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Metabolism and thermoregulation in the Mongolian gerbil *Meriones unguiculatus*

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Oxygen consumption, thermal conductance and body temperature of *Meriones unguiculatus* (Milne-Edwards, 1867) were measured at a temperature range from 5 to 40°C. The lowest mean metabolic rate (BMR) was 2.13 ± 0.14 $mlO_2\ g^{-1} \cdot h^{-1}$, which is higher than the predicted values based on their body mass. The thermal neutral zone (TNZ) was 26 to 38°C. Mean body temperature below the TNZ was 38.4 ± 0.5°C. Mean thermal conductance below the TNZ was 0.179 ± 0.037 $mlO_2\ g^{-1} \cdot h^{-1} \cdot {}^{\circ}C^{-1}$, which is also higher than predicted values based on their body mass. Thermoregulatory characteristics of Mongolian gerbils are very different from that found in arid-adapted small mammals. The extreme severe climate perhaps is the main selective force faced by Mongolian gerbils during their evolution with their macroenvironments.

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Introduction

The Mongolian gerbil *Meriones unguiculatus* (Milne-Edwards, 1867) is a small cricetid rodent native to the desert and semiarid regions of Mongolia and northern China (Walker 1968). Robinson (1959) first measured the metabolic rate of *M. unguiculatus* and reported that this species showed a relative wide thermal neutral zone (TNZ; from 30 to 40°C) and possessed a great tolerance for heat. Thus he concluded that this species had a greater capacity for thermoregulation than other desert rodent species. Luebbert *et al.* (1979) studied the temperature acclimation for this species and found similar properties in many metabolic aspects, but a narrow TNZ.

Most studies on thermoregulation of Mongolian gerbils were on laboratory-bred individuals, and the whole laboratory population of gerbils was raised from only 11 pairs imported to USA from China in 1954 (Robinson 1959, Weiner and Górecki 1981). Weiner and Górecki (1981) studied the metabolic characteristics of wild gerbils from Mongolia and found that *M. unguiculatus* showed some desert-adaptive features such as a narrow TNZ (about 15–18°C) and a steep thermoregulatory curve. In their study temperature range was about 8 to 25°C, and they reported that 25°C was the lethal temperature for those gerbils. It seems that there existed a marked difference in the ecophysiological properties between wild and laboratory populations of *M. unguiculatus*.

Because of the conflicting results reported in literature for Mongolian gerbils, it is necessary and very interesting to study the characteristics of thermal biology for this species. In this study we measured the metabolism of *M. unguiculatus* that were newly caught in the temperate grassland of Inner Mongolia. Climate characteristics of Mongolian desert (ie a hot summer and a long, cold and dry winter) differ from those of hot deserts. Therefore, we predicted that (1) Mongolian gerbils living here may show some different metabolic responses compared with those found in hot desert rodents, and (2) because of the different conditions between field and laboratory, the newly captured gerbils may show different metabolic properties from laboratory-bred gerbils.

Material and methods

Animals

Eight adult Mongolian gerbils (4 males, 4 females) were live-trapped in the semiarid steppe at Xilinhot, Inner Mongolia, China, in spring (April) 1998. The mean body mass was 58.1 ± 8.7 (SD) g. The fluctuation of ambient temperature between day and night is great. In summer the temperature range was from 3°C during the night to 52°C during the day in the sun (Agren *et al.* 1990). The annual mean temperature is –0.4°C, average monthly air temperature in the coldest month (January) is –22.3°C, while 18.8°C during the warmest month (July). The yearly range is –47.5 to 35.3°C. There are four months (December through March) in which the extreme minimum ambient temperature is below –40°C. In April when animals were trapped, the mean ambient temperature is 2.6°C, the maximum ambient temperature is 28.8°C and the minimum is –29.2°C. Annual precipitation is 350 mm and the plant growth period is about 150–180 days (Chen 1988).

After capture, the body mass (Mb), sex and reproductive state of the animals were examined and recorded in the laboratory. Animals were kept in large cages (47.5 × 35 × 20 cm) under natural photoperiod (ca 14L : 10D) and temperature (5–18°C) and were fed laboratory rat chow pellets for about a week. Food and water were supplied *ad lib.*

Measurement procedure

Oxygen consumption rates were measured using the Kalabukhov-Skovortsov closed-circuit respirometer according to Górecki (1975). Temperatures inside the animal chambers submerged in a water both were measured and maintained constant to whin 1°C. Metabolic chamber size was 3.6 dm^3. Mb and rectal temperatures (Tb) of animals were recorded before and after each experiment. Tb was measured by a digital thermometer (Beijing Normal University Instruments Co.) in rectum at depth of 3 cm.

