

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

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**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 ( $\pm 1.0$  °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 today (*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  $T_B$ ?