The Journal of Experimental Biology 207, 41-46
Published by The Company of Biologists 2004
doi:10.1242/jeb.00717

Body temperature and locomotor capacity in a heterothermic rodent

K. Mark Wooden* and Glenn E. Walsberg
School of Life Sciences, Arizona State University, Tempe, AZ 85287-4601, USA
*Author for correspondence (e-mail: wooden@asu.edu)

Accepted 23 September 2003

Summary

We quantify the locomotor capacity of the round-tailed ground squirrel (*Spermophilus tereticaudus*), a mammal that can lower energetic costs by relaxing thermoregulatory limits without becoming inactive. We measured maximum sprint speed, maximum limb cycling frequency and maximum force production in animals at body temperatures ranging from 31°C to 41°C. We found no thermal dependence in any of these parameters of locomotion. Results (means ± S.E.M.) across this range of body temperatures were: sprint speed = 4.73±0.04 m s^{-1}, limb cycling frequency = 19.4±0.1 Hz and maximum force production = 0.012±0.0003 N g^{-1}. The neuro-muscular system of this species may thus be less thermally dependent at these temperatures than that of other mammals, allowing for the maintenance of whole-animal performance across a broader range of body temperatures. The absence of any significant loss of locomotor capabilities associated with either a decrease of 7–8°C or a rise of 3–4°C in body temperature from typical mammalian values raises significant questions regarding our understanding of the evolution and physiology of the mammalian mode of thermoregulation.

Key words: body temperature, thermoregulation, heterothermy, locomotor capacity, sprint speed, limb cycling frequency, force production, round-tailed ground squirrel, *Spermophilus tereticaudus*.

Introduction

The locomotor performance of most animals, like other physiological processes, is strongly affected by core body temperature (T_b). These processes typically slow as T_b is lowered and accelerate as T_b is raised, with temperature coefficients (Q_{10} values) of ~1.5–4.0 (Huey, 1982; Hochachka and Somero, 1984; Cossins and Bowler, 1987; Hill and Wyse, 1989; Bennett, 1990). Most birds and mammals, however, precisely regulate metabolic heat production and heat loss to maintain a high (35–42°C) and stable (±1.0°C) 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). Several investigators have suggested that the preservation of these physiological processes may have been the primary driving force behind the evolution of endothermic homeothermy (Bartholomew, 1977; Heinrich, 1977; Crompton et al., 1978; McNab, 1978; Avery, 1979; Block et al., 1993).

Although endothermic homeothermy is one of the most significant evolutionary alterations involving the relationship between an animal and its environment, it comes with several tradeoffs to the animal. Endothermic homeothermy may offer profound ecological advantages, yet imposes a large energetic burden on the animal (Bennett and Ruben, 1979; Else and Hulbert, 1981). Endothermic homeothermy may also provide a steady state for physiological and biochemical functions, yet restricts the range of body temperatures over which the animal can remain active or even survive (Hochachka and Somero, 1984).

Under most circumstances, endothermic homeotherms are able to maintain T_b. However, when 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), these animals typically respond in one of two ways. Some birds and mammals enter a state of torpor or hibernation, lowering their energetic demand by temporarily, yet substantially, reducing T_b. The T_b of most endothermic homeotherms, however, is tightly coupled to physiological function, and allowing T_b to drop also leaves these animals inactive and unable to respond readily to external stimuli (Schmidt-Nielsen, 1990; Reinertsen, 1996). Most other birds and mammals have no such mechanism by which to lower their energetic demand. For these animals, hypothermia leads to the pathological impairment of physiological function. Complex functions such as coordinated locomotor performance usually become impaired at a drop in T_b of as little as 2°C. A drop in T_b of greater than 5°C commonly leads to widespread physiological impairment and often death (Keller, 1955; Hamilton, 1968; Edholm, 1978; Hayward, 1983; Clark and Edholm, 1985; Reinertsen, 1996).

