.e., they were not using heterothermy at that point). Thus, these individuals were removed from the experiment, rewarmed, and placed back at 25°C with ad libitum food. By the third day of the 12°C, all individuals of this species had been removed. All animal maintenance and experiments were conducted under approval of the University of Pretoria Animal Care and Use Committee (permit number: EC002-10).

Data Analysis

We have included raw data for a representative individual from each species in the online supplementary materials. For analyses, the level of heterothermy (i.e. amount of variation in $T_b$) was estimated using the Heterothermy Index (HI) of Boyles et al. (2011), defined as:

$$HI = \sqrt{\frac{\sum (T_{b-mod} - T_{b-i})^2}{n - 1}}$$

where $T_{b-mod}$ is the modal $T_b$, $T_{b-i}$ is the $T_b$ measurement at time $i$ and $n$ is the number of times $T_b$ is sampled. The HI quantifies deviation away from the optimal temperature for performance as approximated by $T_{b-mod}$ of unstressed animals. We calculated $T_{b-mod}$ for each individual during the 126 hr (630 readings at 12-min intervals) immediately prior to the first temperature treatment. During this period, animals were maintained at 25°C on ad libitum food. We first calculated HI values for each 24-hr period, starting at 12:00 (which was shortly after we fed the animals) so that we could evaluate the effect of keeping animals at each $T_a$ for multiple days. Our preliminary analysis indicated that HI values did not differ between days in either species (see below), so we recalculated HI values for each individual over each five-day $T_a$ treatment. We did not measure metabolic rates to verify animals were actually defending $T_{b}$, so we approximated the active $T_b$ setpoint of each individual during each temperature treatment as $T_{b-mod}$ for individuals that displayed unimodal distributions of $T_b$ and $T_{b-mod}$ at the highest temperature for individuals that displayed bimodal distributions of $T_b$ (McKechnie et al., 2007; Smit and McKechnie, 2010). We excluded the last day of data for any animal that was removed from the experiment after being found lethargic, which resulted in sample sizes of Mashona mole-rats decreasing at 18°C and made statistical analysis of the 12°C treatment impossible for that species. We used calculated energy required to maintain body mass at each temperature by summing the energetic content of food consumed (15.5 kJ/g) adjusted for digestive efficiency (96.3%) (Bennett and Jarvis, 95) and the energetic content of body mass gained or lost during the treatment (Nagy, ’83). Because this is a simple extrapolation, the results were nearly identical to an analysis based only on mass loss and are therefore not shown.

Custom software was used to monitor visits to the nest box by recording whether the treadle was depressed every 100 msec. A wooden step situated at the entrance of the box ensured that the treadle could only be depressed if animals had fully entered the nest box. To eliminate “bounce” events that may have occurred due to the spring-loaded components of the nest boxes, we excluded any nest box visit (hereafter, visit) with a duration of less than 1,000 msec from the analysis. Separate visits were merged into a single event when the interval between them was less than 1,000 msec. While we did not measure activity directly, we assume that increased time outside the nest box and increased visits are likely to be related to increased activity levels. We limited the behavioral analysis to the time period between 14:00 and 10:00 on the following day to eliminate use of the boxes influenced by activity in the room while we were feeding the animals. The animals regularly jammed the treadle mechanism by hoarding food or shavings, so days on which an animal was recorded either spending the entire day in or out of the nest box were removed for that individual. As with HI values, we initially included each day within a $T_a$ treatment separately in analyses, but our preliminary analyses found no effect of day on
behavioral variables, so it was removed to simplify the model and we averaged the values within each \( T_a \) treatment for each individual.

We used repeated-measures analyses of variance to evaluate changes in HI values, \( T_a \) setpoints, and the number of visits and time spent in nest boxes using the PROC MIXED function in SAS (Version 9.2, SAS Inc., Cary, NC) with a type-I error rate of 0.05. To model correlation within experimental units across time and between experimental units, we first determined the appropriate covariance structure for each dataset based on Akaike Information Criterion adjusted for small sizes (AIC\(_C\)) values. When analyzing HI and behavioral data, we first performed double repeated-measures analyses with treatment (shaven or unshaven) as a random factor and \( T_a \) and day within each \( T_a \) treatment considered repeated measures within each individual. Day had no significant effect on HI values or any behavioral variables recorded, so we excluded day from all models and evaluated the effects of \( T_a \) and fur removal on the HI value and behavioral variables over each \( T_a \) treatment. Our a priori experimental design was planned to use the two species as relatively independent replicates to test the predictions of interest, not to quantitatively compare the thermoregulatory patterns of the species. Thus, we chose not to include species as a factor in the model in order to simplify the interpretation of the results in the context of the adaptive framework of thermoregulation using each species separately. We investigated differences between main effects using Fisher’s least significant difference tests (LSD) assuming a type-I error rate of 0.05. When interactions occurred, we performed tests of main effects using the SLICE option in the LSMEANS statement (Schabenberger et al., 2000; Littell et al., 2006). We used the Kenward–Roger method to estimate the degrees of freedom (Kenward and Roger, ’97).

