

Adaptive Thermoregulation in Golden Spiny Mice: The Influence of Season and Food Availability on Body Temperature

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ABSTRACT

We studied the effect of food supplementation during summer and winter in seminatural field conditions on thermoregulation of a desert rodent, the golden spiny mouse *Acomys russatus*. We hypothesized that (a) under natural food availability (control conditions), mice will use less precise thermoregulation (i.e., an increase in the variance of body temperature [T_b]) during winter because of low ambient temperatures (T_a 's) and low food availability and during summer because of low food and water availability; (b) food supplementation will result in more precise thermoregulation during winter, but the effect will be smaller during summer because variation in T_b in summer is also driven by water availability during that period. We found that under natural food availability, spiny mice thermoregulated more precisely during summer than during winter. They spent more time torpid during summer than during winter even when food was supplemented (although summer nights are shorter), allowing them to conserve water. Supplementing food resulted in more precise thermoregulation in both seasons, and mice spent less time torpid. In summer, thermoregulation at high T_a 's was less precise, resulting in higher maximum T_b 's in summer than in winter and when food was supplemented, in accord with the expected effect of water shortage on thermoregulation. Our results suggest that as expected, precise thermoregulation is beneficial when possible and is abandoned only when the costs of homeothermy outweigh the benefits.

Introduction

The cost of maintaining high body temperatures (T_b 's) in homeothermic endotherms is high. It constitutes a substantial component of their resting metabolic rate and is directly related to ambient temperature (T_a). In cold environments, homeothermic endotherms have to use behavioral and physiological strategies to maintain internal T_b at the level of maximum physical performance. These strategies include increasing metabolic rate to produce more heat in proportion to the rate of heat loss to the environment (Geiser 2004a; Heldmaier et al. 2004). This is particularly true in small mammals, whose high surface area to body mass ratios result in relatively high heat loss rates (McNab 2002; Wang et al. 2006).

For years, T_b 's of mammals and birds were considered to be constant. However, it is becoming apparent that this is not the case: T_b 's of almost all endothermic vertebrates fluctuate over time (e.g., Geiser 2004a; Heldmaier et al. 2004) with a controlled reduction in T_b defined as torpor or hibernation. These variations in T_b 's are considered adaptive (e.g., Humphries et al. 2003; Geiser 2004a, 2004b; Ehrhardt et al. 2005).

In a recent article, Angilletta et al. (2010) applied classical conceptual models of thermal adaptation developed for ectotherms to endotherms. They suggested that optimality models, taking into account the costs and benefits of thermoregulation, can explain the qualitative effects of abiotic and biotic factors on thermoregulation, and they constructed a set of predictions regarding the effects of these factors on variations in T_b , thermal sensitivity, and the covariance between them (Angilletta et al. 2010). Here, we studied T_b 's of a desert rodent, the golden spiny mouse *Acomys russatus*, under seminatural field conditions during summer and winter at different resource levels in order to test how these conditions effect thermoregulation. The golden spiny mouse is a diurnally active small desert rodent that inhabits areas where food availability and quality are unpredictable in space and time. It inhabits rock crevices and does not dig burrows or store food (Shkolnik 1966, p. 117). Its preferred dietary item are arthropods (Kronfeld-Schor and Dayan 1999), whose availability and spatial distribution in the golden spiny mouse natural habitat fluctuate daily and seasonally (Vonshak et al. 2009). Recent laboratory studies suggest that the golden spiny mouse is able to defend its body mass by using torpor during food shortage periods and by gaining fat mass when food is plentiful (Merkt and Taylor 1994; Kronfeld-Schor et al. 2000; Ehrhardt et al. 2005; Gutman et al. 2006, 2007, 2008). Such use of daily torpor, which lowers energy and water requirements, may be crucial for survival and reproduction of small insectivorous mammals in the arid zone (Merkt and Taylor 1994; Kronfeld-Schor et al. 2000; Geiser

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2004b; Ehrhardt et al. 2005; Gutman et al. 2006, 2008; Kortner and Geiser 2009).

We used Angilletta's et al. (2010) conceptual model to construct a set of hypotheses predicting the effects of season, water, and food availability on thermoregulation in golden spiny mice. Angilletta et al. (2010) suggested that under low food availability, thermoregulation will be less precise (i.e., the variance of T_b will increase) than under ad lib. food availability; that as T_a deviates from the thermoneutral zone, thermoregulation will be less precise; and that dehydrated animals are expected to thermoregulate less precisely than hydrated animals.

In accord, we hypothesized that under natural food availability (control conditions), golden spiny mice will use less precise thermoregulation during winter because of the low T_a 's and low food availability and during summer because of low food and water availability. We also hypothesized that food supplementation will result in more precise thermoregulation during winter but less so during summer because variation in T_b is also driven by the low water availability and not just food scarcity during that period.

Material and Methods

Experimental Protocol

Experiments were conducted in the summer of 2003 (August and early September) and in the winter of 2004 (January and February) in two field enclosures (see below). In each season, T_b of golden spiny mice was measured under seminatural conditions. Sunflower seeds were added ad lib. to the enclosures for 7 d followed by 10 d with natural food availability.