Although the inability to maintain T_b results in either the suppression or loss of physiological function for most birds and mammals, some species appear to remain alert, responsive and active over changes in T_b of as much as 14°C (see

references in Wooden and Walsberg, 2002). By regulating T_b over such a wide range, these species can reduce thermoregulatory costs to levels below those required in other birds and mammals and thus reduce their overall energetic demand (Mercola-Zwartjes and Ligon, 2000; Wooden and Walsberg, 2002). These species, however, do not enter a torpid state or display any pathological effects with such large changes in body temperature as other birds and mammals do. This raises some very interesting questions. Do these species actually maintain physiological function across this wide range of body temperatures? Is strict homeothermy necessary to maintain physiological function by birds and mammals? Why cannot all birds and mammals lower energetic costs by expanding their thermoregulatory limits?

One of the first signs that an endothermic homeotherm is unable to maintain T_b is the loss of coordinated locomotor performance. Although coordinated locomotor ability among these heterothermic species appears to be maintained over this broad range of body temperatures, this has not yet been quantified. Many investigators have shown that the effects of changes in T_b on the locomotor performance of mammals are similar to those of poikilothermic animals and can be attributed to losses of function at the muscle (Cullingham et al., 1960; Close and Hoh, 1968; Ranatunga, 1977, 1980, 1982, 1984, 1998; Buller et al., 1984; Huey and Kingsolver, 1989; Bennett, 1990; Faulkner et al., 1990; Johnston et al., 1990; Marsh, 1990; Rall and Woledge, 1990; Rome, 1990; Rome et al., 1990; Marden, 1995; Xiang et al., 1996), peripheral nervous system (PNS; Chatfield et al., 1948; Paintal, 1965; Miller and Irving, 1967; Jensen, 1972; MacDonald, 1981; Montgomery and MacDonald, 1990) and/or central nervous system (CNS; Brooks et al., 1955; Roots and Prosser, 1962; Hamilton, 1968; Friedlander et al., 1976; Budnick et al., 1981; Oro and Haghighi, 1992; MacKenzie et al., 1995). Therefore, these birds and mammals should also face a cost to locomotor ability associated with the relaxation of thermoregulatory limits.

Spermophilus tereticaudus, a small desert rodent, inhabits the most barren habitats of the Sonoran and Mohave deserts, where daytime air temperature ranges from less than 5°C in the winter months to as much as 50°C during the summer (K. M. Wooden, unpublished data). T_b of *S. tereticaudus* is much more variable and dependent upon air temperature than that of typical rodents. The T_b of alert and active animals can drop as low as 27.8°C within 45 min of exposure to an air temperature of 10°C. The same period of exposure at an air temperature of 45°C can cause T_b to rise to as much as 41.0°C (Wooden and Walsberg, 2002). *S. tereticaudus* lowers energetic expenditure as much as 50% through this relaxation of thermoregulatory limits (Wooden and Walsberg, 2002). This species also remains active, alert and responsive across this range of body temperatures (Hudson, 1964; Wooden and Walsberg, 2000, 2002). In the present study, we test the hypothesis that this species does experience a significant loss in locomotor capacity associated with the relaxation of thermoregulatory limits.

Materials and methods

Animal collection and maintenance

Fifteen female and six male *Spermophilus tereticaudus* Baird were trapped between June and July 2001 in the Sonoran desert, approximately 25 km north of Gila Bend, Maricopa Co., Arizona, at an altitude of 225 m. Mean body mass at capture was 128.7±3.1 g (mean ± S.E.M., N=21). Animals were housed in a temperature-controlled room that was maintained at 30°C under a 12 h:12 h light:dark photoperiod. Animals were fed Teklad rodent diet (Harlan-Teklad, Madison, WI, USA) and supplied *ad libitum* with water.

Body temperature measurements

We measured T_b (±0.1°C) using temperature transmitters (Mini Mitter, XM-FH; Mini Mitter Co., Inc., Bend, OR, USA; accurate to 0.1°C) surgically implanted into the abdominal cavity of the animals. Transmitters are 1.5 cm-long×1 cm-wide cylinders coated with medical grade silicon rubber (Sylgard). They weigh approximately 1.5 g, or less than 2% of body mass. Transmitter output was received with an AM radio and converted 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 (±0.1°C) in water baths whose temperatures were measured with a type-T (copper–constantan) thermocouple (model HH23 thermometer, calibrated against ice baths and mercury thermometers traceable to the NIST; Omega Scientific, Tarzana, CA, USA). There was no measurable difference in transmitter calibrations before and after the experiments.