**RESULTS**

**Mashona Mole-Rats**

Body temperature generally decreased throughout the experiment among Mashona mole-rats (Fig. 3). Thus, heterothermy increased as \( T_a \) decreased (\( F_{2,21} = 4.92; P = 0.018 \); Fig. 5A), which was driven by a significant difference between HI values at 18 and 30°C (\( t = 3.06, \) d.f. = 21; \( P = 0.006 \)). Fur removal had no effect on the level of heterothermy expressed across all \( T_a \) treatments combined (\( F_{1,21} = 0.21; P = 0.65 \)) or as \( T_a \) decreased (temperature \( \times \) treatment interaction, \( F_{2,21} = 0.21; P = 0.813 \)). The \( T_b\)-mod displayed by Mashona mole-rats decreased as the temperature decreased (\( F_{3,15} = 18.32; P < 0.001 \)) with \( T_b \) decreasing significantly with each decrease in \( T_a \) (\( P < 0.05 \) in all comparisons; Fig. 5B). As with the level of heterothermy expressed, fur removal had no effect on \( T_b\)-mod across \( T_a \) treatments (\( F_{1,9.48} = 0.09; P = 0.766 \)) or as \( T_a \) decreased (temperature \( \times \) treatment interaction, \( F_{3,15} = 0.45; P = 0.719 \)).

There was a significant effect of \( T_a \) on the total duration of visits to nest boxes (\( F_{2,12.2} = 5.51; P = 0.02 \); Fig. 5F), which was driven by animals spending significantly less time in the nest boxes at 24°C than at 30°C (\( t = 3.31, \) d.f. = 12; \( P = 0.006 \)). There was also a significant \( T_a \) \( \times \) treatment interaction effect on the total duration of visits (\( F_{2,12.2} = 6.12; P = 0.014 \)), which was caused by the shaven individuals spending significantly more time in nest boxes at 30°C than any other \( T_a \) and treatment combination (\( P < 0.05 \) in all comparisons). Neither \( T_a \) nor fur removal had any significant effect on the mean duration of visits or the number of visits (Fig. 5D and E).

![Figure 3. Body temperature of a representative Mashona mole-rat over the course of the experiment. Raw data for this figure are in the supplementary materials.](image-url)
There was no difference in initial body mass across treatments ($t = 1.36, \text{d.f.} = 8; P = 0.211$), but there was a significant simple effect of $T_a$ on proportional change in body mass ($F_{2,19} = 18.44; P < 0.0001$; Fig. 5C), which was driven completely by the significant differences between the 30°C treatment and each of the other treatments (i.e., all other comparisons were nonsignificant). Fur removal had no effect on change in body mass ($F_{1,19} = 0.37; P = 0.549$), nor was there a significant interaction between $T_a$ and fur removal ($F_{2,19} = 0.23; P = 0.798$).

Fur removal had no significant effect on the number of days before Mashona mole-rats had to be removed from the experiment ($t = 0.953, \text{d.f.} = 8; P = 0.3687$).

**Highveld Mole-Rats**

Body temperature varied relatively widely in highveld mole-rats (Fig. 4). However, neither $T_a$ ($F_{3,32} = 1.14; P = 0.347$) nor fur removal ($F_{1,32} = 1.36; P = 0.252$) simple effects, or the interaction ($F_{3,32} = 0.85; P = 0.476$) significantly affected the level of heterothermy expressed (Fig. 6A). The $T_b_{-\text{mod}}$ displayed by highveld mole-rats did not change as $T_a$ decreased ($F_{1,32} = 0.42; P = 0.74$; Fig. 6B). However, unshaven individuals maintained significantly higher $T_b$s across all $T_a$ treatments ($F_{1,32} = 10.57; P = 0.003$). The interaction between $T_a$ and fur removal was also nonsignificant ($F_{3,32} = 0.62; P = 0.608$).