Experimental Enclosures

We conducted our field experiment at the Ein Gedi nature reserve in the Judean Desert near the Dead Sea (31°28'N, 35°23'E, 300 m below sea level) in two established 1,000-m² enclosures containing golden spiny mice. The mice were descendants of eight individuals in each enclosure that were trapped in the area in 2001 (for details see Gutman and Dayan 2005) and bred in the enclosures. Over the years, individuals were removed to other enclosures or released to regulate population size, and from time to time, wild-caught individuals were added to the enclosures to avoid inbreeding. The sex ratio of the population within the enclosures was also monitored and was managed at 1 : 1. For identification, each individual was implanted with a PIT (Passive Integrated Transponder, Destron-Fearing) tag. The enclosures were constructed of 10-mm wire mesh buried 3 cm into the ground and standing 70 cm high. Thus, the natural predators (foxes, snakes, owls, and diurnal raptors) and prey (mostly arthropods) of spiny mice could enter and exit the enclosures freely.

During the summer experimental session, the enclosures contained 16 mice (eight mice in each enclosure), and transmitters were implanted in 12 individuals ($n = 6$ in each enclosure, four males and eight females). During the winter experimental session, the enclosures contained 15 mice ($n = 7$

or $n = 8$ in each enclosure), and transmitters were implanted in 13 individuals ($n = 6$ or $n = 7$ in each enclosure, six males and seven females). Of these, we successfully monitored nine individuals during summer and eight individuals during winter under both ad lib. and natural food availability conditions. The sample sizes for all statistical tests are therefore $n = 9$ during summer and $n = 8$ during winter.

Our artificial food patches consisted of six plastic trays (30 cm × 20 cm × 4 cm) containing two liters of finely sifted local soil. Three trays were placed in each enclosure. During the ad lib. session, we placed a large amount of peeled sunflower seeds on each tray and replenished the pile every few days so that food was plentiful during the entire experiment. During the natural food availability session, no food was put in the trays. Because golden spiny mice do not hoard food (Shkolnik 1966, p. 117), we assume the mice were under natural food availability conditions. Frames constructed from heavy wire and fine filament fish netting excluded birds from the trays during the day (details in Jones and Dayan 2000). Mice reached the trays easily by biting through one strand in the net.

Animal Surgery

Mice were trapped, anesthetized with isoflurane in medical-grade oxygen using an anesthetic machine (Ohmeda) and implanted with single-stage transmitters (ca. 2 g; Sirtrack) in the abdominal cavity. Both the abdominal wall and the skin were sutured with absorbable surgical suture with cutting needle (5-0 Dexon), and the incision was treated with topical antibiotic (silver sulfadiazine 1%; Silverol Cream). Prophylactic antibiotics (Baytril 5% 24 mg/kg) and artificial tear ointment (to prevent desiccation) were administered preoperatively. Mice were returned to their enclosures 48 h after capture. After a 1-wk recovery period, T_b 's were monitored continuously.

Monitoring T_b and T_a

Each implanted radio transmitter uses a unique frequency, which enables individual identification. The transmitter uses a comparison circuit against which the pulse period being determined by the temperature is referenced. We used an RX 900 scanner receiver (Televilt) connected to two dipole antennas for data logging. The receiver scanned each frequency for a period of 45 s, and whenever a signal was received, the time, frequency, pulse parameters, active antenna, and signal strength were logged. Hence, data for each transmitter were logged once every 20 min. Before implantation, transmitters were calibrated in a water bath to the nearest 0.1°C using a precision mercury thermometer. We converted the pulse period to a temperature using the calibration curves we produced using five different temperatures.

T_a was measured to the nearest 0.5°C every 30 min using three data-logger thermometers (iButton ds1921 thermochrom). The thermometers were placed in one enclosure under boulders in the shade, representing the microhabitat used most by spiny mice.

Data Analysis

During the experiment we recorded over 150,000 T_b readings for each season. In order to analyze these numerous data efficiently, we developed a computer program that computes T_b according to the transmitter-specific calibration curve and enters the records into an SQL database (R code is available as a text file in the online edition of *Physiological and Biochemical Zoology*). In order to identify any biologically unreasonable T_b readings that should be ignored during data analysis, we included a filter algorithm in the program; if a reading differed from the previous and subsequent readings of the same individual by more than 7°C, it was omitted. We calculated individual mean T_b at each 20-min interval over days during each treatment. T_a measurements were also inserted into the database. We also calculated mean daily rhythms of T_a for each season (at 30 min intervals) and the average T_b for each T_a recorded.

For thermoregulation accuracy analysis, we calculated the daily heterothermy index (HI) for each individual using the HI equation suggested by Boyles et al. (2011):

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

where T_{b-opt} is the optimal T_b for performance, T_{b-i} is the T_b measurement at time i , and n is the number of times T_b is sampled that day. As T_{b-opt} , we used the mean modal T_b during summer and winter (summer: 37.6°C; winter: 36.6°C) as suggested by Boyles et al. (2011). For torpor bouts analysis, we defined the torpor T_b threshold by three different methods (Lovegrove et al. 1999b; McKechnie et al. 2007; Willis 2007). All three methods gave approximately the same T_b thresholds, and we chose to follow the method suggested by Willis (2007), the results of which are exhibited in our figures. We also report the values obtained using the torpor T_b threshold suggested by McKechnie et al. (2007). The torpor T_b thresholds obtained using McKechnie et al. (2007) were 35.1°C and 33.1°C during summer and winter, respectively, and the thresholds by Willis (2007), which change with T_a , were $34.6^\circ \pm 0.4^\circ\text{C}$ (mean \pm SD) and $33.8^\circ \pm 0.3^\circ\text{C}$ during summer and winter, respectively. We calculated individual average torpor bout duration, total time torpid per day, and the number of torpor bouts per day for each season. Bout duration was determined as the time between the beginning of the torpor bout (first data point when T_b was below the torpor threshold), until the animal's T_b returned to normothermy range (the first data point when T_b increased above the torpor threshold). Torpor calculations were made after omitting the first 3 d of each treatment (see below). We also calculated the timing of torpor entry and arousal (presented as the frequency of torpor entry or arousal for each half hour during the diel cycle) and T_b distribution.

