

METABOLISM AND THERMAL RESPONSE IN WINTER-ACCLIMATIZED PYGMY RABBITS (*BRACHYLAGUS IDAHOENSIS*)

TODD E. KATZNER, KATHERINE L. PARKER, AND HENRY H. HARLOW

Department of Zoology and Physiology, P.O. Box 3166, University of Wyoming, Laramie, WY 82071

Present address of KLP: Faculty of Natural Resources and Environmental Studies,

University of Northern British Columbia, 3333 University Way,

Prince George, British Columbia, V2N 4Z9 CANADA

Resting metabolic rate of pygmy rabbits ($0.89 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) was high compared to other eutherian mammals, but not unusual among lagomorphs. The estimated size of the zone of thermoneutrality was ca. $8\text{--}9^\circ\text{C}$, with the lower critical temperature occurring between 15 and 20°C , depending on body mass. Minimum thermal conductance was lower and mean body temperature was higher than predicted for similarly sized mammals. Body temperature fluctuated $>1^\circ\text{C}$ within a 24-h period, but showed no circadian patterns. Pygmy rabbits are thermally stressed during harsh winters in Wyoming, but low thermal conductance, a high-energy source of food, and favorable microenvironments enhance survival.

Key words: *Brachylagus idahoensis*, pygmy rabbit, metabolism, body temperature, thermoregulation, conductance, thermoneutral zone

Species in north-temperate regions experience wide ranges in ambient and operative temperatures during winter. Extended periods of extremely cold temperatures, in particular, place high energy demands on animals in northern latitudes. Endotherms living in these climates usually enhance their chances of survival by adaptive changes in food habits, metabolic rate, and quality of insulation (Scholander et al., 1950a; Wang et al., 1973). Because the insulation attainable by smaller mammals is limited, they must employ various behavioral and physiological mechanisms to minimize energetic losses in such cold environments (Pyomila et al., 1992).

Leporids in sagebrush-steppe habitat often are more directly exposed to the environment than other small mammals that spend much of the winter under the snow or in forested habitats protected from wind (Rogowitz, 1990). Pygmy rabbits (*Brachylagus idahoensis*) are among the smallest leporids in the world (300–500 g), and subsist almost exclusively on big sagebrush

(*Artemisia tridentata*) during winter (Green and Flinders, 1980; Katzner, 1994; Wilde, 1978). Despite such a limited diet and small body size, these animals survive harsh winters throughout much of their range from southeastern Oregon and northeastern California across southern Idaho, northern Nevada and Utah, into southwestern Wyoming (Campbell et al., 1982; Green, 1978; Pritchett et al., 1987); a small remnant population also exists in southeastern Washington (Dobler and Dixon, 1992). Pygmy rabbits have no known food-caching behaviors or depressed metabolic rates such as are observed in other cold-adapted lagomorphs (MacArthur and Wang, 1973; Wang et al., 1973). In southwestern Wyoming, pygmy rabbits may use subnivean burrows to ameliorate thermal extremes, yet still spend $>60\%$ of daylight hours above the surface of snow in spite of a high ratio of surface area to volume (Katzner, 1994). Field studies in this region, which includes the coldest climates in their geographic range, indicate that animals are active during all

24 h of the winter day in temperatures ranging from -26 to $+9^{\circ}\text{C}$ (Katzner, 1994). An understanding of the thermal requirements and energetic needs of pygmy rabbits in relation to habitat requirements is particularly important at this time because numbers of rabbits are believed to be declining in all known populations (Dobler and Dixon, 1992; Groombridge and Baily, in press). This decline is associated with the degradation and disappearance of sagebrush ecosystems throughout arid western North America.

In a previous study, Katzner (1994) described the role that habitat plays in influencing the thermal environment and consequent effects on patterns of activity by pygmy rabbits. The purpose of the present study was to define their thermoregulatory requirements. Our specific objectives were to determine the energetic costs associated with thermoregulation by pygmy rabbits, to examine the relationships between body temperature and thermal conductance under a wide range of ambient temperatures, to monitor and describe the relationship between body temperature of pygmy rabbits and the thermal environment in a simulated natural setting, and to examine these characteristics relative to other lagomorphs and in the context of conservation of the pygmy rabbit.

