Standard Metabolic Rate and Thermoregulation in Five Species of Mongolian Small Mammals

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Summary. Oxygen consumption was measured over a range of ambient temperatures in 5 species of Mongolian small mammals: *Microtus brandti, Alticola argentatus, Phodopus sungorus, Meriones unguiculatus*, and *Ochotona daurica* (Tables 1 and 2). The measurements were made in the field, the animals being adjusted to natural environmental conditions. All the species studied coexist in the same arid steppe ecosystem. A variety of climatic adaptations was found.

Introduction

Preliminary studies were undertaken on the role of small mammals in an arid steppe ecosystem during the geographical expedition to Central Mongolia in summer 1977. Metabolic rates of the five most common species of mammals were measured in order to estimate population energy flows and food consumption (Weiner et al. 1982a). Four species of *Cricetidae* rodents: Brandt's vole, *Microtus brandti* Radde, 1861; Asiatic mountain vole, *Alticola argentatus* Severtzov, 1879 (Microtinae); Djungarian hamster, *Phodopus sungorus* Pallas, 1770 (Cricetinae); Mongolian gerbil, *Meriones unguiculatus* Milne-Edwards, 1867 (Gerbillinae); and a lagomorph, the Dahurian pika, *Ochotona daurica* Pallas, 1776 (Ochotonidae) are the subjects of this study.

For several years the Mongolian gerbil and Djungarian hamster have been used in the laboratory for physiological studies (e.g. Robinson 1959; McManus and Mele 1969; Mele 1972; Heldmaier 1975; Luebbert et al. 1979; Herberg et al. 1980, and others). However, the laboratory populations of these two species have been raised from only a few specimens imported from Asia (Schwentker 1964; Figala et al.

1973) and it is very likely that they differ in metabolic adaptations from the native Mongolian populations. The metabolism of the remaining three species apparently has never been studied.

The studies presented below were carried out in the field in the area of the original occurrence of the species. This made it possible to examine the adaptations to the local microenvironmental conditions and to compare the results obtained from the wild populations with those taken in laboratory investigations.

Materials and Methods

Study Area. The specimens were trapped in their natural habitats in eastern Mongolia, 150 km south from Ulan Bator (latitude 47°03′ N, longitude 107°38′ E, altitude 1,370 m above sea level). The area belongs to the zone of arid steppes with sagegrass and *Caragana*. The density of vegetation is variable, depending on exposition and local soil and water conditions. In the area of our studies the biomass standing crop during summer reached 200–290 g dry mass per square meter, but only 69–130 g dry mass × m⁻² seemed available for rodents (Weiner et al. 1982b). In spite of the moderate latitude, permafrost occurs in many places in the area (Klimek and Tserensodnom 1977) and the climate is severe. Average monthly air temperature in January is −24 °C and during the warmest month (July) it averages +16 °C. The yearly amplitude spans from −45 to +36 °C. Average temperatures on the ground surface during summer oscillates around 20 °C, below the surface at depths of 20, 50 and 100 cm the temperatures average 18, 16 and 14 °C, respectively. Thermal summer (av. daily temp. >15 °C) lasts for only 22 days; vegetation period (av. daily temperature >5 °C) for 141 days. Annual precipitation approaches 250 mm (90% falling during summer, when the humidity is very low and evaporation extremely rapid; Kowanetz and Olecki, 1980).

The species studied occupy slightly different habitats, but occur in close proximity to one other (within 12 square km; Weiner and Górecki 1982). The Brandt's voles live in large and very dense colonies in a shrub steppe with *Caragana microphylla*; the hamsters live in single burrows and prefer rather more arid patches with *Caragana pygmaea*. The numerous small tectonic scarpes built of basalt rocks and man-made cult piles of stones ('obo's') provide a favourite habitat for *Alticola argentatus*, a species which does not burrow (Obidina 1972). The pikas and gerbils live in small colonies with a preference for rather light, sandy soils. Both *Alticola*