Statistical Analysis

Mixed effects modeling was used because it appropriately acknowledges correlations in the outcome matrix that result from repeated observations of individuals. We analyzed data using the R statistical programming language (ver. 2.9.0; R Development Core Team 2009), using the lme function from the nlme package (ver. 3.1-90; Pinheiro et al. 2008). We started each model with the full model. Then we identified the optimal residual variance structure and the optimal random structure (Zuur et al. 2009). We tested for the fit of subjects, enclosures, and days under treatment as random factors. Random factors were removed from the model if they did not increase the fit of the model. Model selection of the optimal residual variance structure and the optimal random structure was based on the Akaike Information Criterion, which measures goodness of fit and model complexity (see Burnham and Anderson 1998). We examined (1) the effect of season and food availability on T_b ; (2) the effect of T_a on T_b ; and (3) the effect of season and food availability on HI, daily mean torpor bout duration, total time torpid, and the number of torpor bouts per day. Because the relationship between T_a and T_b was not linear, in test 2 we used Generalized Additive Mixed Models technique using the gamm function from the mgcv package (ver. 1.52; Wood 2008). In order to further explore the effect of T_a on T_b within each treatment, we used linear regression tests on each experimental session using the lm R function. All calculations were made at the individual level and then averaged for the figures.

In order to test on what day acclimation occurred during ad lib. and natural food availability treatments (i.e., when variables did not change any more), we ran test 1 with the days under treatment as a continuous covariate and omitted days beginning from the first day of treatment until there was no significant effect of day (tests not shown). Our tests showed that acclimation occurred after 3 d of treatment, and therefore we used the data from day 4 and on for each treatment. All results are presented as mean or estimate \pm SD.

Results

Mean body mass of golden spiny mice did not differ between seasons (summer: 53.9 ± 10.8 g; winter: 47.2 ± 6.5 g; Student t -test: $t = 1.56$, $df = 13.32$, $P = 0.14$).

T_a

T_a showed pronounced seasonal variations in our study area (Fig. 1). Average maximum T_a 's ($39.2^\circ \pm 2.0^\circ\text{C}$ in the shade under boulders) were recorded during summer around 1700 hours. Average minimum T_a 's ($15.8^\circ \pm 1.7^\circ\text{C}$) were recorded during winter at around 0700 hours. Minimum T_a 's were always recorded around sunrise, while maximum T_a 's were recorded around 1700 hours during summer and 1600 hours during winter. In both seasons, a distinct day/night variation in T_a was observed (T_a amplitude was $13.7^\circ \pm 3.7^\circ\text{C}$ in winter and $10.0^\circ \pm 0.82^\circ\text{C}$ in summer).