MATERIALS AND METHODS

Eight pygmy rabbits (four males, four females) were trapped with double-door livetraps (15 by 15 by 60 cm, Tomahawk Live Trap Co., Tomahawk, WI) 8 km S of Superior, Sweetwater Co., Wyoming ($41^{\circ}6'N$ $109^{\circ}W$) and transported to the Red Buttes Environmental Laboratory of the University of Wyoming, 15 km S of Laramie, Wyoming ($41^{\circ}10'N$ $106^{\circ}35'W$). They were maintained in an outdoor enclosure that was 2 m high and 12.3 m^2 ; it was constructed with 1.25-cm wire mesh, which roofed the enclosure and also extended 1 m below the ground surface underneath the enclosure. The wire served to deter predation by carnivorous birds and mammals, and prevented escape during excavation of burrows. The ground surface was mounded and

planted with sagebrush and grasses to simulate natural habitat conditions. Sagebrush (harvested from the Medicine Bow National Forest east of Laramie), commercial guinea pig pellets (containing 18% crude protein, 4% crude fat, 16% crude fiber, and mineral supplement; Lab Diet Brand Guinea Pig diet 5025, PMI Feeds Inc., St. Louis, MO) and water were supplied ad lib. Polyvinylchloride (PVC) tubing (11–18 cm diameter; ≤ 2 m in length) was placed in the ground for use as burrows to a maximum depth of 1 m, and wooden nest boxes (30.5 by 20 by 17 cm) with removable backs supplied additional cover for the animals above ground. The enclosure was sheltered from prevailing winds, and sagebrush branches were allowed to accumulate; nevertheless, the outdoor site exposed the animals to a natural photoperiod and temperature regime. Pygmy rabbits initially lost weight when first placed in captivity, but quickly recovered and maintained weight throughout the period of experimentation. Body mass ($\bar{X} \pm 1SD$) obtained from measurements made weekly during that period (which began 4–8 weeks after capture) was 432 ± 40 g (range, 370–490 g). Experimental trials were conducted 0730–1230 h during 30 November 1995–29 February 1996; ambient temperatures outdoors ranged from -33.2 to 16.7°C .

Animals were habituated to the experimental protocol before data collection began. When the PVC tunnels in the enclosure were blocked off, the rabbits generally ran into the nest boxes where they were easily captured. Subject animals were transported to the laboratory in a nest box, placed in a cloth bag and weighed on a top-loading balance, and then released into a metabolic chamber. The chamber was made from a 15-l opaque, polyethylene, processed-food container, for which we fabricated a close-fitting acrylic plastic lid, which bolted to the container, and a metal screen flooring raised 2 cm above the bottom surface. Each chamber was large enough that an animal could move easily about. The metabolic chamber was placed in an environmental chamber (Model 745145, Forma Scientific, Marietta, OH) with simulated daytime photoperiod and temperatures set between $+25$ and -15°C .

Oxygen consumption was measured using an open-circuit system (Hill, 1972). Instruments for analysis were located in a room adjacent to the environmental chamber. Air from the metabolic

chamber was evacuated by vacuum pump (Neptune Dyna-flow; Neptune Products Inc., Dover, NJ); the rate of air flow, as measured by a Matheson flow-meter system (Transducer Model 814, Flow Meter Readout Model 8143, Montgomeryville, PA), was kept constant at ca. 3500 cm³/min during all trials. Gas concentrations were analyzed for oxygen (Applied Electrochemistry S-3A/I Oxygen Analyzer, N-22M Oxygen Sensor, R-I Flow Control, Ametek, Pittsburgh, PA) and carbon dioxide (Anarad infrared gas analyzer AR-400 series, Santa Barbara, CA) after removing moisture using anhydrous calcium sulfate. Temperatures in the environmental and metabolic chambers were monitored to the nearest 0.01°C with copper-constantan thermocouples. Data (percentage O₂, percentage CO₂, flow rate, air-flow temperature at the gas analyzers, and environmental and metabolic chamber temperatures) were recorded every second and averaged over each minute by a CR21X datalogger (Campbell Scientific, Logan, UT). Oxygen consumption for each minute was determined with the following formula (Withers, 1977):

$$VO_2 = V_E(FIO_2 - FEO_2)/[1 - (1 - RQ)FIO_2]$$

where V_E is the volume of air flowing out of the chamber (at standard temperature and pressure), FIO_2 and FEO_2 are the fractional concentrations of oxygen in the air entering and leaving the chamber, respectively, and RQ is the respiratory quotient, calculated from the amount of CO₂ produced as a fraction of the amount of O₂. Gas concentrations of ambient air pulled into the metabolic chamber were monitored for 10 min before and after each trial without the rabbit; those data were averaged and considered to be the fractional concentrations of oxygen and carbon dioxide entering the chamber during the experiment.

