

Effect of environmental temperature on body temperature and metabolic heat production in a heterothermic rodent, *Spermophilus tereticaudus*

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Summary

This study quantifies the thermoregulatory ability and energetics of a mammal, the round-tailed ground squirrel *Spermophilus tereticaudus*, that can relax thermoregulatory limits without becoming inactive. We measured body temperature and metabolic rate in animals exposed for short periods (1 h) to air temperatures ranging from 10 to 45 °C and for long periods (8 h) to air temperatures ranging from 10 to 30 °C. Within 45 min of exposure to air temperatures ranging from 10 to 45 °C, the mean body temperatures of alert and responsive animals ranged from 32.1 °C ($T_{\text{air}}=10$ °C) to 40.4 °C ($T_{\text{air}}=45$ °C). This thermolability provided significant energetic savings below the thermoneutral zone, ranging from 0.63 W (18 %) at 10 °C to 0.43 W (43 %) at 30 °C. When exposed for 8 h to air temperatures between 10 and 30 °C, animals

varied their body temperature significantly over time. At all air temperatures, the lowest body temperature (maintained for at least 1 h) was 31.2 °C. The highest body temperatures (maintained for at least 1 h) were 33.6 °C at 10 °C, 35.3 °C at 20 °C and 36.3 °C at 30 °C. The energetic savings realized by maintaining the minimum rather than the maximum body temperature was 0.80 W (25 %) at 10 °C, 0.71 W (33 %) at 20 °C and 0.40 W (47 %) at 30 °C. This study demonstrates in several ways the ability of this species to adjust energy expenditure through heterothermy.

Key words: thermoregulation, heat transfer, heterothermy, metabolic heat production, body temperature, round-tailed ground squirrel, *Spermophilus tereticaudus*.

Introduction

Endothermic homeothermy is one of the most significant evolutionary alterations involving the relationship between an animal and its environment (Hayes and Garland, 1995; Hensel et al., 1973). Many birds and mammals precisely regulate metabolic heat production (MHP) and heat loss to maintain a high (35–42 °C) and stable (± 1.0 °C) core body temperature (T_B) over a broad range of environmental conditions. This provides them with a 'thermodynamic freedom' that is unavailable to other species (Burton and Edholm, 1955; Crompton et al., 1978; McNab, 1978). Endothermic homeothermy provides a steady state for physiological and biochemical functions (e.g. locomotion, enzymatic activity, membrane and action potentials, digestion, growth, excretion) and offers profound ecological consequences by allowing these animals to be active for longer periods and over a wider range of habitats (Bartholomew, 1977; Heinrich, 1977; Crompton et al., 1978; Avery, 1979; Block et al., 1993; Somero et al., 1996).

Endothermic homeothermy also imposes a large energetic burden on the animal. At rest within the animal's thermoneutral zone, maintenance of the metabolic machinery necessary for increased activity and thermogenic capacity results in a basal metabolic rate that is 8–10 times higher than the standard metabolic rate of a similar-sized ectotherm

(Bennett and Ruben, 1979; Else and Hulbert, 1981). When exposed to air temperatures below the thermoneutral zone, these animals further increase metabolic rate, as much as eightfold above basal metabolic rate, to maintain a constant T_B (Hinds et al., 1993). The energetic requirements for an endothermic homeotherm to maintain such a constant T_B is a function of the animal's thermal conductance and the temperature gradient that must be overcome. Small and poorly insulated animals have the highest area-specific thermal conductances and, therefore, are most likely to experience conditions in which the energetic demand of maintaining a constant T_B exceeds supply (e.g. extreme thermal conditions, limited resource availability, inadequate ability to acquire or process sufficient resources).

Instability of body temperature due to exposure has mostly been studied in humans and domestic animals (Keller, 1955; Hamilton, 1968; Edholm, 1978; Hayward, 1983; Clark and Edholm, 1985; Reinertsen, 1996). For these species as well as other non-domesticated forms (e.g. *Neotoma lepida*, *Dipodomys merriami*; K. M. Wooden, personal observation), hypothermia of more than 2 °C results in the loss of coordinated locomotory performance, impairment of physiological function and loss of consciousness. Hypothermia of more than 5 °C often results in death. Thus, for many small

and poorly insulated animals, survival mechanisms have evolved that allow them temporarily to abandon tight thermoregulatory control. Through hibernation, torpor or estivation, these animals reduce thermoregulatory demand, lower metabolic rate and realize substantial energetic savings. However, because the T_B of most endothermic homeotherms is tightly coupled to physiological function, allowing T_B to drop also leaves these animals inactive and unable to respond readily to external stimuli (Schmidt-Nielsen, 1990; Reinertsen, 1996).