Surgical procedures

Surgery was performed under aseptic conditions. Animals were anesthetized using metophane. Transmitters were sterilized by immersion in Cidex solution (Advanced Sterilization Products, Miami, FL, USA) and rinsed with saline solution prior to implantation. Transmitters were positioned between the liver and stomach through an incision approximately 1.5 cm wide in the lateral abdominal wall. The abdominal wall was closed using 4.0 silk sutures. The dermis and epidermis were closed using surgical staples. Animals were allowed to recover for 7–10 days and had returned to, at minimum, their mass at the time of capture prior to experimental use. Mean body mass during the experimental procedures was 131.4±2.1 g (mean ± S.E.M., N=21).

Experimental procedures

We tested all animals at body temperatures of 30–32°C, 36–38°C and 40–42°C, randomizing the sequence of temperature exposure for each animal. We brought the animals to the desired T_b by placing them in a walk-in environmental chamber for 30–60 min. The environmental chamber was set at 10°C to achieve a T_b of 30–32°C, at 35°C to achieve a T_b of 36–38°C and at 45°C to achieve a T_b of 40–42°C. Experiments were conducted on a 5 m-long×10 cm-wide track at room temperature (23°C). One side wall of the track was made of clear acrylic plastic and the other side wall was made

of plywood with markings every centimeter. The track was lined with a short-napped carpet to maximize traction. A darkened box at the end of the track served as a target refuge into which the animals could escape from the sound of compressed air hissing out of a plastic tube at the beginning of the track. For three days prior to the start of the experiments, animals were run on the track to familiarize them with the track and accustom them to the procedure. All experimental procedures were completed between 08:00 h and 17:00 h, and no animal was used for more than one experimental condition per day or on consecutive days. All animals were tested three times in one day at each T_b and the results reported are the maximum values that an individual achieved.

Sprint speed and limb cycling frequency

Animals were video taped (Panasonic camera model 456) at a rate of 60 frames s^{-1} as they ran along the track. Framing rates were measured continuously by simultaneously recording a digital stopwatch. Upon removal from the environmental chamber, animals were immediately placed on the track, T_b was taken and the animal was stimulated to run by the sound of compressed air hissing out of a plastic tube at the beginning of the track and the sight of a darkened refuge at the end of the track. T_b was taken again at the end of each run and the animal was returned to the environmental chamber for a minimum of 30 min as it awaited its next trial at that T_b range. Frame-by-frame analysis of the films was performed with a Desktop Editor video cassette recorder (Panasonic Model AG-1980). Results reported from this experiment include maximum sprint speed (m s^{-1}) achieved over any 1 m section of track and limb cycling frequency for at least four strides over that same portion of the run.

Force production

Upon removal from the environmental chamber, animals were placed into a nylon harness fitted around the body and secured snugly with Velcro™. The harness was constructed to fit over the torso and not interfere with limb motion or respiration. As soon as the animal was placed on the track, body temperature was taken and the harness was attached to a thin wire that ran over pulleys and connected to 5 m of fine-linked chain, piled vertically below the pulley, on the floor. The animal was stimulated to start pulling by the sound of compressed air hissing out of a plastic tube at the beginning of the track and the sight of a darkened refuge at the end of the track. As the animal proceeded down the track, it lifted a greater length of chain (greater mass) off the floor. Each animal was video-taped and the maximum distance the animal was able to move itself down the track was recorded. Maximum distance pulled equaled the maximum length of chain lifted and was determined as the point at which any further attempt to progress forward resulted in the weight of the chain pulling the animal backwards. The opposing force was the weight of the chain lifted, calculated as the product of the maximum number of links of chain lifted and the mass of each link. Self-lubricating ball-bearing pulleys were used to minimize frictional resistance. A chain with links that were 1.2 cm long and weighed 0.92 g provided sufficient opposing force for most animals. Several of the larger animals, however, required a chain with links that were 2.2 cm long and had a mass of 2.56 g. In each case, the resolution of the weight of a single link to the weight lifted was less than 1%. Body temperature was again measured and compared with that prior to the run. At the beginning and end of each day, calculated forces at various intervals along the track were compared with those measured by a force displacement transducer (model FT03; Grass, West Warwick, RI, USA) calibrated against known weights. The calculated force differed from that measured by the force transducer by less than 1%. Results reported are the individual's maximum force exerted.