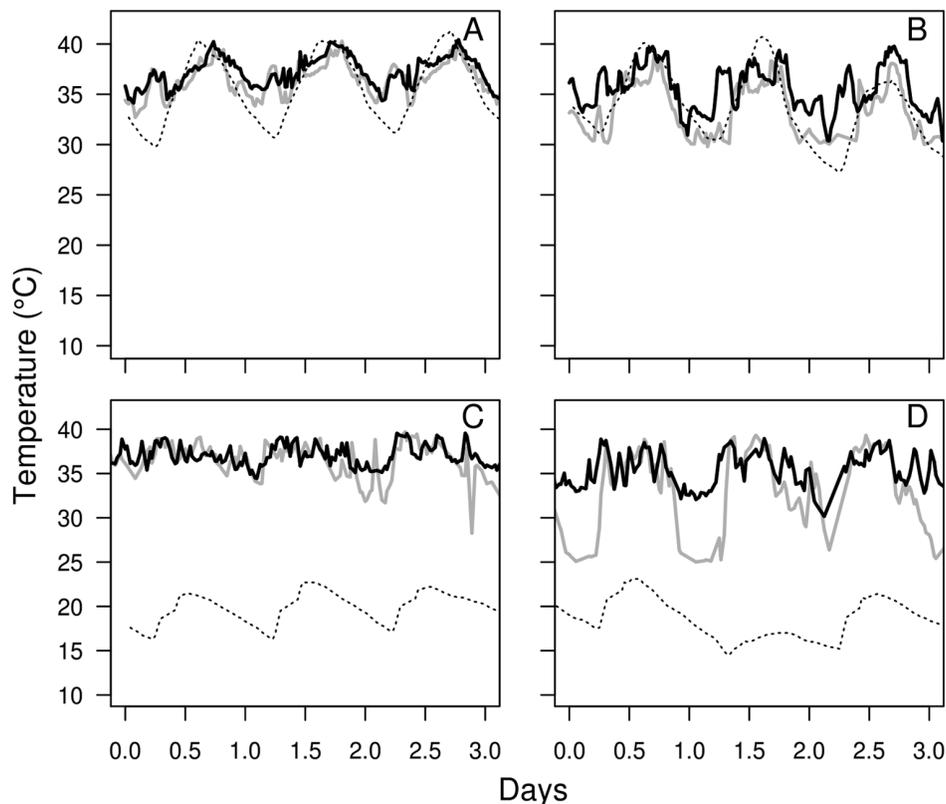


Figure 1. T_b rhythms of two golden spiny mice expressing the most (gray) and least (black) torpor during the summer under ad lib. (A) and natural (B) food availability and during the winter under ad lib. (C) and natural (D) food availability over 3 d. Dotted line represents corresponding T_a .

Effect of Season and Food Availability on Daily T_b Rhythm and HI

Added food resulted in a significant increase in average, minimum, and maximum T_b (Figs. 1, 2) and a significant decrease in HI. During summer under ad lib. food availability, average T_b was $36.8^\circ \pm 0.3^\circ\text{C}$, and it decreased by $2.6^\circ \pm 0.3^\circ\text{C}$ when food was naturally available ($df = 122$, $t = -28.91$, $P < 0.001$); maximum T_b was $40.0^\circ \pm 0.3^\circ\text{C}$ and decreased by $0.7^\circ \pm 0.3^\circ\text{C}$ ($df = 122$, $t = -7.09$, $P < 0.001$); minimum T_b was $33.8^\circ \pm 0.3^\circ\text{C}$ and decreased by $3.5^\circ \pm 0.3^\circ\text{C}$ ($df = 122$, $t = -26.88$, $P < 0.001$); and HI was 1.85 ± 0.27 and increased by 2.19 ± 0.24 ($df = 147$, $t = 26.82$, $P < 0.001$). The effect of food supplementation on average and minimum T_b properties and on HI was significantly stronger during winter; under ad lib. food availability, average T_b was $36.9^\circ \pm 0.28^\circ\text{C}$, and it decreased by $3.5^\circ \pm 1.13^\circ\text{C}$ when food was naturally available (food availability \times season: $df = 122$, $t = -2.43$, $P < 0.05$); minimum T_b was $35.1^\circ \pm 0.57^\circ\text{C}$ and decreased by $9.4^\circ \pm 1.4^\circ\text{C}$ (food availability \times season: $df = 122$, $t = -17.82$, $P < 0.001$); and HI was 1.44 ± 0.46 and increased by 3.37 ± 0.47 (food availability \times season: $df = 147$, $t = 3.07$, $P < 0.01$). However, the effect of natural food availability on maximum T_b was significantly weaker during winter; under ad lib. food

availability, maximum T_b was $39.2^\circ \pm 0.3^\circ\text{C}$ and decreased by $0.3^\circ \pm 0.8^\circ\text{C}$ (food availability \times season: $df = 122$, $t = 2.66$, $P < 0.01$). Moreover, under ad lib. food availability, HI was significantly higher during summer than winter by 0.43 ± 0.28 ($df = 147$, $t = -4.56$, $P < 0.001$).

The distribution of frequencies of each T_b was different between the seasons and between treatments (Fig. 3). More than 50% of the T_b records were between 35° and 39°C except during the summer when food was naturally available (summer, ad lib.: $80.1\% \pm 4.4\%$; summer, natural food availability: $40.5\% \pm 5.9\%$; winter, ad lib.: $88.2\% \pm 10.5\%$; winter, natural food availability: $52.8\% \pm 17.6\%$), when the most frequent T_b was lower, the T_b amplitude was lower, and T_b frequencies were more evenly distributed. The effect of food availability on the distribution of frequencies was stronger in winter than in summer.

Effect of T_a on T_b

The relationships between T_a and average T_b had significant nonlinear components at all treatments (summer, ad lib.: $edf = 4.3$; summer, natural food availability: $edf = 4.9$; winter, ad lib.: $edf = 6.7$; winter, natural food availability: $edf = 6.1$;