At least one species of bird (*Todus mexicanus*, Mercola-Zwartjes and Ligon, 2000) and several species of mammal (*Bradypus cuculliger*, Wislocki, 1933; *Bradypus griseus*, Britton and Atkinson, 1961; *Pipistrellus hesperus*, Bradley and O'Farrell, 1969; *Myotis thysanodes*, *Myotis lucifugus*, Studier and O'Farrell, 1972; *Eptesicus fuscus*, Hirshfeld and O'Farrell, 1976; *Antrozous pallidus*, *Myotis californicus*, *Pipistrellus hesperus*, *Plecotus townsendii*, Nelson et al., 1977; *Heterocephalus glaber*, Buffenstein and Yahav, 1991; *Nycticeius humeralis*, *Lasiurus intermedius*, Genoud, 1993; *Geogale aurita*, Stephenson and Racey, 1993; *Murina leucogaster ognevi*, Choi et al., 1997; *Spermophilus tereticaudus*, Hudson, 1964; Wooden and Walsberg, 2000) can, however, maintain normal activity and display no pathological effects over changes in T_B as large as 14 °C. Of these species, the energetics of this phenomenon has only been studied in the Puerto Rican tody (*Todus mexicanus*) (Mercola-Zwartjes and Ligon, 2000). *T. mexicanus* remains fully alert, responsive to external stimuli and capable of flight at body temperatures ranging from 28 to 42 °C. When exposed to an air temperature (T_{air}) of 15 °C, the body temperature of this species ranges between 32 and 33.4 °C. By lowering T_B by only 1.4 °C from 33.4 to 32 °C, this species reduces energetic cost by 28 %. At a T_{air} of 30 °C, *T. mexicanus* maintains an active-phase T_B of only 36.7 °C. This allows them to expend 33 % less energy for thermoregulation than that required to maintain the T_B reported for other coraciforms of 40 °C (Prinzinger et al., 1991).

Our current study addresses the energetics and thermoregulatory ability of a mammal, the round-tailed ground squirrel (*Spermophilus tereticaudus*), that like *T. mexicanus* relaxes thermoregulatory limits without becoming inactive. This diurnal rodent inhabits the most barren areas of the Sonoran and Mohave Deserts, where daytime air temperature ranges from less than 5 °C in the winter months to 50 °C during the summer (K. M. Wooden, unpublished data). *S. tereticaudus* has a very sparse coat (Walsberg, 1988) and consequently a very high thermal conductance (Wooden and Walsberg, 2000). Metabolic rate at rest within the thermoneutral zone is approximately 60 % of that predicted by mass, and this species remains active and alert over body temperatures ranging from 30 to 42 °C (Hudson, 1964; Wooden and Walsberg, 2000). The primary questions addressed by this study are as follows. (i) How does T_{air} affect metabolic heat production and T_B ? (ii) How much control over T_B does this species have at a given T_{air} ? (iii) How do changes in T_B relate to changes in metabolic

heat production? (iv) Are there energetic savings associated with changes in T_B ?

Materials and methods

Animal collection and maintenance

Male *Spermophilus tereticaudus* Baird were trapped between March and April in the Sonoran Desert, approximately 25 km north of Gila Bend, Maricopa County, Arizona, USA, at an altitude of approximately 225 m. Mean body mass at capture was 129.1 ± 2.7 g (mean ± S.E.M., $N=11$). Animals were housed in a temperature-controlled room that was maintained at 30 °C under a 12h:12h light:dark photoperiod. Animals were fed Teklad rodent diet and supplied *ad libitum* with water.

Within 1 week of capture, all animals were drinking water freely and began gaining mass. At this time, temperature transmitters were inserted into the abdominal cavity and positioned just below the liver (anesthesia, metofane). The incision (approximately 2 cm long) was closed with silk sutures. We began the experimental procedures when all animals had fully recovered from the surgery (2 weeks). Mean body mass during the experimental procedures was 131.4 ± 2.1 g (mean ± S.E.M., $N=11$).