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. Values presented are means ± S.E.M. (N=21).

Results

There were no significant effects on any of the major parameters of locomotor performance (sprint speed, limb cycling frequency or force production) over a 10°C range of body temperatures. Values presented for each parameter are the means of maximum performance by each animal from three trials at each T_b. Individual maximum performance occurred randomly across the three trials. Changes in T_b resulting from physical exertion during these experiments were less than 0.2°C for each animal, as measured immediately before and after each run. Mean T_b during measurements of sprint speed and limb cycling frequency were 30.9±0.9°C, 37.1±0.1°C and 40.9±0.1°C for trials at individual body temperatures in the range of 30–32°C, 36–38°C and 40–42°C, respectively. Sprint speed at these body temperatures was 4.71±0.06 m s^{-1}, 4.74±0.06 m s^{-1} and 4.76±0.09 m s^{-1}, respectively (Fig. 1). Limb cycling frequencies at these body temperatures were 19.5±0.14 Hz, 19.4±0.20 Hz and 19.6±0.16 Hz, respectively (Fig. 2).

Mean T_b during measurements of force production was 30.8±0.2°C, 36.9±0.1°C and 40.6±0.1°C for trials at individual body temperatures in the range of 30–32°C, 36–38°C and 40–42°C, respectively. In each trial, animals moved forward along the track with all feet firmly grasping the carpeted floor. Animals continued to move away from the hissing sound at the beginning of the track and towards the darkened box at the end of the track until they were unable to move forward any further. At this point, all animals held the carpet firmly so as not to be pulled backwards. Body mass was correlated with force production (r^2=0.8 at T_b=30–32°C, r^2=0.7 at T_b=36–38°C and r^2=0.6 at T_b=40–42°C. Therefore, we removed the mass effect and report the mass-specific force production as

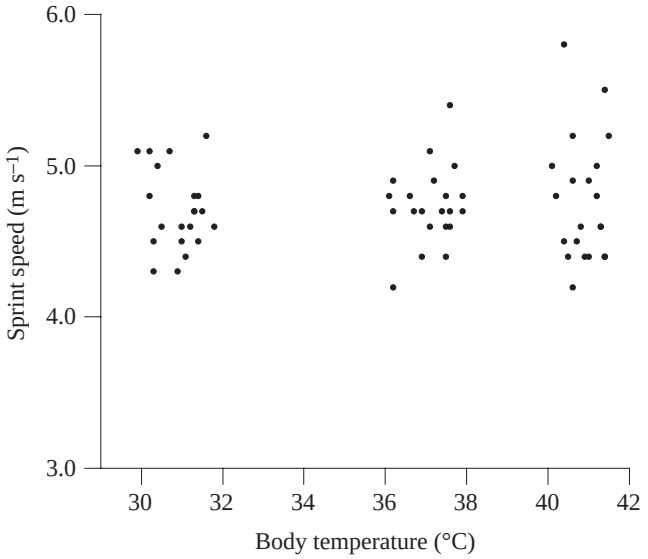

Fig. 1. Sprint speed as a function of body temperature. Values presented are maximum individual values (*N*=21).

0.13±0.0004 N g^{-1}, 0.12±0.0005 N g^{-1} and 0.12±0.0006 N g^{-1} for trials at individual body temperatures ranging from 30°C to 32°C, 36°C to 38°C and 40°C to 42°C, respectively (Fig. 3).

Discussion

Because locomotor performance involves such complex interactions at the neuro-muscular biomechanical level, and body temperature has such a strong influence on neural, muscular and biochemical performance, one would expect these animals to experience similar costs to locomotor capacity as do poikilothermic animals. To evaluate the effects of body temperature on locomotor capacity we attempted to stimulate maximal effort from the animals. The maximal sprint speeds attained in this study are similar to those found by other investigators for *S. tereticaudus*, other similar-sized species of ground squirrel and other rodents (Djawdan and Garland, 1988).