Table 1. Metabolism and thermoregulation in 5 species of Mongolian small mammals

Age class (n)	Av. body weight (g)	Range (g)	Regression equation		
			$Y = mlO_2\,g^{-1}\,h^{-1}$: $t = °C$	r	S_{x_y}
Microtus brandti					
Adults (12)	40.2	33.2–41.5	$Y = 6.68 - 0.1716\,t$	−0.82	0.83
Subadults (15)	27.9	26.5–30.8	$Y = 8.07 - 0.2151\,t$	−0.89	0.70
Semiadults (20)	19.9	18.8–22.3	$Y = 10.44 - 0.2554\,t$	−0.83	0.78
Juveniles (14)	15.7	13.3–17.4	$Y = 12.29 - 0.3004\,t$	−0.87	0.88
Alticola argentatus					
Subadults (11)	37.4	33.6–45.1	$Y = 5.37 - 0.1356\,t$	−0.64	0.37
Phodopus sungorus					
Adults (9)	33.2	32.0–34.0	$Y = 6.12 - 0.1793\,t$	−0.91	0.60
Subadults (18)	22.2	21.3–23.9	$Y = 8.15 - 0.2378\,t$	−0.90	0.78
Juveniles (17)	14.3	11.0–17.2	$Y = 10.83 - 0.2941\,t$	−0.78	1.73
Meriones unguiculatus[a]					
Adults (11)	66.9	60.2–77.9	$Y = 5.67 - 0.3023\,t$	−0.88	0.57
Subadults (8)	32.1		$Y = 8.33 - 0.3955\,t$	−0.99	0.18
Ochotona daurica					
Adults (12)	127.7	113.3–156.2	$Y = 4.24 - 0.1190\,t$	−0.76	0.41

[a] See text for comments

and *Meriones* occur synanthropically, *Alticola* living in solid buildings and *Meriones* in felt tents (yurts) of the native inhabitants.

The rate of oxygen consumption was measured using a modified Kalabuchov-Skvortzov closed circuit respirometer, following the usual procedure (Górecki 1975). During a measurement the animals were kept in small cages ($4 \times 4 \times 9$ or $6 \times 6 \times 10$ cm for rodents and $11 \times 15 \times 32$ cm for pikas) and were placed in plexiglas chambers of 1.2 and 9.0 l capacity, respectively. The size of the cages allowed for postural changes of all the animals studied. However, for gerbils the space of $6 \times 6 \times 10$ cm might have been too small. A water bath provided constant temperatures in the range 5 °C to 30 °C. The temperature was measured inside the chambers. The field conditions did not allow for a larger range of experimental temperatures, nor for the measurements of body temperatures.

The animals were kept outdoors in large cages for a few days after they were captured. Before each experiment the animals were fasted for 4–6 h and weighed to the nearest 0.1 g.

All measurements were made between 10 a.m. and 2 p.m. and each trial lasted for approximately 30 min. The lowest records of oxygen consumption, taken during periods of complete rest, were used for subsequent evaluation. Oxygen consumption values were reduced to standard conditions.

Since the body temperatures of experimental animals could not be measured, it was difficult to determine properly the critical temperatures and the heat transfer coefficients (sensu: Calder and King 1974, or thermal conductance: Herreid and Kessel 1967). In the cases when the oxygen consumption dropped continuously with the rise of ambient temperature, linear regression equations were calculated for all the data within the range of temperatures studied. In other cases, separate curves were drawn for each individual and the temperature at which the curves started to level or rise, was considered as the lower limit of the thermoneutral zone.

Linear regressions were computed excluding the data recorded at temperatures above this limit. It is assumed that slope coefficients of these regressions represent heat transfer coefficients.

Results

The average values of the minimal metabolism of fasted animals (basal metabolic rate, BMR), as well as the regression equations referring to the thermoregulatory slopes are presented in Table 1, and in Fig. 1–5.

In *Microtus, Phodopus* and *Meriones* several age classes were distinguished (Table 1). In *Microtus* and *Phodopus* no distinct zones of thermoneutrality were observed within the range of temperatures applied (Figs. 1 and 3). On the other hand, fairly broad thermoneutral zones were found for *Alticola* and *Ochotona* (Figs. 2 and 5). The Mongolian gerbils showed the greatest metabolic response with falling T_a, of all the species studied (Table 1, Fig. 4). Below and above 15 and 18 °C, respectively, the metabolic rate increased sharply, and a temperature of about 25 °C appeared to be lethal for this species in the given experimental conditions (Fig. 4). Four animals died, and the remaining 6 displayed marked signs of a thermal discomfort.

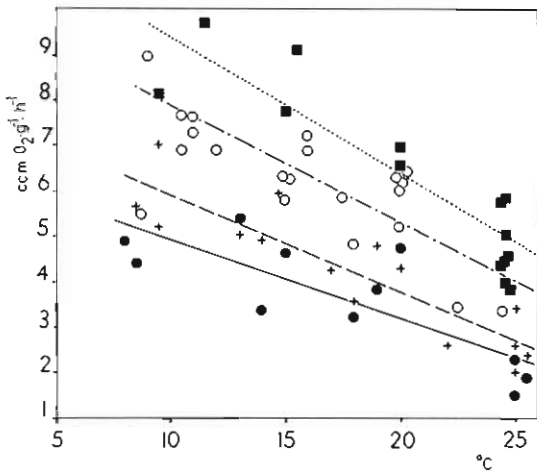The relatively wide range of the body weights of