Procedures

We conducted two studies using the same animals. In both studies, measurements were taken from post-absorptive animals resting quietly for at least one 99 % equilibration period of the chamber (Lasiewski et al., 1966). The regime of temperature exposure was randomized, and no animal was used on consecutive days. Studies conducted during the active phase of the animals' daily cycle were completed between 08:00h and 17:00h. Those conducted during the animal's resting phase were completed between 20:00h and 05:00h. The first study measured metabolic heat production (MHP) and T_B during the active phase, over short-term (approximately 1 h) exposure to air temperatures ranging from 10 to 45 °C. Values of MHP are the mean of the first 5 min following at least 45 min under the experimental conditions. Values of T_B reported were taken immediately following metabolic measurements. The second study measured the same variables over longer periods of exposure to air temperatures below the thermoneutral zone (during both the active and resting phases of the animals) to determine the thermoregulatory ability of this species and to quantify energetic costs. In this study, animals were exposed to air temperatures of 10, 20 and 30 °C for 8 h. Active- and resting-phase measurements were taken on different days. Measurements of T_B were taken every 20 min. Values reported are the 8 h average $T_{B,min}$ and $T_{B,max}$ ($T_{B,min}$ and $T_{B,max}$ are the means of the lowest and highest T_B maintained within 0.2 °C for at least 1 h, respectively). Metabolic measurements were recorded every 10 min over the 8 h period. Values reported are the 8 h average maximum and minimum (maximum and minimum measurements are 5 min averages taken 30 min into

the hours in which the minimum and maximum body temperatures were maintained).

Body temperature

We measured T_B ($\pm 0.1^\circ\text{C}$) using temperature transmitters (AVM Corp., model SM-1) implanted into the abdominal cavity of the animals and a radiotelemetry receiver (AVM Corp., model LA12-Q). We converted transmitter output into T_B by timing 100 pulses with a digital stopwatch. Both prior to implantation and after removal from the animal, we calibrated the transmitters ($\pm 0.1^\circ\text{C}$) in water baths whose temperatures were measured with a type-T (copper–constantan) thermocouple (Omega Scientific, model HH23 thermometer, calibrated against ice baths and mercury thermometers traceable to the NIST). There was no measurable difference in transmitter calibrations before and after the experiments.

Metabolic rate

Measurements of metabolic rate were made using 800 ml respirometry chambers constructed of transparent acrylic plastic. Air temperature was regulated by placing these chambers into a temperature-controlled room. Animals were exposed to fluorescent lighting that allowed normal vision but was thermally insignificant (irradiance $< 3 \text{ W m}^{-2}$) for measurements taken during their active phase. During the resting phase, measurements were made in total visual darkness, and subjects were monitored under infrared light using a CCD camera (Magnavox 18MC205T). Metabolic rate was determined from rates of CO_2 production and O_2 consumption. Influent air was scrubbed of CO_2 and dried by an air purifier (Puregas CDA1) before being sent through rotameters (Omega FL3402C-HRV, calibrated against a soap-film flowmeter). Flow rates were adjusted so that there was an approximately 1% reduction in oxygen concentration, measured at a downstream oxygen analyzer (Applied Electrochemistry, S-3A). At the lowest flow rate used, the entire respiratory apparatus equilibrated in 19 min (Lasiewski et al., 1966). A 150 ml min^{-1} subsample of gas was dried with anhydrous calcium sulfate and passed to a CO_2 analyzer (LiCor, 6252) which has a resolution of 1 p.p.m. The analyzer was calibrated daily with both CO_2 -free air and a calibration gas known to contain 2840 p.p.m. CO_2 . Instrument signals were recorded on a Campbell CR21x datalogger and averaged at 1 min intervals. Carbon dioxide production was calculated using equation 3 of Walsberg and Wolf (1995) and corrected to STP (0°C , 101 kPa).

This calculation and subsequent conversion to units of energy requires knowledge of the respiratory exchange ratio (RER). Carbon dioxide production and oxygen consumption were recorded and averaged simultaneously using a Campbell CR21x datalogger. The O_2 concentration of air entering and leaving the chamber was determined from a 50 ml min^{-1} subsample of effluent air from the chamber using an Applied Electrochemistry S3a oxygen analyzer. The oxygen analyzer was calibrated daily, as described by Walsberg and Wolf (1995), against the general atmosphere.