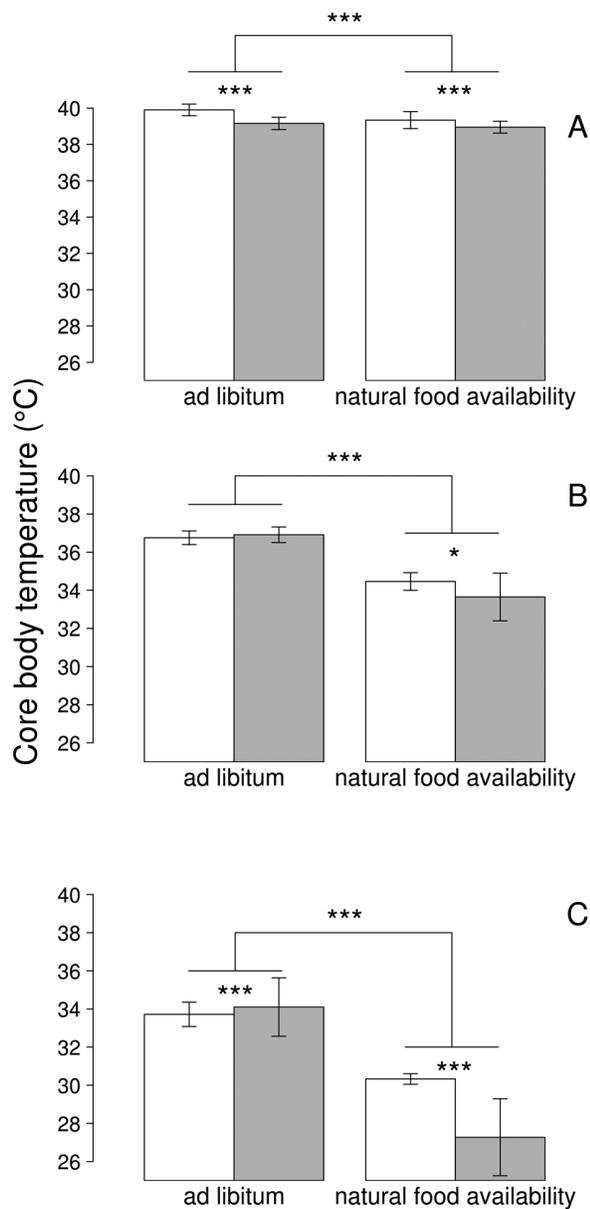


Figure 2. Daily core T_b properties (mean \pm SD) of golden spiny mice under ad lib. and natural food availability (A, maximum T_b ; B, average T_b ; C, minimum T_b) during the summer (unfilled bars, $n = 9$) and winter (filled bars, $n = 8$) after 3 d of acclimation to each food treatment. One asterisk, $P < 0.05$; three asterisks, $P < 0.001$.

all treatments: $P < 0.001$; Fig. 4). During summer, when food was available ad lib., average T_b decreased with T_a with a slope of $0.4^{\circ}/1^{\circ}\text{C}$ (multiple $R^2 = 0.58$, $P < 0.001$) until it reached 35°C at T_a of 33°C , after which it started to increase even though T_a decreased with a slope of $0.8^{\circ}/1^{\circ}\text{C}$ (multiple $R^2 = 0.86$, $P < 0.01$). When food was naturally available, highest average T_b 's were recorded at T_a 38°C . At higher T_a , average T_b decreased. Between T_a 38° and 29°C , average T_b dropped with a slope of $0.7^{\circ}/1^{\circ}\text{C}$ (multiple $R^2 = 0.94$, $P < 0.001$) until they

reached 31°C . Below that T_a , average T_b started to increase again (Fig. 4A).

During winter under ad lib. food availability, mice kept their average T_b around 37°C at the higher range of T_a 's. Between T_a 25° and 19°C , average T_b dropped with a slope of $0.4^{\circ}/1^{\circ}\text{C}$ (multiple $R^2 = 0.98$, $P < 0.001$) until it reached 36°C , after which it increased back to around 37°C . When food was naturally available, mice kept their average T_b around 37°C at the higher range of T_a 's. Between T_a 25° and 19°C , average T_b dropped with a slope of $1.2^{\circ}/1^{\circ}\text{C}$ (multiple $R^2 = 0.93$, $P < 0.001$) until it reached 31°C , after which it did not drop any more even at lower T_a (Fig. 4B).

Analysis of Torpor Bouts

Occurrence of torpor bouts varied between summer and winter and between natural and ad lib. food availabilities (Fig. 5). There were 0.63 ± 0.5 more bouts/day (0.29 ± 0.13 , using McKechnie et al. 2007) during summer than during winter ($df = 118$, $t = -3.55$, $P < 0.001$) and 0.81 ± 0.46 (0.67 ± 0.14 , using McKechnie et al. 2007) more torpor bouts/day during natural food availability than during ad lib. food availability ($df = 118$, $t = -5.27$, $P < 0.001$; food availability \times season: -0.26 ± 0.94 , $df = 117$, $t = -0.78$, $P = 0.43$ [no. bouts]). The average duration of each torpor bout did not differ significantly between seasons (winter effect: 0.31 ± 89.4 , $df = 95$, $t = 0.01$, $P = 0.99$ [min]) but increased during natural food availability by 348.77 ± 102.4 (322.9 ± 31.7 , using McKechnie et al. 2007) min ($df = 95$, $t = 10.22$, $P < 0.001$; food availability \times season: -50.42 ± 217.3 , $df = 94$, $t = -0.66$, $P = 0.51$ [min]). The average time/day each individual spent torpid increased under natural food availability by 633.15 ± 140.3 (526.95 ± 40.5 , using McKechnie et al. 2007) min compared with ad lib. food availability ($df = 117$, $t = -13.54$, $P < 0.001$ [min]). The time spent torpid during natural food availability was lower by 266.87 ± 242.5 (197.72 ± 50.3 , using McKechnie et al. 2007) min ($df = 117$, $t = -3.11$, $P < 0.01$) during winter than during summer. Under ad lib. food availability, there was no significant season effect (winter effect: -39.32 ± 112.7 , $df = 117$, $t = -0.99$, $P = 0.33$ [min]).

During summer, the times of torpor entry (Fig. 6A) and times of arousal from torpor (Fig. 6B) occurred during the first half of the day and during the entire night, starting at sunset. During winter, individuals entered torpor mainly during the hours before sunset but also at the beginning of the night and the beginning of the day (Fig. 6C), while arousal occurred mainly during the few hours after sunrise but was also scattered throughout both the day and night (Fig. 6D).