A metabolic trial was conducted for each rabbit at intervals of 5°C between -15 and 25°C. The air temperature for each trial was selected to represent conditions similar to those in the outdoor enclosure on that day to avoid major acclimation effects. Animals were given ≥1 h to adjust to the metabolic chamber before each trial, and oxygen consumption was recorded for 1–2 h after this equilibration. Resting oxygen consumption for each air temperature was determined from the continuous 18–22-min period of the trial when metabolism was lowest. Because

of the difficulty in fasting animals in the outdoor enclosure and the danger of starving such small animals on a regular basis (MacArthur and Wang, 1973), the animals were provided with sagebrush and guinea pig pellets during the measurements. In a separate set of experiments, we compared metabolic rates for each rabbit with access to food (at 20°C) to metabolic rates obtained 5 h after food had been removed (also at 20°C) to check for possible differences between metabolism in fed and fasted states. Basal metabolic rate is assumed to be achieved when an animal is calm, in muscular repose, in a thermoneutral environment, and in a postabsorptive state. Heat production by nonfasted animals under similar conditions of rest and no thermal stress is termed resting metabolic rate.

To determine lower critical temperature (the ambient temperature below which metabolic rate increases linearly with decreasing ambient temperature as the animal regulates body temperature within acceptable limits) and upper critical temperature (the ambient temperature above which metabolic rate increases as the animal minimizes thermal heat stress), we compared metabolic rates at ambient temperatures where oxygen consumption was lowest and at the next higher and lower temperatures, using Student's *t*-test. The temperature range between upper and lower critical temperatures was assumed to be the animal's thermoneutral zone.

We described the rate of increase in oxygen consumption with decreasing air temperatures below lower critical temperature using least-squares regression analysis. To avoid pseudoreplication from repeated measurements on the same animal, we regressed data from each individual rabbit and averaged the slope and intercept from those regression equations to obtain an average rate of increase. We calculated conductance (C) using the Scholander-Irving model, $C = VO_2/(T_b - T_a)$, at each experimental temperature, where VO_2 is the volume of oxygen consumed, T_b is body temperature, and T_a is air temperature (McNab, 1970; Scholander et al., 1950*b*). This model assumes that the level that body temperature is held above ambient temperature depends on the ratio of heat production (metabolic rate) to cooling rate (conductance).

We anaesthetized four pygmy rabbits with a mixture of ketamine-xylazine hydrochloride and then surgically implanted radiotransmitters, into the peritoneal cavity, for which frequency of the

signal was calibrated with body temperature ($\pm 0.1^\circ\text{C}$; CHP1-H, Telonics, Mesa, AZ). During metabolic trials, transmission signals were monitored with a Telonics (Model TR-2) receiver located in the adjacent instrument room, and attached to an H-antenna in the environmental chamber. Readings were taken three times per minute, time between signals was converted to millivolts with a Telonics signal processor (Model TDP-2), and that information was then stored by a CR10 datalogger (Campbell Scientific, Logan, UT). Regression equations developed for each transmitter were used to convert the millivolt readings into body temperatures, which were averaged for each minute of the trial.

Body temperature also was monitored in the rabbits implanted with temperature sensors when they were in the outdoor enclosure. Signals were received with an omnidirectional antenna (Model V-2R; Telex, Minneapolis, MN) at the rabbit enclosure and a Telonics receiver-scanner-processor system (Models TR-2, TS-1, and TDP-2, respectively, Telonics, Mesa, AZ), and recorded on a CR10 datalogger. Body temperatures for each animal were taken six times within each 15-min period throughout the day and averaged for that period. We monitored concurrent air temperature, wind speed, and solar radiation (measured with a Temp 107 probe thermistor, a Met One anemometer, Model 014A, and a LiCOR solarimeter, Model Li-2000s; Campbell Scientific, Logan, UT) for every second and averaged them over the same 15-min period at a weather station located 10 m from the rabbit enclosure. We used an α level of 0.05 for statistical significance in all analyses. Means are presented as $\bar{X} \pm 1 SE$.