Highveld mole-rats spent significantly less total time in nest boxes as $T_a$ decreased ($F_{3,145} = 21.88; P < 0.0001$; Fig. 6F), with significant differences between all $T_a$ comparisons except 18 and 24°C. Ambient temperature did not significantly affect the number of visits ($F_{1,144} = 2.30; P = 0.08$; Fig. 6D) or the mean duration of each visit ($F_{3,146} = 2.32; P = 0.078$; Fig. 6E). Fur removal had no effect on the number of visits ($F_{1,7,66} = 0.29; P = 0.603$), the total duration of visits ($F_{1,7,98} = 0.29; P = 0.603$), or the mean duration of visits ($F_{1,8,98} = 1.14; P = 0.14$). Similarly, the interaction between $T_a$ and fur removal was nonsignificant for all three variables.

There was no difference in initial body mass across treatments ($t = 0.03, \text{d.f.} = 8; P = 0.977$), but there was a significant simple effect of $T_a$ on proportional change in body mass ($F_{1,32} = 16.28; P < 0.0001$; Fig. 6C), which was driven by significant differences between the 30°C treatment and each of the other treatments ($P < 0.05$ in all comparisons) and a significant difference between the 12 and 24°C treatments ($t = 2.57, \text{d.f.} = 32; P = 0.015$). There was no effect of fur removal on change in body mass ($F_{1,32} = 0.8; P = 0.379$) or a significant interaction between $T_a$ and fur removal ($F_{1,32} = 0.19; P = 0.904$).

**DISCUSSION**

Our experiment provides a novel test of theoretical predictions about how thermoregulatory challenges affect the control of $T_b$ in relatively homeothermic endotherms (Angilletta et al., 2010). Although our results generally fit well into the overall framework of adaptive thermoregulation, we also showed that none of the three predictions we tested herein apply equally well to even the two closely related mole-rat species. This solidifies the suspicions of Angilletta et al. (2010) that adjustments to thermoregulatory patterns will be species- or population-specific; researchers should therefore attempt to examine multiple aspects of thermoregulation whenever possible.

Studies on $T_b$ in endotherms often revolve around the relationship between energy expenditure and $T_b$. However, because $T_b$ also affects performance of endotherms, it is likely to play a role in the fitness of endotherms in exclusion of energetic considerations. For example, muscle performance is strongly tied to temperature in humans, a classic homeotherm.
THERMOREGULATION IN MOLE-RATS

Given that mole-rats generally maintain relatively constant $T_b$ (Streicher et al., 2011), some of the $T_b$s recorded in our study could lead to a decrease in performance and therefore could lead to decreased foraging efficiency or predator avoidance. Thus, experiments such as ours testing explicit predictions about when the cost of maintaining high and constant $T_b$s outweighs the benefits are important in the future.

Mashona mole-rats decreased thermoregulatory precision (i.e., increased heterothermy) as $T_a$ decreased. This conforms well to short-term measurements, which suggest Mashona mole-rats show decreased $T_b$ at temperatures below the TNZ (approximately 28°C) (Bennett et al., '93). Conversely, and contrary to predictions, highveld mole-rats maintained a constant level of homeothermy as $T_a$ decreased. Interestingly, fur removal did not lead to an increase in heterothermy or rate of body mass loss in either species, even when the $T_a$ was well below the TNZ. As predicted (Angilletta et al., 2010), Mashona mole-rats displayed lowered $T_{b\text{--mod}}$ as $T_a$ decreased; conversely, highveld mole-rats maintained a constant $T_{b\text{--mod}}$

Figure 5. Physiological and behavioral measures of thermoregulation in unshaven (black bars) and shaven (grey bars) Mashona mole-rats (Fukomys darlingi) across a range of ambient temperatures (mean ± SE). Boxes are: (A) expression of heterothermy; (B) modal body temperature; (C) proportional change in body mass; (D) number of visits to the nest box; (E) mean duration of visits to the nest box; and (F) total duration of visits to the nest box. Bars that share any letter are not significantly different.
across all temperature treatments. Similarly, the removal of fur led to contradictory results between the two species. In Mashona mole-rats, shaving had no effect on \( T_{b\_mod} \) or the number of days before they had to be removed from the experiment, but it caused shaven highveld mole-rats to maintain significantly lower \( T_{b\_mod} \) than the unshaven controls in all \( T_a \) treatments. Finally, our behavioral data show that when faced with a \( T_a \) below the TNZ, both species become more active (i.e. spent less time in the nest boxes), either in search of food or in an attempt to increase thermogenesis. Fur removal had relatively little effect on the level of activity (at least as measured herein) in either species.