Metabolic rate measurements were made over a temperature range from 5 to 40°C and each measurement lasted for 40 min after the animals had been in the metabolic chamber for about 1 h. Before each experiment food was witheld 3 hours to minimize the specific dynamic action of food and gerbils were weighed to the nearest 0.1 g. Records of oxygen consumption due to animal's activity in the chamber were discarded when computing the metabolic rate of each individual.

All measurements were made daily between 08.30 h and 19.00 h. Metabolic rates were expressed as $mlO_2 \cdot g^{-1} \cdot h^{-1}$ and corrected to STP conditions. Obviously pregnant or lactating animals were not used in the experiments.

Thermal conductance

Overall thermal conductance (C, $mlO_2 \cdot g^{-1} \cdot h^{-1} \cdot {}^{\circ}C^{-1}$) was calculated at temperatures below the thermal neutral zone using the formula:

$$C = MR/(Tb - Ta)$$

where MR is metabolic rate (in $mlO_2 \cdot g^{-1} \cdot h^{-1}$), Tb is body temperature (in °C), and Ta is ambient temperature (in °C). This formula has been suggested by McNab (1980) as well as Bradley and Deavers (1980) for calculating conductance at any given ambient temperature.

Statistics

Data were analyzed using SPSS package (1998). Differences between groups were determined by Student's *t*-test and $p < 0.05$ was taken to be statistically significant. Regression equations were determined by the method of least squares using all data points. All values were presented as mean ± SD.

Results

Body temperature (Tb)

Fig. 1 shows the changes of Tb with ambient temperature (Ta). Mean Tb was 38.8 ± 0.9°C after experiments and ranged from a mean of 38.2 ± 0.3°C at 28°C to 41.0 ± 1.2°C at 40°C. Tbs were fairly constant between 5 and 32°C (ie 38.4 ± 0.5°C), but increased above 34°C. At 40°C, 25% of the gerbils died at the end of metabolic determination.

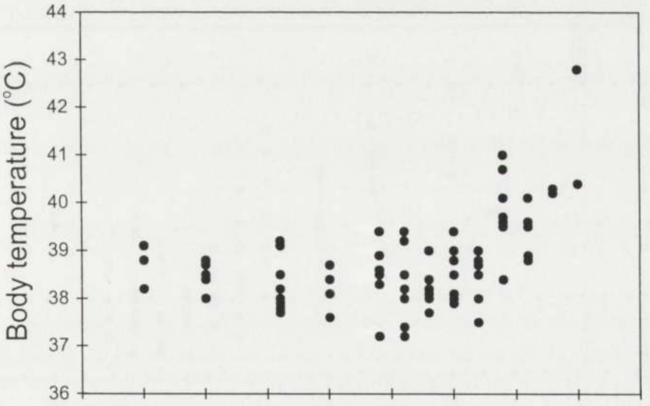

Fig 1. Body temperatures of Mongolian gerbil *Meriones unguiculatus* at different ambient temperatures. $n = 8$.

Metabolic rate

Metabolic rates of gerbils measured over the Ta range from 5 to 40°C are shown in Fig. 2. Metabolic rates were kept stable from 26 to 38°C. Although there was no significant difference for metabolic rates between 24 and 26°C, the difference between 24 and 36°C was significant ($p < 0.01$). Iterative fitting method also showed that 26°C is the "turning point" of the line between metabolic rates and Ta. Thus, 26°C was thought to be the lower critical temperature. Above 38°C, metabolic rate significantly increased ($p < 0.05$) and was regarded as the upper critical temperature. Thus the thermal neutral zone (TNZ) during the present study extended from 26 to 38°C. Metabolic rates within this temperature zone are regarded as basal metabolic rate (BMR). The mean BMR was 2.13 ± 0.14 $\mathrm{mlO_2 \cdot g^{-1} \cdot h^{-1}}$, ie 172% and 163% of the values predicted by Kleiber (1961: $\mathrm{BMR} = 3.42\mathrm{M}^{-0.25}$ for eutherian mammals, where M is body mass in g) and Hayssen and Lacy (1985: $\mathrm{BMR} = 4.98\mathrm{M}^{-0.33}$ for rodent species), respectively.