RESULTS

The lowest mean level of oxygen consumption, representing resting metabolic rate in winter-acclimatized pygmy rabbits, occurred at 20°C ($0.89 \pm 0.034 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$; Fig. 1). No readily apparent pattern distinguished males from females; rather, three of the largest animals (2 females and 1 male) tended to have lower metabolic rates than the five other ones ($\text{VO}_2 = 1.169 - 0.00184M$, where VO_2 is the volume of oxygen consumed in $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, and M is body mass in g; Fig. 1 inset). Respiratory

quotients (RQ) at 20°C averaged 0.79 ± 0.018 .

Food deprivation did not have a statistically significant impact on metabolic rates at 20°C (for rabbits that had been fed, $\bar{X} = 1.07 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$; for fasted rabbits, $\bar{X} = 1.03$; $t = 2.431$, $d.f. = 6$, $P = 0.051$) or on respiratory quotients ($t = 1.518$, $d.f. = 6$, $P = 0.180$, although the rabbits lost 0.7–2.4% ($1.2 \pm 0.23\%$) of their body weight when starved for 5 h. We were unable, therefore, to determine a quantifiable difference between resting and basal metabolic rates. Animals with free access to food may not necessarily have been in a fed state; further, fasted animals undoubtedly consumed cecal and fecal pellets during the experimental period because few pellets were found in the chamber at the end of the trial.

Oxygen consumption was significantly greater ($t = 3.56$, $d.f. = 7$, $P = 0.005$) at 15°C than at 20°C , and it continued to increase at lower ambient temperatures (Fig. 1; $\text{VO}_2 = 1.1757 - 0.0157 * \text{air temperature in } ^\circ\text{C}$). From these data, and assuming no discernible differences between animals that were fed and fasted, we conclude that lower critical temperature for pygmy rabbits was between 15 and 20°C . Oxygen consumption was greater at 25°C than at 20°C for six of the eight rabbits, but the averages for all rabbits at those two temperatures were not significantly different ($t = 1.43$, $d.f. = 6$, $P = 0.100$). The dataset at 25°C represents only seven animals, because the largest rabbit became heat stressed and was removed from the metabolic chamber before the trial was completed.

Thermal conductance for the four rabbits implanted with temperature sensors increased at air temperatures $>0^\circ\text{C}$ (Fig. 2a). Conductance did not change significantly at temperatures $<0^\circ\text{C}$, representing a minimum value of $0.027 \pm 0.014 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ } ^\circ\text{C}^{-1}$. Body temperatures of these animals in the metabolic chamber were relatively constant at air temperatures of -15 to 15°C (Fig. 2b) and averaged $38.3 \pm 0.2^\circ\text{C}$ ($n = 4$). At higher ambient temperatures, body