Our results show no thermal dependence for sprint speed, limb cycling frequency or maximum force production across the range of body temperatures studied. We found that sprint speed at body temperatures ranging from 30°C to 35°C, like that of lizards, shows no thermal dependence (Marsh and Bennett, 1985; Kaufmann and Bennett, 1989; Xiang et al., 1996). One striking difference, however, is that the performance of this mammalian species is maintained at body temperatures up to ~41°C whereas the sprint speed of lizards commonly declines above 35°C. One possible explanation for these findings is the one that has been used to explain the low thermal dependence of whole-animal locomotion in lizards despite the high thermal dependence of the isolated muscle fibers. Farley (1997) demonstrated that maximum sprint speed in lizards is limited by something other than the maximum mechanical power output of the muscular system. If maximum exertion of all muscle fibers is not required to attain maximum sprint speed at higher temperatures, then performance may be maintained at lower body temperatures by greater muscle fiber output or the recruitment of additional muscle fibers.

Maximum performance in activities such as lifting a load, however, requires the simultaneous recruitment of all fibers in the relevant muscles and thus the maximum mechanical power output of the muscular system (Rome, 1990). Activities such as this should, therefore, be as temperature dependant as isolated muscles with temperature coefficients of ~1.5–4.0 (Rome, 1990). In the present study, ground squirrels lifted a progressively heavier load to the point that the load

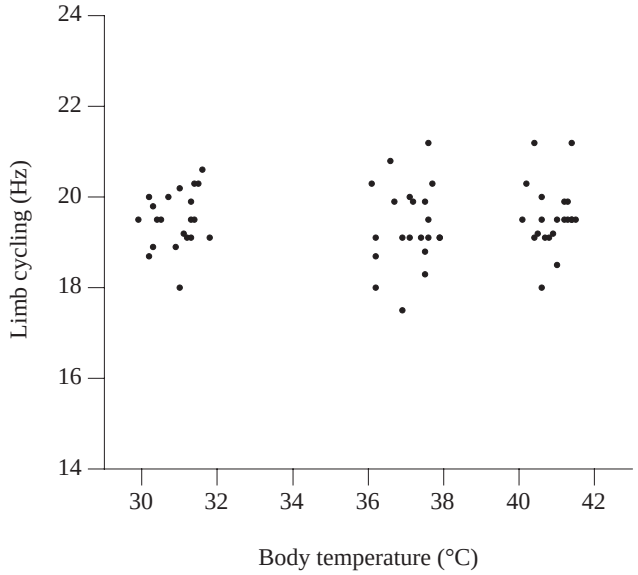

Fig. 2. Limb cycling frequency as a function of body temperature. Values presented are maximum individual values (*N*=21).

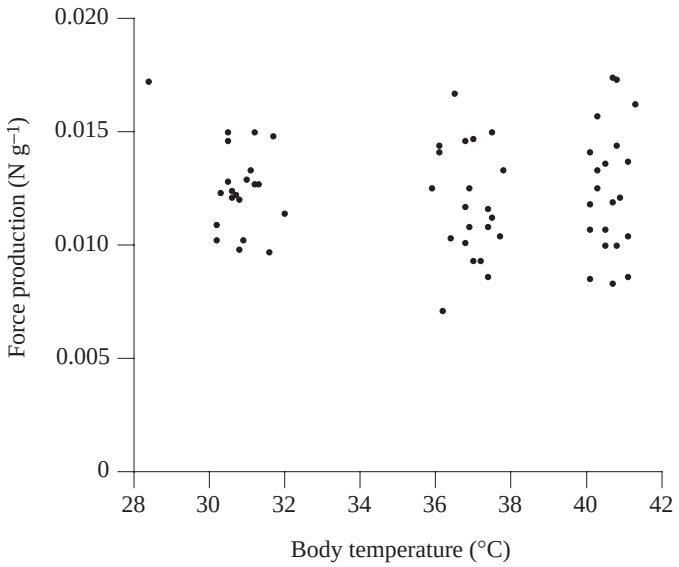

Fig. 3. Force production as a function of body temperature. Values presented are mass-specific maximum individual values (*N*=21).

overwhelmed the mechanical power output of the muscular system. These animals were most certainly utilizing the maximum power output of the muscles and, therefore, should not be able to compensate through motor unit recruitment at varying temperatures. Our findings, however, show that maximum force production in this species is also temperature independent over a range of ~10°C. Perhaps in this species, like that of another heterothermic mammal (*Murina leucogaster*), the neuro-muscular system is less temperature dependent at these temperatures than in other animals, allowing for the maintenance of whole-animal performance across a broader range of body temperatures (Choi et al., 1997).