Below the TNZ, metabolic rates increased with decreasing Ta (Fig. 2), the relationship between resting metabolic rates (RMR) and Ta is described by:

$\mathrm{RMR}\ (\mathrm{mlO_2 \cdot g^{-1} \cdot h^{-1}}) = 5.47\ (\pm\ 0.188) - 0.108\ (\pm\ 0.010)\ \mathrm{Ta}\ (r = -0.9827, p < 0.001)$.

Thermal conductance (C)

The variations of overall thermal conductance with Ta for gerbils are shown in Fig. 3. Below the TNZ, the average C was 0.179 ± 0.037 $\mathrm{mlO_2 \cdot g^{-1} \cdot h^{-1} \cdot {}^\circ C^{-1}}$, which is 137% and 133% of that predicted by Herreid and Kessel (1967: $\mathrm{C} = 1.0\mathrm{M}^{-0.50}$, where M is body mass in g) and Bradley and Deavers (1980: $\mathrm{C} = 0.76\mathrm{M}^{-0.43}$), respectively, based on body mass.

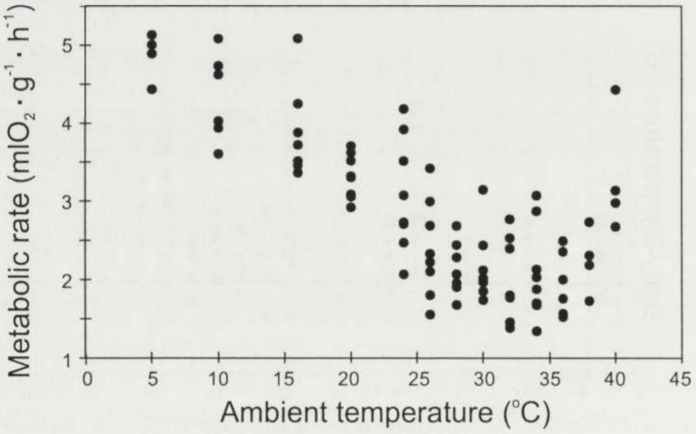

Fig. 2. Relationship between metabolic rates and ambient temperatures in Mongolian gerbil *Meriones unguiculatus*. $n = 8$.

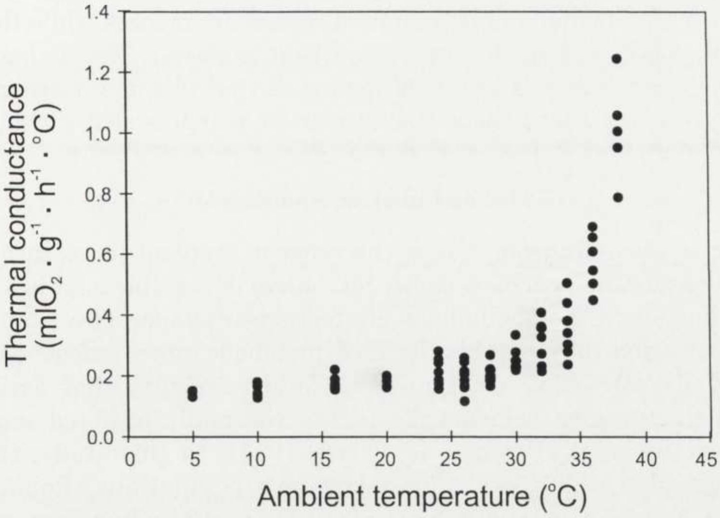

Fig. 3. Thermal conductance of Mongolian gerbil *Meriones unguiculatus* at different ambient temperatures. $n = 8$.

Within and above the TNZ, C increased significantly with increasing Ta, and sharply increased from 38°C (1.01 ± 0.17 mlO$_2$ · g^{-1} · h^{-1} · °C^{-1}), reaching 5.89 ± 2.91 mlO$_2$ · g^{-1} · h^{-1} · °C^{-1} at 40°C (not shown in Fig. 3).

Discussion

The following characteristics are typical for desert animals: (1) a relatively low BMR, (2) a steep thermoregulatory curve, (3) a narrow and hard-to-define thermoneutral zone (TNZ), and (4) a high lower critical temperature (Weiner and Górecki 1981, Degen 1997). Webb and Skinner (1996) stated that gerbils (subfamily Gerbillinae) have low BMR and average minimum thermal conductance when compared to other rodents and other mammals of the same body mass. In this study, Mongolian gerbils had neither a lowered BMR and thermal conductance nor a narrow TNZ but they do inhabit a semiarid environment.