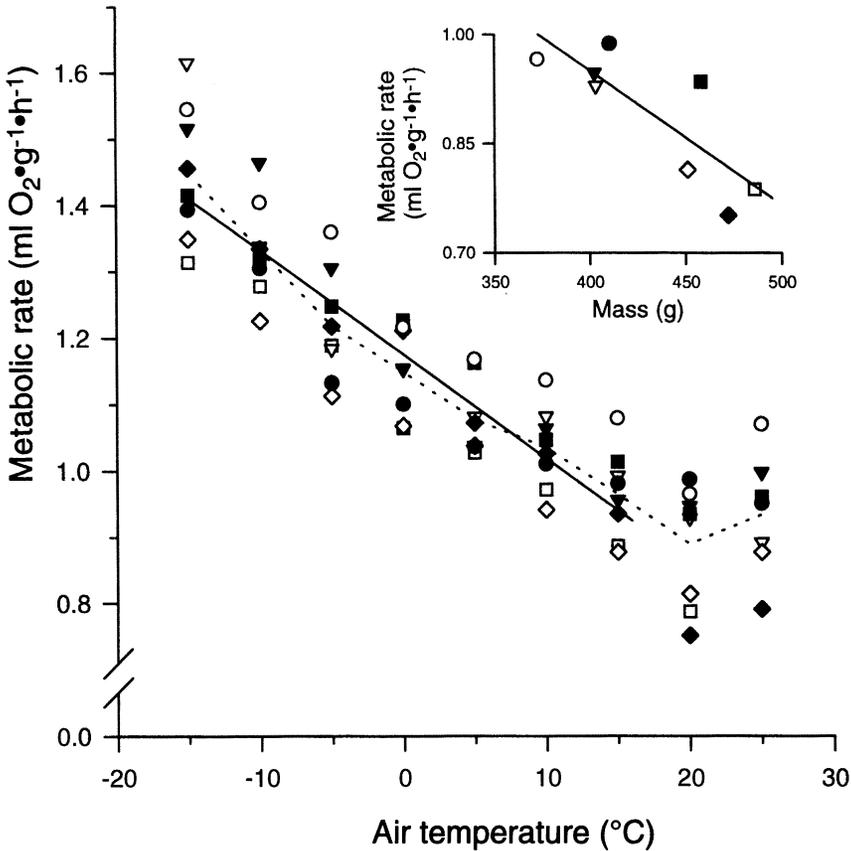


FIG. 1.—Oxygen consumption for eight pygmy rabbits at rest in relation to air temperature. Symbols show values for individual rabbits; solid symbols for males, open symbols for females. The dotted line connects mean oxygen consumption at each temperature. The solid line is the average of the regression lines for each rabbit at temperatures below the lower critical temperature. Inset shows resting metabolic rate at 20°C relative to body mass for the same eight rabbits.

temperatures tended to increase, exceeding 41°C for the one animal that became heat stressed at 25°C. Within the thermoneutral zone (at 20°C), body temperature averaged $38.7 \pm 0.2^\circ\text{C}$.

In the outdoor enclosure, body temperatures of pygmy rabbits ranged from 35.8 to 40.5°C ($\bar{X} = 38.47 \pm 0.16$). Body temperatures showed no consistent relationship with air temperature (-33.2 to 16.7°C), wind speed (14.2 m/s maximum), solar loads (1,089 W/m² maximum), or to a standard operative temperature calculated from combinations of micrometeorological variables (Katzner, 1994). Body temperatures of pygmy rabbits regularly fluctuated $>1^\circ\text{C}$

over 24-h periods, but consistent circadian rhythms were not evident in these fluctuations.

DISCUSSION

Under conditions that were not thermally stressful, resting metabolic rate of pygmy rabbits ($0.89 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) was higher than would be predicted for a 432-g eutherian mammal ($0.75 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ —Kleiber, 1975), but similar to that predicted by models for lagomorphs ($0.93 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ —Hayssen and Lacy, 1985; $0.92 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ —Rogowitz, 1990). These higher rates of metabolism may be specific to this order of mammals, and also could reflect the heat