Thermal conductance

Total conductance (C) was calculated at ambient temperatures below thermoneutrality by using the following equation derived, for biological application, from Fourier's law of heat flow by Burton (1934):

$$\text{MHP} = C(T_B - T_{\text{air}}), \quad (1)$$

where MHP is metabolic heat production (W), C is whole-animal thermal conductance ($\text{W } ^\circ\text{C}^{-1}$), T_B is core body temperature ($^\circ\text{C}$) and T_{air} is air temperature ($^\circ\text{C}$).

Statistical analyses

Statistical analyses were performed using StatView 5.0 for Macintosh. Analyses were accomplished using a repeated-measures analysis of variance (ANOVA) followed by a *post-hoc* multiple-comparison test (Tukey type) for pairwise comparisons among groups. All reported values are significant at $P < 0.05$. Values are given as means ± 1 S.E.M.

Results

Short-term exposure

The mean respiratory exchange ratio (RER) under post-absorptive conditions was 0.704 ± 0.004 ($N=11$), suggesting near-total reliance upon lipids as a catabolic substrate (Kleiber, 1961). On the basis of this value, the thermal equivalent of carbon dioxide produced is estimated as 27.4 J ml^{-1} (Withers, 1992). T_{air} had a significant effect on both T_B ($F_{10,80}=107.504$, $P < 0.0001$) and MHP ($F_{10,80}=75.192$, $P < 0.0001$). As T_{air} was increased from 10 to 45°C , T_B increased from 32.1 to 40.4°C (Fig. 1). MHP, below 30°C , increased from 0.57 to 2.79 W and, above 35°C , from 0.44 to 1.14 W (Fig. 2). No differences in MHP occurred between 30 and 35°C (thermoneutral zone) or between 10 and 15°C ($P < 0.05$). Mean total thermal

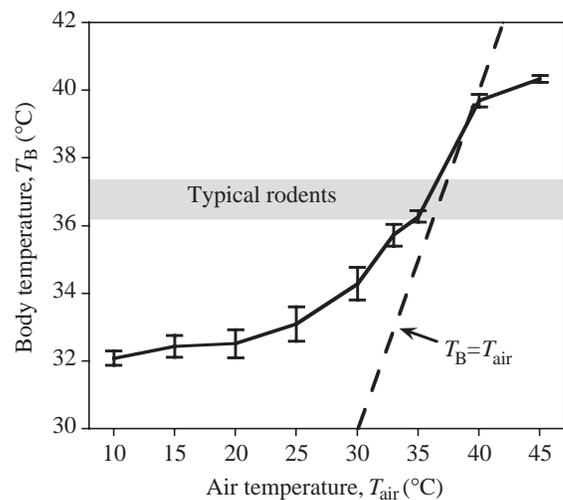


Fig. 1. Body temperature as a function of air temperature (1 h exposure). Also shown are the body temperature range of typical rodents and a line of equality (dashed). Values are means \pm S.E.M. ($N=11$).

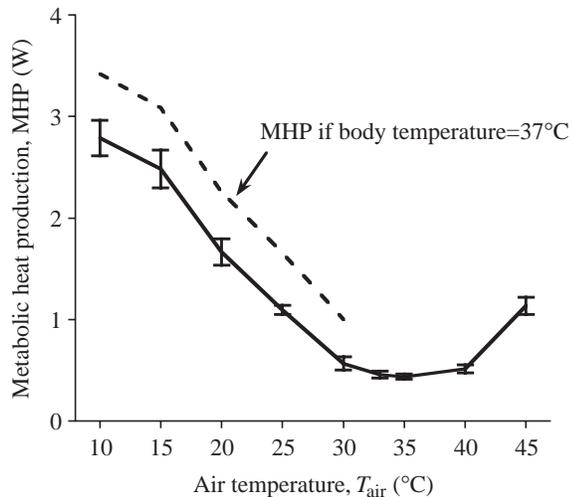


Fig. 2. Metabolic heat production as a function of air temperature (1 h exposure). Also shown is the estimated metabolic heat production as calculated from equation 1, setting $C=0.14 \text{ W } ^\circ\text{C}^{-1}$ and $T_B=37^\circ\text{C}$. Values are means \pm S.E.M. ($N=11$).

conductance was constant at $0.14 \pm 0.01 \text{ W } ^\circ\text{C}^{-1}$ ($N=11$), across all air temperatures below thermoneutrality ($P<0.05$).