The mixed results can likely be explained by species-specific characteristics. The Mashona mole-rat is a highly social, subterranean species from a tropical climate that is unlikely to experience temperatures below the TNZ. Further, Mashona mole-rats are relatively small endotherms with a high surface/volume ratio. Therefore, this species may lack the thermogenetic capacity to maintain homeothermy under thermal stress associated with cold \( T_a \). Our results corroborate previous evidence from

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Figure 6. Physiological and behavioral measures of thermoregulation in unshaven (black bars) and shaven (grey bars) highveld mole-rats (Cryptomys hottentotus pretoriae) across a range of ambient temperatures (mean ± SE). Boxes are: (A) expression of heterothermy; (B) modal body temperature; (C) proportional change in body mass; (D) number of visits to the nest box; (E) mean duration of visits to the nest box; and (F) total duration of visits to the nest box. Bars that share any letter are not significantly different.
short-term exposure to cold that this species has difficulty thermoregulating below 25°C (Bennett et al., ’93) and anecdotal observations of animals found lethargic suggest they may not have the capacity to rewarm after $T_a$ falls below normal levels. Further, mole-rats are known to have high thermal conductance compared to similar-sized mammals (Bennett, 2009), which may prevent overheating in enclosed burrow systems (McNab, ’66). The effect of fur removal on thermoregulation, at least to the extent that fur was removed in this experiment, was minimal on thermoregulation in Mashona mole-rats. The general lack of effect contradicts theoretical predictions and suggests that fur may be relatively unimportant for thermoregulation below the TNZ in this species.

The highveld mole-rat is also highly social and subterranean, but occurs in a sub-tropical climate at high altitude where nighttime winter temperatures frequently drop below the species’ TNZ, although extended exposure to cold is still unlikely. It is a slightly larger species than the Mashona mole-rat and is thought to have more precise thermoregulatory control under short-term exposure to cold $T_a$s (Haim and Fairall, ’86). Highveld mole-rats do not increase heterothermy even when faced with considerable thermoregulatory costs associated with decreased $T_a$ and/or increased heat loss, but they do lower their $T_a$ in response to increased heat loss. This suggests that fur may be more important for thermoregulation in highveld mole-rats than in Mashona mole-rats, which is not surprising as highveld mole-rats have, qualitatively speaking, longer and denser fur than Mashona mole-rats.

Given the loss of mass in both unshaven and shaven individuals during $T_a$ treatments below the TNZ, it appears that the energetic benefits gained from lessening control of $T_b$ as $T_a$ decreased (in Mashona mole-rats) or heat loss increased (in highveld mole-rats) could not offset increased energy expenditure associated with the likely increases in activity and/or thermogenesis under the food restriction regime to which we exposed the animals. This is again likely related to the subterranean nature and environmental temperatures where these two species occur, which mean these species are unlikely to experience temperatures below TNZ for five consecutive days as they did in our experiment. Therefore, in the wild, these mole-rats may preferentially metabolize fat reserves to maintain high and constant $T_b$ during the brief periods they are under thermal stress instead of decreasing energy expenditure through alterations to physiological thermoregulation or increased activity. Conversely, the social nature of mole-rats may allow them to behaviorally thermoregulate in a manner not tested herein.

The goal of our study was to explicitly test predictions about the effects of increased thermoregulatory costs on the pattern of $T_b$ expressed by two relatively homeothermic species of mole-rats, not to measure the energetic benefit of fur to small mammals. Both species conformed to at least some of the predictions made within an adaptive thermoregulatory framework. This suggests that attempts to use the framework used for a long time to predict thermoregulatory patterns in ectotherms (Huey and Slatkin, ’76; Angilletta, 2009) have at least some merit and should be explored further. However, our results also demonstrate that generalizations about the effects that different costs will have on thermoregulatory patterns may be difficult, considering that even two closely related species responded to thermoregulatory challenges in different ways. The inconsistent response to similar thermoregulatory challenges may relate to the limited thermoregulatory flexibility of highly homeothermic species (when compared to heterotherms). Therefore, manipulative experiments addressing these predictions among a group of species displaying a gradient of thermoregulatory patterns (from homeothermy to heterothermy) will be of particular importance in the future.

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**LITERATURE CITED**


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