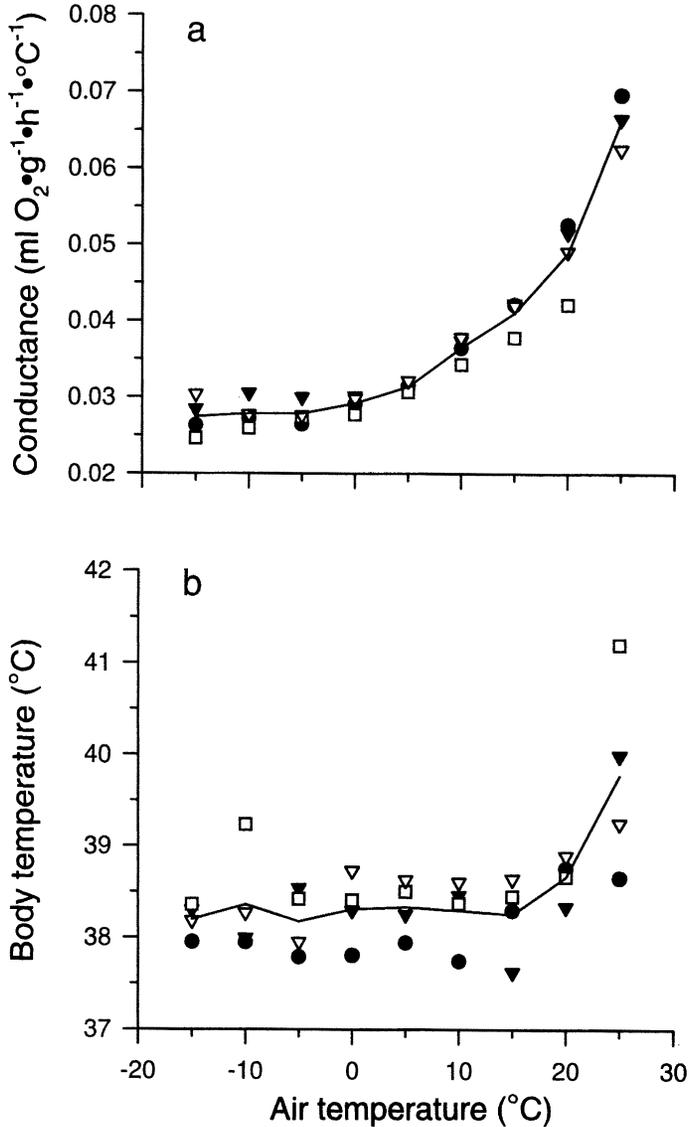


FIG. 2.—Thermal conductance (a) and body temperature (b) of four pygmy rabbits at rest in relation to air temperature in a metabolic chamber. The solid line represents the average conductance and body temperature at each air temperature; solid symbols are males, open symbols are females.

increment associated with digesting food. Most studies of the metabolism of lagomorphs either assume that reasonably short periods (<5 h) of fasting are needed to reach a postabsorptive state, or do not fast the animals at all to reduce stress (Hinds, 1973, 1977; Kronfeld and Shkolnik, 1996; MacArthur and Wang, 1973; Wang et al., 1973). Because lagomorphs reingest cecal

and fecal pellets when food stressed (Hirakawa, 1994; Wang et al., 1973), it is difficult to know when they are truly postabsorptive. The metabolic rates and respiratory quotients of pygmy rabbits given ad lib. access to food were not distinguishable from basal rates obtained after 5 h without food.

Pygmy rabbits did not exhibit a classical

metabolic response to different air temperatures with precisely defined lower and upper critical temperatures (Fig. 1), although our data suggest trends similar to the metabolic profiles of other lagomorphs (Hinds, 1973, 1977; Kronfeld and Shkolnik, 1996; MacArthur and Wang, 1973). We believe that the 5°C temperature increments chosen during experimentation were too large, and consequently it is likely we sampled metabolism only once within the thermoneutral zone of the rabbits.

Metabolic rate and body size influence an animal's resistance to high and low thermal extremes. The width of an animal's thermoneutral zone has been directly related to the climatic environment it experiences (Kronfeld and Shkolnik, 1996; Scholander et al., 1950b; Wang et al., 1973). Animals in tropical habitats, where temperatures are relatively stable over the course of a year, have limited thermoneutral zones. In temperate regions, animals must cope with more variability in temperatures, and consequently tend to have a thermoneutral zone with wider limits. Body mass among animals outside the tropics should be a determinant of the range of thermoneutrality, because larger animals have more mass and a greater insulative capacity, which thereby increases resistance to cold temperatures. Larger animals also have proportionately less surface area over which heat gain can occur, increasing tolerance to high temperatures (Vaughan, 1986).

A log-linear relationship exists among North American lagomorphs found in cold climates between body size and the range of thermoneutrality achieved per unit of heat production during winter (Fig. 3). We scaled the width of the thermoneutral zone (°C) by the metabolic rate of the animal (its heat production; ml O₂ g⁻¹ h⁻¹) because some lagomorphs (most notably Arctic hares, *L. arcticus*) have adaptive basal metabolic rates that are higher or lower than would be expected based on body mass (Wang et al., 1973), making singular estimates of thermal tolerance from body size

impractical. Likely, our relationship includes both basal and resting metabolic rates because a truly postabsorptive state is difficult to achieve in lagomorphs with coprophagic habits. Using a regression developed from three studies that empirically determined the upper and lower limits of thermoneutrality (Hinds, 1973; MacArthur and Wang, 1973; Wang et al., 1973), the predicted thermoneutral range for an average-sized (432 g) pygmy rabbit would be 8.4°C. This is only slightly less than is predicted (9.2°C) by a regression for six cold-adapted North American lagomorphs that includes cases for which we estimated upper critical temperature from the published data (Hart et al., 1965; Pyornila et al., 1992; Rogowitz, 1990).