Long-term exposure

There was no difference in body temperature or metabolic heat production between studies conducted during the active and resting phases of the animals' daily cycle ($P<0.05$). Therefore, reported values are for studies conducted during the active phase only. All animals remained awake and rested quietly for the entire 8 h at each temperature. At every air temperature, animals maintained (within 0.2°C), for at least 1 h, significantly different minimum ($T_{B,\text{min}}$) and maximum

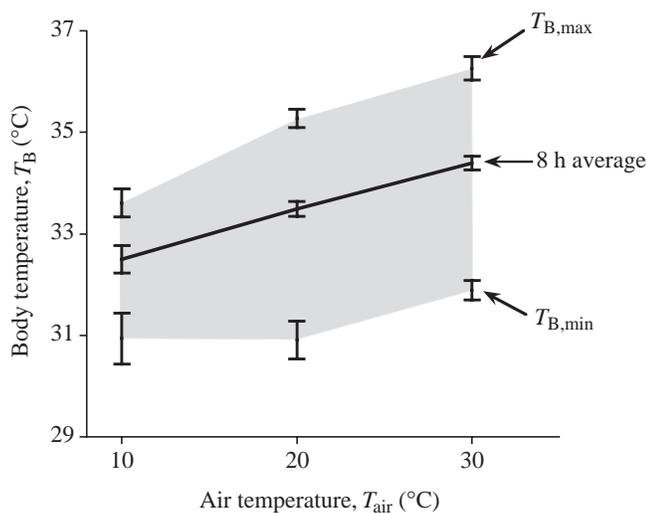


Fig. 3. Body temperature as a function of air temperature (8 h exposure). Also shown are the minimum and maximum body temperatures maintained within 0.2°C for at least 1 h and the average body temperature over 8 h. Values are means \pm S.E.M. ($N=9$).

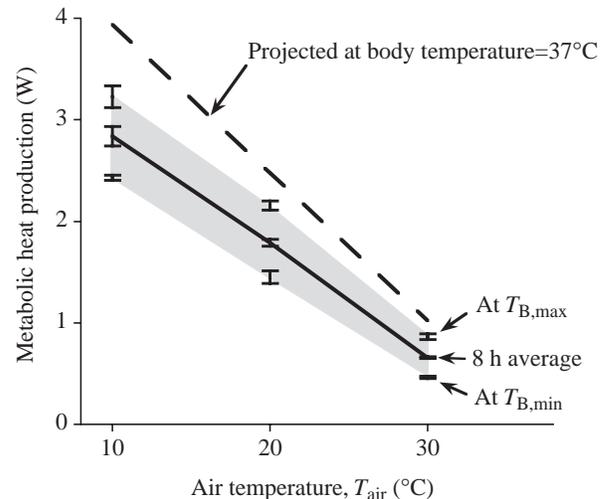


Fig. 4. Metabolic heat production as a function of air temperature (8 h exposure). Minimum and maximum values are those measured 30 min into the periods in which the reported minimum and maximum body temperatures occurred. Average values are body temperatures averaged over the entire 8 h period. Also shown is the estimated metabolic heat production as calculated from equation 1, setting $C=0.14 \text{ W } ^\circ\text{C}^{-1}$ and $T_B=37^\circ\text{C}$. Values are means \pm S.E.M. ($N=9$).

($T_{B,\text{max}}$) body temperatures (10°C , $F_{2,16}=19.462$, $P<0.0001$; 20°C , $F_{2,16}=43.423$, $P<0.0001$; 30°C , $F_{2,16}=152.726$, $P<0.0001$) (Fig. 3). There was no apparent pattern to the direction of T_B changes, the number of times an animal changed T_B or the duration for which a given T_B was maintained. $T_{B,\text{min}}$ was constant across all air temperatures at 31.2°C ($P<0.05$). The 8 h average and $T_{B,\text{max}}$ increased from 32.5 and 33.6°C at 10°C to 34.4 and 36.3°C at 30°C respectively (8 h average, $F_{2,16}=36.362$, $P<0.0001$; $T_{B,\text{max}}$, $F_{2,16}=55.697$, $P<0.0001$). MHP was lower at $T_{B,\text{min}}$ than at $T_{B,\text{max}}$ across all air temperatures (10°C , $F_{2,16}=20.584$, $P<0.0001$; 20°C , $F_{2,16}=46.362$, $P<0.0001$; 30°C , $F_{2,16}=106.302$, $P<0.0001$) (Fig. 4). As T_{air} decreased, the MHP corresponding to $T_{B,\text{min}}$ increased from 0.46 W at 30°C to 2.43 W at 10°C ($F_{2,16}=213.354$, $P<0.0001$) and that corresponding to $T_{B,\text{max}}$ increased from 0.86 W at 30°C to 3.23 W at 10°C ($F_{2,14}=290.658$, $P<0.0001$). Mean total thermal conductance across all conditions was $0.146 \pm 0.004 \text{ W } ^\circ\text{C}^{-1}$ ($N=9$; $P<0.05$).