The results of our study suggest the need for further investigation at the tissue and cellular levels to explain how this mammal can maintain whole-animal performance across such a broad range of body temperatures and avoid any significant loss of locomotor capabilities associated with either a decrease of 7–8°C or a rise of 3–4°C in body temperature from typical mammalian values. A popular view regarding the evolution of endothermic homeothermy is that birds and mammals expend large amounts of energy to maintain high and stable body temperatures so as to be able to remain active over a broad range of environmental conditions (Crompton et al., 1978; Block et al., 1993). This hypothesis suggests that homeothermy allows for the maintenance of activity over varying environmental conditions by providing greater biochemical stability, greater enzyme specialization and, consequently, improved metabolic efficiency (Heinrich, 1977; Avery, 1979; Hochachka and Somero, 1984).

Our results argue against the view that strict homeothermy is required to maintain activity over a broad range of environmental conditions. *S. tereticaudus* maintains its capacity for intense activity over environmental temperatures ranging from at least 5°C to 50°C and does so over a wide range of body temperatures (30–42°C). Similarly, the ability to maintain neuro-muscular activity over such a broad range of body temperatures together with the energetic savings provided by changes in body temperature argue against the need for homeothermy to render biochemical stability and metabolic efficiency.

In summary, the temperature independence of locomotor performance and the associated reduction in energy expenditure characteristic of this mammal raises significant questions regarding our understanding of the evolution and physiology of the mammalian mode of thermoregulation. If some species, such as round-tailed ground squirrels, can realize large energetic benefits by allowing body temperature to vary by ~12°C without accruing costs in their capacity for intense activity, why do not all birds and mammals do this?

We thank Jon Harrison and Jeff Hazel for their critical comments and suggestions on earlier drafts of this article. We also thank Ty Hoffman and Dale DeNardo for their technical assistance. This research was supported by National Science Foundation Grant IBN-9725211.

References

Avery, R. A. (1979). *Lizards – A Study in Thermoregulation.* Baltimore: University Park Press.

Bartholomew, G. A. (1977). Body temperature and energy metabolism. In *Animal Physiology: Principles and Adaptations* (ed. M. S. Gordon), pp. 364-449. New York: Macmillan.

Bennett, A. F. (1990). Thermal dependence of locomotor capacity. *Am. J. Physiol.* **259**, R253-R258.

Bennett, A. F. and Ruben, J. A. (1979). Endothermy and activity in vertebrates. *Science* **206**, 649-654.

Block, B. A., Finnerty, J. R., Stewart, A. F. R. and Kidd, J. (1993). Evolution of endothermy in fish: mapping physiological traits on a molecular phylogeny. *Science* **260**, 210-213.

Brooks, C. M., Koizumi, K. and Malcolm, J. L. (1955). Effects of changes in temperature on reactions of spinal cord. *J. Neurophysiol.* **18**, 205-216.

Budnick, B., McKeown, K. L. and Wiederholt, W. C. (1981). Hypothermia-induced changes in rat short latency somatosensory evoked potentials. *Electroenceph. Clin. Neurophysiol.* **51**, 19-31.

Buller, A. J., Kean, J. C., Ranatunga, K. W. and Smith, J. A. (1984). Temperature dependence of isometric contractions of cat fast and slow skeletal muscles. *J. Physiol.* **355**, 25-31.

Burton, A. C. and Edholm, O. G. (1955). *Man in Cold Environment.* London: Edward Arnold.

Chatfield, P. O., Battista, A. F., Lyman, C. P. and Garcia, J. P. (1948). Effects of cooling on nerve conduction in a hibernator (golden hamster) and non-hibernator (albino rat). *Am. J. Physiol.* **155**, 179-185.

Choi, I., Cho, Y., Oh, Y. K., Jung, N. and Shin, H. (1997). Behavior and muscle performance in heterothermic bats. *Physiol. Zool.* **71**, 257-266.

Clark, R. P. and Edholm, O. G. (1985). Responses to cold. In *Man and His Thermal Environment*, pp. 155-172. London: Edward Arnold.

Close, R. and Hoh, J. F. Y. (1968). Influence of temperature on isometric contractions in rat skeletal muscles. *Nature* **217**, 1179-1180.