Body temperature (Tb)

Within the TNZ most desert rodents have a Tb of 37°C or lower, whereas most nondesert rodents have a Tb of 37°C or above. Lower Tbs of desert species represents an increased ability to maintain a small temperature differential during periods of high Ta (Bradley and Yousef 1972). But, for adult Mongolian gerbils kept below the TNZ, mean resting body temperatures were 38.4°C. Luebbert *et al.* (1979) reported that laboratory-bred Mongolian gerbils could maintain their Tbs above 38°C over a wide Ta range.

A rise in the Tb of small desert mammals often commences while the animal is still within its TNZ, and in this way some heat is stored. This is more common among the larger of the small diurnal mammals and in some nocturnal rodents. Mongolian gerbils increased their Tbs from 34°C, which is still within the TNZ.

Thermal neutral zone (TNZ)

According to the definition, TNZ is the range of ambient temperature at which temperature regulation is achieved only by control of sensible heat loss, ie without regulatory changes in metabolic heat production or evaporative heat loss (IUPS Thermal Commission 1987). Within the TNZ, metabolic rate is independent with Ta.

High and narrow TNZ are typical of desert rodents that avoid extreme temperature fluctuations behaviorally in the thermally buffered microenvironments of their burrows (Downs and Perrin 1994). In this study, the TNZ for Mongolian gerbil was 26–38°C. For laboratory populations, Robinson (1959) reported that the TNZ extended from 30 to 39 or 40°C. Luebbert *et al.* (1979) reported that the TNZ was 32–34°C for 24°C-acclimated gerbils, 30–36°C for 5°C -acclimated gerbils and 32–38°C for 35°C-acclimated gerbils. Compared with the above mentioned data, this study indicated that the lower critical temperature is low, whereas the upper critical temperature is similar. However, Weiner and Górecki (1981) found that in wild Mongolian gerbils the TNZ was only about 15–18°C and 25°C was the lethal temperature. They explained that this is perhaps a metabolic difference between field- and laboratory-bred populations. It is very interesting that the climate characteristics of our research site are somewhat similar to that of Weiner and Górecki (1981). Thus, it is difficult to interpret this great difference between their and our findings.

Bartholomew (1977) stated that high thermal conductance and tolerance of hyperthermia cause the TNZ to move to a higher Ta. This reduces the need for high water loss and large expenditure of energy for cooling at high Ta (Roxburgh and Perrin 1994). Thus, a higher upper critical temperature would be a beneficial adaptation, specifically for water conservation.

Thermoregulation and metabolism

This study showed that Mongolian gerbils have a high level of metabolism (2.127 $mlO_2 \cdot g^{-1} \cdot h^{-1}$, ie 72% higher than predicted value), higher than that previously reported for this species, and are not conformable with the general rule of the thermoregulatory pattern of arid and semi-arid rodent species.

Robinson (1959) found that BMR (calculated from the equation of MR to Ta at the lower end, 30°C) of the Mongolian gerbil was 1.43 $mlO_2 \cdot g^{-1} \cdot h^{-1}$. Luebbert *et al.* (1979) found that this species is capable of acclimating to a wide range of ambient temperatures and its BMR (1.42 $mlO_2 \cdot g^{-1} \cdot h^{-1}$) is not below that predicted for the body size, even following heat acclimation, significantly differing from the desert species. They also found that cold-acclimated gerbils have a significantly higher BMR than non-acclimated controls, increasing to 1.94 $mlO_2 \cdot g^{-1} \cdot h^{-1}$, which is similar to our measurements for newly captured gerbils.

It has been argued that a lower than predicted BMR would be advantageous for animals inhabiting arid areas as it would reduce energy requirements, heat production and evaporative water loss (Borut and Shkolnik 1974). Indeed, many desert mammals have been reported to have a BMR lower than predicted values based on their body mass. Goyal and Ghosh (1983) reported that, among desert rodents, the maximum and average decreases of BMR from expected values were 37 and 16%, respectively, whereas in non-desert rodents, the maximum and average increases of BMR from expected values were 88 and 34%, respectively. A lower than predicted BMR has been reported for desert mammals in all deserts of the world (Degen 1997). A similar conclusion was obtained for the gerbil species (Webb and Skinner 1996). Haim and Harari (1992) suggested that some of the inter-specific variation in BMR within the Gerbillinae might be attributable to inter-specific variation in habitat.