Discussion

Most birds and mammals that have been studied maintain a very stable body temperature regardless of environmental conditions. For these species, physiological function is so closely tied to body temperature that hypothermia greater than 2°C is usually characterized initially by loss of coordination and locomotory performance resulting from impairment of both neural and muscular function (Keller, 1955; Hamilton, 1968; Edholm, 1978; Hayward, 1983; Clark and Edholm, 1985; Reinertsen, 1996). As the duration of these states is

prolonged or the degree of perturbation approaches 5 °C, there is increased loss of coordinated locomotory performance, depletion of energetic reserves, widespread impairment of cellular and physiological function and loss of consciousness. With deviations of T_B greater than 5 °C, death may ensue unless T_B is returned to normal within a short period (Hensel et al., 1973). To survive energetically stressful periods, a diverse assemblage of birds and mammals have evolved temporarily to abandon thermoregulation at their normal T_B . These animals significantly reduce energetic expenditure by regulating T_B at a lower value, often just slightly above ambient temperature (Hill and Wyse, 1989; Withers, 1992). These episodes of facultative hypothermia represent a highly refined state of endothermic thermoregulation in which rates of heat production and levels of body temperature are controlled on a much more flexible basis than in most birds and mammals. This adaptation allows these animals to survive periods when energy supply from the environment does not meet the demand of maintaining a constant T_B (Reinertsen, 1996). However, this strategy also requires the downregulation of many physiological functions, rendering these animals inactive and removing them from the environment for intervals ranging from hours (daily torpor) to months (deep hibernation) (see pp. 134–138 in Cossins and Bowler, 1987).

We found that the T_B of *S. tereticaudus* is much more variable and dependent upon T_{air} than that of typical rodents. Within 45 min of exposure to air temperatures ranging from 10 to 45 °C, mean body temperatures ranged from 32.1 °C to 40.4 °C respectively (Fig. 1). These animals, however, remained alert and responsive at all body temperatures. One individual experienced changes in body temperature ranging from 27.8 °C at 10 °C to 41.0 °C at 45 °C. The thermal conductance for *S. tereticaudus* remained constant under both short-term and long-term exposure to air temperatures below the thermoneutral zone at approximately 0.14 W °C⁻¹. This value is the same as that from our previous study in which we found that the thermal conductance of *S. tereticaudus* was 45 % higher than predicted by Aschoff's (1981) allometric equation and was the highest reported of 17 species of rodents ranging in mass from 100 to 200 g as measured during the active phase of their daily cycle (Wooden and Walsberg, 2000).

S. tereticaudus can both estivate and enter torpor when circumstances do not permit the maintenance of energetic balance (Hudson, 1964); however, they are commonly found above ground and active year-round (Dengler, 1967; Drabek, 1973; Vorhies, 1945; K. M. Wooden, personal observation). This diurnal rodent must survive high air temperatures in the summer and arid conditions throughout most of the year. In an arid desert environment when T_{air} is high, allowing T_B to rise above T_{air} is advantageous as it maintains the driving force ($T_B - T_{air}$) for non-evaporative heat loss and conserves body water by eliminating the need for evaporative cooling. Similarly, when T_{air} exceeds T_B , a rise in T_B reduces the rate of heat influx ($T_{air} - T_B$) and conserves both the water and energy required to eliminate the incoming heat through active evaporative cooling. In winter and early spring, *S. tereticaudus*

faces air temperatures that drop below 5 °C (K. M. Wooden, unpublished data). By allowing T_B to drop when T_{air} is low (Fig. 1), non-torpid individuals may conserve body water in two ways. First, as oxygen requirements for metabolic heat production are reduced, ventilation rate and respiratory water loss should decrease. Second, as body temperature is lowered, exhaled air is cooler (carrying less water vapor per unit volume) and transcutaneous water loss presumably decreases as a result of lowered skin temperature.