Discussion

As predicted by the optimal thermoregulation model suggested by Angilleta et al. (2010), under natural food availability, golden spiny mice thermoregulated more precisely during summer than during winter, when T_a 's deviated significantly below the golden spiny mouse thermoneutral zone lower critical point

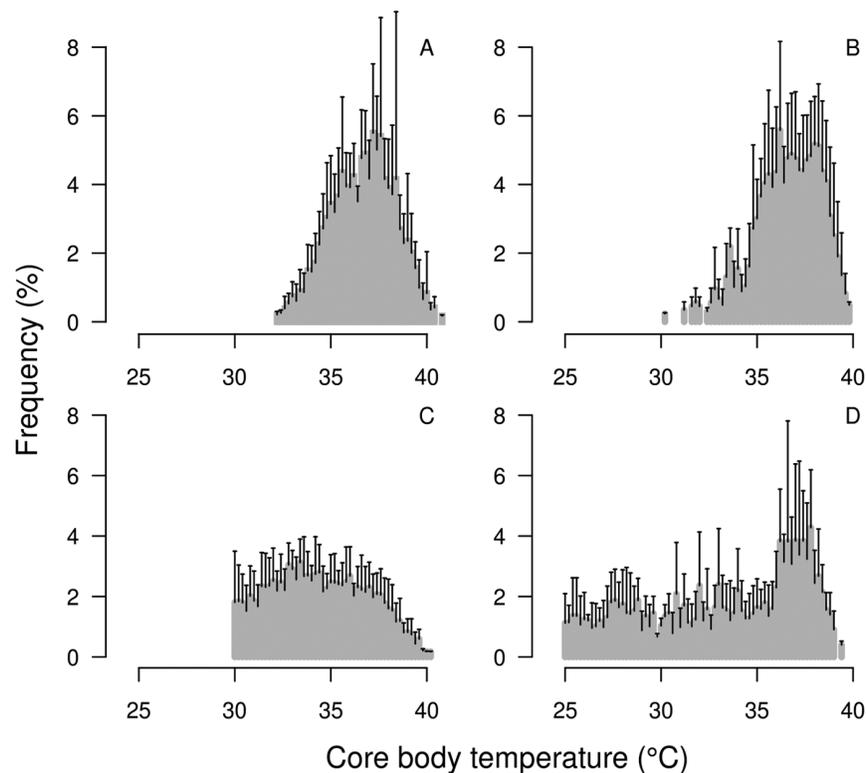


Figure 3. Daily frequencies (mean + SD) of golden spiny mice individual T_b 's during summer and winter when food was offered ad lib. (A, summer; B, winter) and under natural food availability (C, summer; D, winter); $n = 9$ and $n = 8$ during summer and winter, respectively.

(30°C; Shkolnik 1971). This result was also apparent from the higher HI during winter compared with summer. Nevertheless, using several different definitions for torpor thresholds, we found that spiny mice spent more time torpid during summer than during winter, although summer nights are shorter than winter nights. The increase in torpor length resulted from an increase in torpor frequency, while torpor bout duration did not differ between seasons (Fig. 5). Most species studied to date use torpor more frequently during winter than summer as an adaptation to winter conditions (reviewed by Geiser 2004a; Heldmaier et al. 2004). To the best of our knowledge, the only other species where an increase in the use of torpor during summer was described is the subtropical blossom bat (*Syconycteris australis*; Coburn and Geiser 1998).

Supplementing food resulted in more precise thermoregulation and a lower HI in both seasons, and the mice spent significantly less time torpid. A similar effect of food availability on the precision of thermoregulation was described in free-ranging eastern chipmunks *Tamias striatus*, where experimental supplementation of food hoards or high food availability led to reduced torpor expression (Humphries et al. 2003; Landry-Cuerrier et al. 2008), and in the subtropical blossom bat *S. australis*, where the more pronounced torpor during summer was ascribed to low or unpredictable food availability during this season (Coburn and Geiser 1998).

Interestingly, thermoregulation at high T_a 's was less accurate

during summer, resulting in significantly higher maximum T_b 's in summer than in winter. This did not change when food was supplemented and is in accord with the expected effect of water shortage on thermoregulation. Furthermore, golden spiny mice spent more time torpid during summer than during winter even when food was supplemented. Adaptive thermoregulation is important for water conservation, especially for mammals of arid regimes (Schmid and Speakman 2000; Geiser 2004b; Cooper et al. 2005). It allows golden spiny mice to conserve water in two ways. First, by allowing T_b to decrease, the animal reduces metabolic rate, food consumption, and activity, which results in a parallel reduction in evaporative, fecal, and urinary water loss (Cooper et al. 2005). The higher use of torpor during summer in golden spiny mice, even when food was supplemented, is probably used as a water-saving strategy. Second, by allowing their T_b 's to increase to higher levels during summer, the mice delay the onset of evaporative cooling as a strategy for conserving water. Coupled with other water-conserving adaptations of the golden spiny mouse (Shkolnik and Borut 1969; Shkolnik 1971; Kam and Degen 1993; Kronfeld-Schor et al. 2000, 2001c), use of adaptive thermoregulation likely increases its survival during prolonged periods of low water availability.