Cossins, A. R. and Bowler, K. (1987). *Temperature Biology of Animals.* New York: Chapman and Hall.

Cullingham, P. J., Lind, A. R. and Morton, R. J. (1960). The maximal isometric tension developed by mammalian muscle, *in situ*, at different temperatures. *Quart. J. Exp. Physiol.* **45**, 142-156.

Crompton, A. W., Taylor, C. R. and Jagger, J. A. (1978). Evolution of homeothermy in mammals. *Nature* **272**, 333-336.

Djawdan, M. and Garland, T., Jr (1988). Maximal running speeds of bipedal and quadrupedal rodents. *J. Mamm.* **69**, 765-772.

Edholm, O. G. (1978). *Man – Hot and Cold. The Institute of Biology's Studies in Biology 97.* London: Edward Arnold.

Else, P. L. and Hulbert, A. J. (1981). Comparison of the "mammalian machine" and the "reptile machine": energy production. *Am. J. Physiol.* **240**, R3-R9.

Farley, C. T. (1997). Maximum speed and mechanical power output in lizards. *J. Exp. Biol.* **200**, 2189-2195.

Faulkner, J. A., Zerba, E. and Brooks, S. V. (1990). Muscle temperature of mammals: cooling impairs most functional properties. *Am. J. Physiol.* **259**, R259-R265.

Friedlander, M. J., Kotchabhakdi, N. and Prosser, C. L. (1976). Effects of cold and heat on behavior and cerebellar function in goldfish. *J. Comp. Physiol.* **112**, 19-45.

Hamilton, J. B. (1968). The effect of hypothermic states upon reflex and central nervous system activity. *Yale J. Biol. Physiol.* **9**, 327-332.

Hayward, J. S. (1983). The physiology of immersion hypothermia. In *The Nature and Treatment of Hypothermia* (ed. R. S. Pozos and L. E. Wittmers), pp. 3-19. Minneapolis: University of Minnesota.

Heinrich, B. (1977). Why have some animals evolved to regulate a high body temperature? *Am. Natr.* **111**, 623-640.

Hill, R. W. and Wyse, G. A. (1989). *Animal Physiology.* New York: Harper and Row.

Hochachka, P. W. and Somero, G. N. (1984). *Biochemical Adaptations.* Princeton: Princeton University Press.

Hudson, J. W. (1964). Temperature regulation in the round-tailed ground squirrel, *Citellus tereticaudus*. *Ann. Acad. Sci. Fenn. Ser. A* **15**, 219-233.

Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. In *Biology of the Reptilia* vol. 12 (ed. C. Gans and F. H. Pough), pp. 25-91. New York: Academic Press.

Huey, R. B. and Kingsolver, J. G. (1989). Evolution of thermal sensitivity of ectotherm performance. *Trends Ecol. Evol.* **4**, 131-135.

Jensen, D. W. (1972). The effect of temperature on transmission at the

neuromuscular junction of the sartorius muscle of *Rana pippins*. *Comp. Biochem. Physiol. A* **41**, 685-695.

Johnston, I. A., Fleming, J. D. and Crockford, T. (1990). Thermal acclimation and muscle properties in cyprinid fish. *Am. J. Physiol.* **259**, R231-R236.

Kaufmann, J. S. and Bennett, A. F. (1989). The effect of temperature and thermal acclimation on locomotor performance in *Xantusia vigilis*, the desert night lizard. *Physiol. Zool.* **62**, 1047-1058.

Keller, A. D. (1955). Hypothermia in the unanesthetized dog. In *Physiology of Induced Hypothermia* (ed. R. D. Dripps), pp. 61-79. Washington: National Academy of Sciences.

Macdonald, J. A. (1981). Temperature compensation in the peripheral nervous system: Antarctic vs temperate poikilotherms. *J. Comp. Physiol.* **142**, 411-418.

MacKenzie, M. A., Vingerhoets, D. M., Colon, E. J., Pinckers, A. J. L. G. and Notermans, S. L. H. (1995). Effect of steady hypothermia and normothermia on multimodality evoked potentials in human poikilothermia. *Arch. Neurol.* **52**, 52-58.