Inhabiting the most barren habitats of the Sonoran Desert also subjects *S. tereticaudus* to periods of several months in which the only available vegetation may be creosote bush (*Larrea tridentata*). This plant contains toxic phenols (Rhoades and Cates, 1976; Mabry et al., 1977), and dependence upon it as a primary food source may severely limit energy, nutrient and water intake (Karasov, 1989; Meyer and Karasov, 1989). By reducing the gradient between T_B and T_{air} , *S. tereticaudus*, in addition to conserving water, also reduces the energetic cost required to maintain T_B . We estimated the MHP required to achieve a T_B of 37 °C using equation 1, setting $C=0.14$ W °C⁻¹ and $T_B=37$ °C. By lowering T_B at air temperatures below the thermoneutral zone, *S. tereticaudus* realizes a short-term energetic saving ranging from 0.63 W (18 %) at 10 °C to 0.43 W (43 %) at 30 °C (Fig. 2). It is important to note that this lowering of T_B does not reflect an inability to generate sufficient heat because the animal is demonstrably capable of higher rates of heat production (Fig. 2). Rather, this implies a controlled mechanism for reducing energetic demand.

The results of long-term exposure to air temperatures between 10 and 30 °C offer additional evidence of an ability to adjust energetic expenditure through body temperature regulation. During long-term exposure to air temperatures of 10, 20 and 30 °C, animals again demonstrate the ability to generate sufficient heat to raise T_B at 20 and 30 °C well above that typical of other rodents (37 °C) (Fig. 4). By averaging body temperatures over 8 h of 32.5 °C at 10 °C, 33.5 °C at 20 °C and 34.4 °C at 30 °C rather than 37 °C, these animals potentially realize long-term energetic savings of 1.1 W (28 %), 0.69 W (28 %) and 0.35 W (34 %) respectively (Fig. 4).

During the 8 h of exposure to each temperature, individuals also demonstrated the ability to vary their body temperature over time by as much as 9.0 °C. The occurrences of a minimum and maximum body temperatures at each T_{air} (during which T_B did not vary by more than 0.2 °C for at least 1 h) occurred randomly both within the runs of individual animals and among animals. At all air temperatures studied, animals allowed $T_{B,min}$ to drop to a mean of 31.2 °C (Fig. 3). The $T_{B,min}$ was significantly lower than the average T_B in all cases and correlates to additional energetic savings of 0.41 W (10 %) at 10 °C, 0.34 W (14 %) at 20 °C and 0.20 W (20 %) at 30 °C from that projected to maintain a T_B of 37 °C (Fig. 4).

Our data show that *S. tereticaudus* did not maintain a T_B typical of other rodents at any air temperature below their thermoneutral zone. We estimate (as described above) that these animals, even at their maximum body temperatures, expended 0.71 W (18 %) at 10 °C, 0.32 W (13 %) at 20 °C and 0.16 W

(16%) less energy than would be required if they maintained a T_B of 37°C. Although these animals did not maintain body temperatures comparable with those other rodents, at each T_{air} , the maximum body temperature maintained was significantly higher (2.7°C at 10°C, 4.4°C at 20°C and 4.4°C at 30°C) than $T_{B,min}$ (Fig. 3). The reason for this variation in T_B at a given T_{air} is unknown. However, these animals realized a significant energetic savings of 0.8 W (25%) at 10°C, 0.71 W (33%) at 20°C and 0.40 W (47%) at 30°C by maintaining the minimum rather than the maximum T_B (Fig. 4).

With respect to avian and mammalian thermoregulation, *S. tereticaudus* and the Puerto Rican tody (Mercola-Zwartjes and Ligon, 2000) are unusual: both species have independently evolved to remain alert, responsive and active over a very broad range of body temperatures. This adaptation provides a mechanism to reduce energetic costs to levels below those required in other birds and mammals. In the light of the current hypotheses regarding the costs and benefits of homeothermy, this gives rise to several interesting questions. Are there costs, relative to other birds and mammals, associated with this adaptation? What mechanisms allow for the maintenance of physiological function over such a broad range of body temperatures? Why have not all birds and mammals lowered energetic costs by expanding their thermoregulatory limits? We suggest that further investigation at the tissue, cellular and biochemical levels, using these species as models of comparison, might significantly advance our understanding of mammalian and avian physiology.

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