Assuming that lower critical temperature for pygmy rabbits is between 15 and 20°C (Fig. 1), upper critical temperature is likely between 23 and 28°C. Specific lower and upper critical temperatures probably vary with individual size and pelage characteristics. For example, the largest rabbit in our study became heat stressed at 25°C and would have died with continued exposure. We are confident that 25°C was above the upper critical temperature for that animal. Observations on the other seven rabbits at 25°C indicated that they were minimizing heat production by not moving and were behaviorally dissipating body heat by assuming postures to maximize exposed surface area. It is likely that some of these rabbits were thermally stressed, and that others were in the upper range of their thermoneutral zones. Given the overall thermal response to a wide range of ambient temperatures, pygmy rabbits probably are cold stressed for most of a winter in Wyoming (Katzner, 1994). Nevertheless, despite their small size, pygmy rabbits do not appear to have physiological adaptations, such as depressed metabolic rates or body temperatures, which would set them apart from other lagomorphs.

It generally is assumed that below lower critical temperature a constant minimum

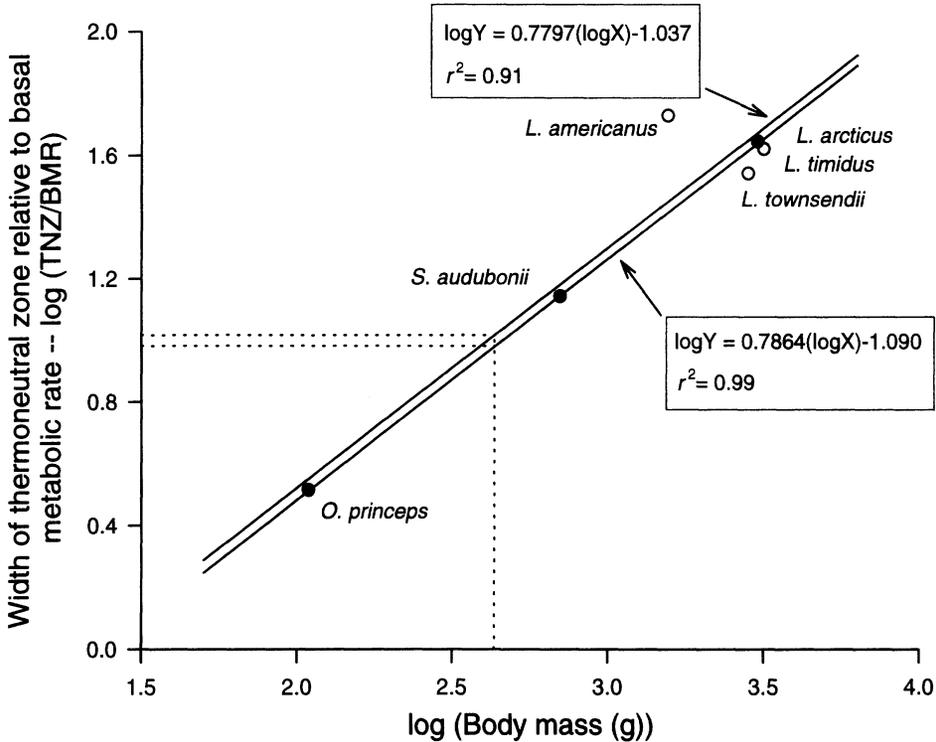


FIG. 3.—Width of the thermoneutral zone (TNZ; °C) per unit of basal metabolic rate (BMR; ml O₂ g⁻¹ h⁻¹) in relation to body mass for six North American lagomorphs (*Lepus americanus*, ca. 43°C, 0.80 ml O₂ g⁻¹ h⁻¹—Hart et al., 1965; *L. arcticus*, 16°C, 0.36 ml O₂ g⁻¹ h⁻¹—Wang et al., 1973; *L. timidus*, ca. 31°C, 0.74 ml O₂ g⁻¹ h⁻¹—Pyornila et al., 1992; *L. townsendii*, ca. 22°C, 0.63 ml O₂ g⁻¹ h⁻¹—Rogowitz, 1990; *Sylvilagus audubonii*, 11°C, 0.79 ml O₂ g⁻¹ h⁻¹—Hinds 1973; *Ochotona princeps*, 5°C, 1.53 ml O₂ g⁻¹ h⁻¹—MacArthur and Wang, 1973). Least-squares regressions are shown for six species (all symbols, upper line), and for the three species for which the thermoneutral zone was explicitly defined (solid symbols, lower line). The dotted lines represent predicted values for pygmy rabbits (432 g).