Small mammals from cold deserts are exposed to environmental conditions that differ substantially from those of hot deserts and, in consequence, tend to show different metabolic responses (Degen 1997). Weiner and Górecki (1981) reported that BMR in field-caught gerbils was 1.15 $mlO_2 \cdot g^{-1} \cdot h^{-1}$, close to predicted value and lower than the results of others and ours. This difference is due to, at least in part, the different seasons and different geographic distributions. The relatively low BMR of field-caught gerbils is perhaps because they were summer-acclimatized animals. In summer, the arid steppe of eastern Mongolia is characterized by typical hot desert conditions. Luebbert *et al.* (1979) showed that heat-acclimated gerbils had a lower BMR than non-acclimated controls.

Various factors have been suggested as determinants of BMR, including body size, phylogeny, climate, and one of the most important, food habits (McNab 1986). The following possible reasons might account for the high metabolic rate of our gerbils: (1) Mongolian gerbils in our studies prefer to live at the interface of farming and grazing (ecotone) and have the habit of storing seeds of grass and crops. Thus, their food is available throughout the year in sufficient abundance to support a high rate of metabolism. (2) Although Mongolian gerbil is a seed-eating rodent, grass leaves and tender stems are their dominant food during spring and summer (Zhou *et al.* 1988). It has been shown that mammals eating herbs have high basal metabolic rate (McNab 1986). (3) The standard interpretation of low BMRs in desert rodents is that they contribute to water conservation. Therefore, Mongolian gerbils feeding on green vegetation, with its high water and relative low protein contents, might not be required to have low BMR. (4) It is still cold in spring. In April, the mean ambient air temperature is only 2.6°C (see Material and methods). The temperature fluctuation between day and night is large. Low temperature could cause animals to increase metabolic rates. (5) Our study site is a semiarid habitat and is different from the hot desert. Animals living here do not have as great a need for water conservation as animals inhabiting desert areas, and a reduced metabolic rate is not essential for survival.

Thermal conductance

In general, desert rodents have conductance lower than expected values based on their body mass. Although the thermal conductance of desert rodents was lower than that of non-desert rodents (Goyal and Ghosh 1983), some of the higher values were reported among the desert rodents and gerbils (Webb and Skinner 1996). Haim and Izhaki (1993) found a significant positive correlation between resting metabolic rate and thermal conductance. Thus, because of the high BMR in our studies, Mongolian gerbils should have slightly higher thermal conductance than predicted. Weiner and Górecki (1981) reported that Mongolian gerbils have a high thermal conductance (regression equation slope between metabolic rates and Tas), and thus different from the results obtained by Robinson (1959) and Luebbert *et al.* (1979). They found that Mongolian gerbils have moderate thermal coefficients, similar to our results which were slightly higher than predicted values. The higher slope value in Weiner and Górecki's (1981) equation is perhaps because of their narrow Ta range (5–18°C). Interestingly, all the reports for Mongolian gerbils showed that their thermal conductance is not below the predicted values. Combined with the high higher critical temperature, our results support the prediction of Robinson (1959) that Mongolian gerbils might be active even during summer days. Direct field observations confirmed this conclusion (Agren *et al.* 1990; D. Wang, pers. obs.). This is also contrary to the observations of Weiner and Górecki (1981).

Mongolian gerbils are reported to have a high level of BMR, a moderate thermal conductance, a lower critical temperature of about 25°C, a higher upper critical temperature, and a high heat tolerance (Robinson 1959, McManus and Mele 1969, Luebbert *et al.* 1979). Our results are consistent with these conclusions. This study showed that there is not marked metabolic differences between field and laboratory gerbils. They showed however, somewhat different metabolic properties from hot desert rodents and field-caught Mongolian gerbils studied by Weiner and Górecki (1981).

In conclusion, the characteristics of thermal biology for *Meriones unguiculatus* are: both BMR and thermal conductance are higher than predicted values based on their body mass, a wide TNZ, low lower critical temperature (although higher than that reported by Weiner and Górecki 1981) and high upper critical temperature – all typical adaptive characteristics of both desert and arctic species. Our results support the conclusion of Robinson (1959) that *M. unguiculatus* is not a true desert form. Perhaps extreme severe climate is the main selective force faced by Mongolian gerbils during their evolution with their macroenvironments.

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