Although less precise thermoregulation considerably reduces energy expenditure, it also involves physiological and ecological costs, including the cost of arousal from torpor, or returning to normothermia (Tucker 1965; Kortner and Geiser 2000;

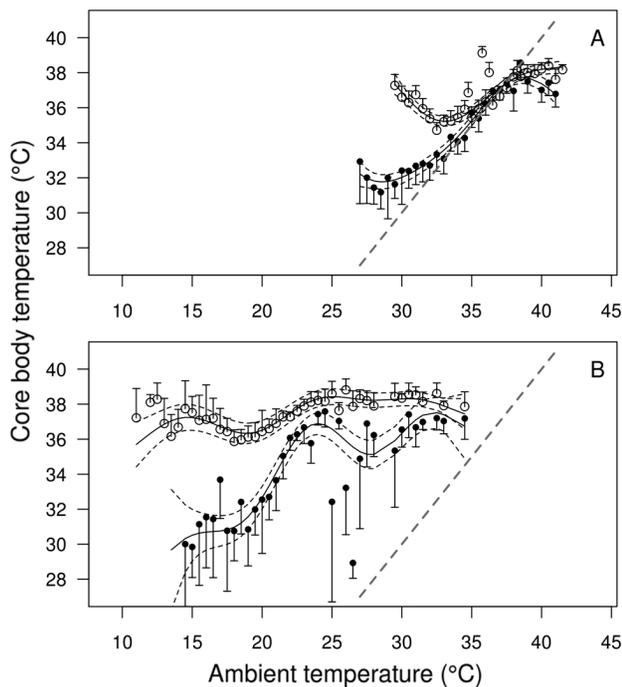


Figure 4. Core T_b of golden spiny mice (mean \pm SD) across a range of T_a 's during summer (A) and winter (B) under ad lib. (unfilled circles) and natural (filled circles) food availability sessions. The solid lines are the estimated smoothing curves fitted from a Generalized Additive Mixed Model. The black dotted lines are the 95% confidence bands; the gray dotted lines are $T_a = T_b$.

Boyles et al. 2007; Landry-Cuerrier et al. 2008). One of the parameters affecting the energetic cost of arousal from torpor is T_a . Therefore, it is expected that the energetic cost of arousal will be much higher during winter than during summer (Lovegrove et al. 1999a; Geiser and Drury 2003; Wojciechowski et al. 2007). In accord, winter field-trapped as well as short-day-acclimated golden spiny mice have higher nonshivering thermogenesis capacity (Kronfeld-Schor et al. 2000). However, golden spiny mice may also use passive rewarming or basking (Geiser and Pavey 2007; Pavey and Geiser 2008), taking advantage of the increase in T_a in the morning, which is $\sim 15^\circ\text{C}$ higher during summer than during winter, resulting in a further decrease in the cost of torpor. Accordingly, during winter, golden spiny mice usually entered torpor a few hours before sunset, possibly because of the decrease in T_a , and were aroused from torpor usually a few hours after sunrise, when T_a increased. The use of passive rewarming is also clearly evident when looking at the daily rhythm of T_b in relation to T_a on a daily basis (Fig. 1).

Use of adaptive thermoregulation as an energy- and water-conserving measure in field populations must have significant effects on foraging decisions of individuals and interspecific interactions of populations. Golden spiny mice respond to the absence of their nocturnal congener, the common spiny mouse, by shifting some of their activity into the night (Shkolnik 1971;

Gutman and Dayan 2005). This phenomenon coupled with the endogenous rhythmicity of a nocturnal species suggests that common spiny mice have competitively displaced golden spiny mice into diurnal activity (Shkolnik 1971; Kronfeld-Schor et al. 2001a; Kronfeld-Schor and Dayan 2003; Cohen and Kronfeld-Schor 2006; Levy et al. 2007; Cohen et al. 2009). Golden spiny mice have evolved adaptations to cope with high summer T_a during the day (e.g., Koskela et al. 1989; Kronfeld-Schor et al. 2000, 2001b, 2001c), enabling them to use temporal partitioning as a mechanism of coexistence. The ability to use