thermal conductance is maintained by the animal and oxygen consumption increases with decreasing air temperature ($C = VO_2 / (T_b - T_a)$)—McNab, 1980). However, species that do not rigidly distinguish between physical and chemical thermoregulation may vary both conductance and oxygen consumption simultaneously (McNab, 1980; Pyornila et al., 1992). Pygmy rabbits increased oxygen consumption at temperatures less than their presumed lower critical temperature (15–20°C, Fig. 1), but also continued to make thermal adjustments in conductance at ambient temperatures as low as 0°C (Fig. 2a). Minimum thermal-conductive properties ($C = 0.027$ ml O₂ g⁻¹ h⁻¹ °C⁻¹)

were less than would be expected for placental mammals (0.05779 ml O₂ g⁻¹ h⁻¹ °C⁻¹—Bradley and Deavers, 1980; 0.0477 ml O₂ g⁻¹ h⁻¹ °C⁻¹—Herreid and Kessel, 1967), but again, were more similar to other leporids (*L. americanus* = 0.022 ml O₂ g⁻¹ h⁻¹ °C⁻¹—Hart et al., 1965; *L. townsendii* = 0.014 ml O₂ g⁻¹ h⁻¹ °C⁻¹—Rogowitz, 1990; *Oryctolagus cuniculus* = 0.026 ml O₂ g⁻¹ h⁻¹ °C⁻¹—Gonzales et al., 1971; *Sylvilagus audubonii* = 0.036 ml O₂ g⁻¹ h⁻¹ °C⁻¹—Hinds, 1977).

In conjunction with this low thermal conductance relative to similarly sized eutherians, body temperatures of lagomorphs (including pygmy rabbits) are also often high-

er than predicted by allometric models. Pygmy rabbits have low body temperatures (38.47°C) in comparison to most other lagomorphs (*L. americanus* = 39.8°C—Hart et al., 1965; *L. arcticus* = 38.9°C—Wang et al., 1973; *L. californicus* = 38.7°C—Hinds, 1977, 39.2°C—Schmidt-Nielsen et al., 1965; *L. timidus* = 39.7°C—Pyornila et al., 1992; *L. townsendii* = 38.9°C—Rogowitz, 1990; *O. princeps* = 40.1°C—MacArthur and Wang, 1973; *S. audubonii* = 38.5°C—Hinds, 1973). Maintaining a low body temperature would contribute to strategies for conserving energy, particularly for such a small species in one of the coldest regions of the United States.

Pygmy rabbits in the outdoor enclosure showed no circadian rhythms in body temperature regulation associated with ambient temperature or activity as are seen in other mammals (e.g., Pauls, 1979) and some lagomorphs (Hinds, 1977; Shoemaker et al., 1976). In accordance with the lack of a circadian body temperature profile, Katzner's previous work shows that pygmy rabbits were active at all hours of the day and night (Katzner, 1994).

There are several consequences of such a small mammal maintaining a high metabolic rate and living in a continuously stressful thermal environment. They must ingest either large quantities of low-energy food or proportionately smaller amounts of higher-energy food to offset high metabolic expenditures. Sagebrush, the exclusive winter forage of pygmy rabbits (Green and Flinders, 1980; Katzner, 1994) has a high energy content, despite plant-defense strategies that include the production of large quantities of terpenoids (White et al., 1982). Because they spend a large proportion of time above the snow surface, pygmy rabbits potentially can lose large amounts of heat through convective and radiative processes. Physiological and behavioral adaptations that minimize heat loss are, therefore, important to survival. The relatively low thermal conductance of pygmy rabbits and their use of specialized habitats are essential ad-

aptations. In previous work, Katzner (1994) observed that pygmy rabbits exclusively occupied habitats with extensive structure of sagebrush, composed of both living and dead vegetative material. These structural features provide thermally favorable micro-environments that minimize energy expenditures (Taylor and Buskirk, 1994), and permit survival in otherwise inhospitable conditions.

Results and implications from this study are important to our understanding of the physiology and ecology of pygmy rabbits. This species exhibits metabolic and insulative characteristics that are typical of lagomorphs, but exclusive dietary and habitat choices set it apart from most other species in the order. The multifaceted, obligate relationship that pygmy rabbits have with sagebrush suggests that they cannot tolerate extensive habitat alteration. Indeed, population declines have been related to degradation and loss of sagebrush habitat. These issues should be of particular concern in the most eastern portions of the Great Basin, where harsh winters place pygmy rabbits under more extreme physiological stress than they encounter in other areas of their range.

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