Marden, J. H. (1995). Evolutionary adaptation of contractile performance in muscle of ectothermic winter-flying moths. *J. Exp. Biol.* **198**, 2087-2094.

Marsh, R. L. (1990). Deactivation rate and shortening velocity are determinants of contractile frequency. *Am. J. Physiol.* **259**, R223-R230.

Marsh, R. L. and Bennett, A. F. (1985). Thermal dependence of isotonic contractile properties of skeletal muscle and sprint performance of the lizard *Dipsosaurus dorsalis*. *J. Comp. Physiol. B* **155**, 541-551.

McNab, B. K. (1978). The evolution of homeothermy in the phylogeny of mammals. *Am. Nat.* **112**, 1-21.

Mercola-Zwartjes, M. and Ligon, J. D. (2000). Ecological energetics of the Puerto Rican Tody: heterothermy, torpor, and intra-island variation. *Ecology* **81**, 990-1003.

Miller, L. K. and Irving, L. (1967). Temperature-related nerve function in warm- and cold-climate muskrats. *Am. J. Physiol.* **213**, 1295-1298.

Montgomery, J. C. and MacDonald, J. A. (1990). Effects of temperature on nervous system: implications for behavioral performance. *Am. J. Physiol.* **259**, R191-R196.

Oro, J. and Haghighi, S. S. (1992). Effects of altering core temperature on somatosensory and motor evoked potentials in rats. *Spine* **17**, 498-503.

Paintal, A. S. (1965). Effects of temperature on conduction velocity in single vagal and saphenous myelinated nerve fibers of the cat. *J. Physiol.* **180**, 20-49.

Rall, J. A. and Woledge, R. C. (1990). Influence of temperature on mechanics and energetics of muscle contraction. *Am. J. Physiol.* **259**, R197-R203.

Ranatunga, K. W. (1977). Changes produced by chronic denervation in the temperature-dependent isometric contractile characteristics of rat fast and slow twitch skeletal muscles. *J. Physiol.* **273**, 255-262.

Ranatunga, K. W. (1980). Influence of temperature on isometric tension development in mouse fast-and slow-twitch skeletal muscles. *Exp. Neurol.* **70**, 211-218.

Ranatunga, K. W. (1982). Temperature dependence of shortening velocity and rate of isometric tension development in rat skeletal muscle. *J. Physiol.* **329**, 465-483.

Ranatunga, K. W. (1984). The force-velocity relation of rat fast-and slow-twitch muscles examined at different temperatures. *J. Physiol.* **351**, 517-529.

Ranatunga, K. W. (1998). Temperature dependence of mechanical power output in mammalian (rat) skeletal muscle. *Exp. Physiol.* **83**, 371-376.

Reinertsen, R. E. (1996). Physiological and ecological aspects of hypothermia. In *Avian Energetics and Nutritional Ecology* (ed. C. Carey), pp. 125-157. New York: Chapman and Hall.

Rome, L. C. (1990). Influence of temperature on muscle recruitment and muscle function *in vivo*. *Am. J. Physiol.* **259**, R210-R222.

Rome, L. C., Funke, R. P. and Alexander, R. M. (1990). The influence of temperature on muscle velocity and sustained performance in swimming carp. *J. Exp. Biol.* **154**, 163-178.

Roots, B. I. and Prosser, C. L. (1962). Temperature acclimation and the nervous system in fish. *J. Exp. Biol.* **39**, 617-629.

Schmidt-Nielsen, K. (1990). *Animal Physiology: Adaptation and Environment*, pp. 276-282. Cambridge: Cambridge University Press.

Wooden, K. M. and Walsberg, G. E. (2000). Effect of wind and solar radiation on metabolic heat production in a small desert rodent, *Spermophilus tereticaudus*. *J. Exp. Biol.* **203**, 879-888.

Wooden, K. M. and Walsberg, G. E. (2002). Effect of environmental temperature on body temperature and metabolic heat production in a heterothermic rodent, *Spermophilus tereticaudus*. *J. Exp. Biol.* **205**, 2099-2105.

Xiang, J., Weiguo, D. and Pingyue, S. (1996). Body temperature, thermal tolerance, and influence of temperature on sprint speed and food assimilation in adult grass lizards, *Takydromus septentrionalis*. *J. Therm. Biol.* **21**, 155-161.