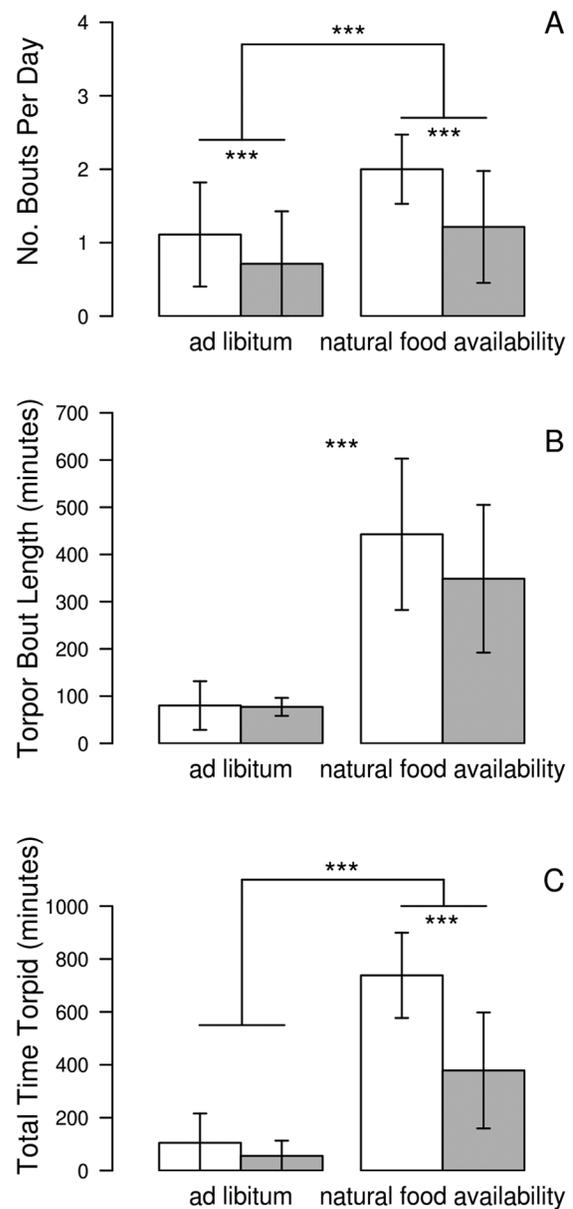


Figure 5. Daily number (mean \pm SD) of bouts per day (A), torpor bout duration (B), and total time torpid (C) per individual in golden spiny mice during summer (unfilled bars, $n = 9$) and winter (filled bars, $n = 8$) under natural food availability. Three asterisks, $P < 0.001$.

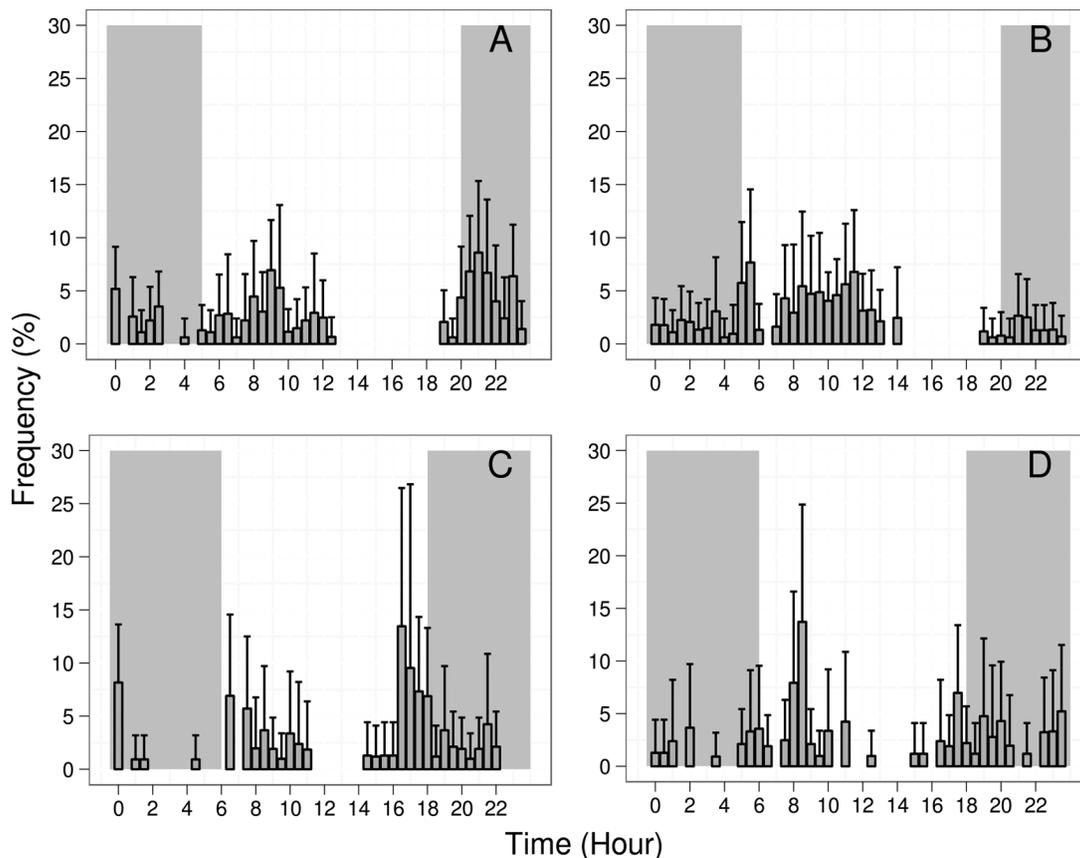


Figure 6. Distribution (% mean \pm SD) of time of entry (A, summer; C, winter) and arousal (B, summer; D, winter) from torpor in golden spiny mice under natural food availability; $n = 9$ and $n = 8$ during summer and winter, respectively. Gray shading represents dark hours.

adaptive thermoregulation and to undergo torpor, an additional mechanism of coping with heat stress and the need for water conservation (Shkolnik and Borut 1969; Kronfeld-Schor et al. 2001a, 2001b), may well be equally significant for promoting coexistence between the golden spiny mouse and its congener. Thus, this physiological mechanism may well have community-level implications.

The fact that when possible, mice kept homeothermia (when food availability was high during winter) supports the hypothesis that the adaptive thermoregulation results from an optimization between its costs and benefits (Humphries et al. 2003; Angilletta et al. 2010). These include both physiological and ecological parameters, such as variation in energy availability, water availability, physiological costs of foraging, costs of interspecific interactions (predation, competition), and the physiological costs of torpor.

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