Fig. 1. Oxygen consumption (mlO$_2$ g^{-1}h^{-1}) vs ambient temperature (°C) in *Microtus brandti*: —●—, adults (body weight 36.1 g); --+--, subadults (26.8 g); ·—·○·—·, semiadults (19.9 g); ---■---, juveniles (15.7 g)
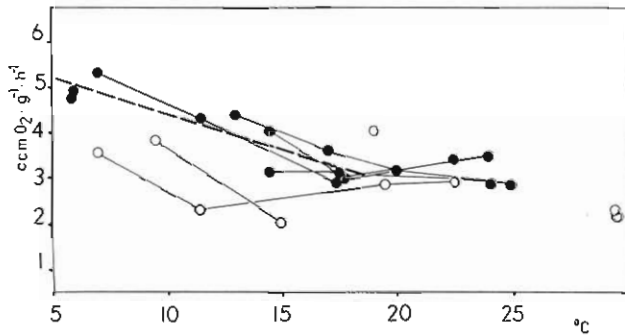

Fig. 2. Oxygen consumption (mlO$_2$ g^{-1}h^{-1}) vs ambient temperature (°C) in *Alticola argentatus*: ○, adults (52.9 g); ●, subadults (37.4 g)
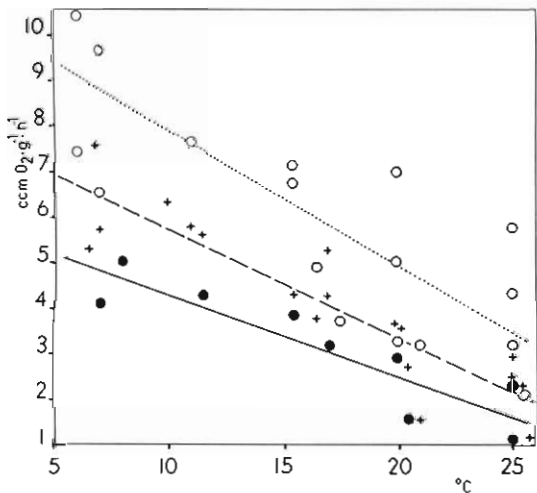
Fig. 3. Oxygen consumption (mlO$_2$ g^{-1}h^{-1}) vs ambient temperature (°C) in *Phodopus sungorus*: —●—, adults (33.2 g); --+--, subadults (21.2 g); ---○---, juveniles (14.3 g)
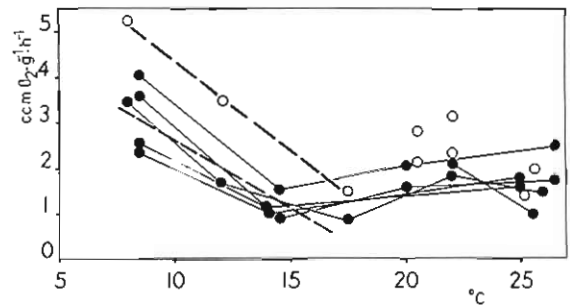

Fig. 4. Oxygen consumption (mlO$_2$ g^{-1}h^{-1}) vs ambient temperature (°C) in *Meriones unguiculatus*: ●—, adults (66.9 g); --○--, subadults (32.1 g)

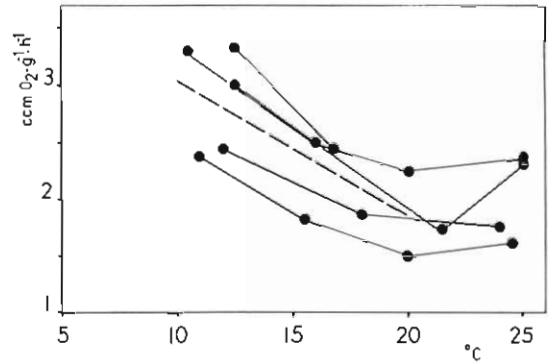Fig. 5. Oxygen consumption (mlO$_2$ g^{-1}h^{-1}) vs ambient temperature (°C) in *Ochotona daurica*

voles examined at near-basal conditions (13.3–41.5 g, $n=15$) made it possible to estimate the relationship between the body weight and the basal metabolism in this species. This relationship was almost linear:

$$BMR\ [mlO_2\ g^{-1}h^{-1}] = 65.8\ W^{-0.97} \qquad (r = -0.91).$$

A linear rather than hypometric function of basal metabolism in relation to body weight seems to be characteristic for growing animals (Adamson et al. 1969).

Discussion

The environmental conditions of the steppe zone of Central Asia are a severe challenge for small mammals in regard to their metabolic and thermoregulatory adaptations. One may presume that a hot and arid summer, scarce vegetation and the lack of water must result in adaptations typical of desert animals. On the other hand, a long and cold winter, the occurrence of permafrost, relatively high altitude, and again, a poor vegetation, more closely resemble alpine or arctic conditions. However, due to the variability of microhabitats in the study area, climatic adaptations typical of mammals found in either of the above
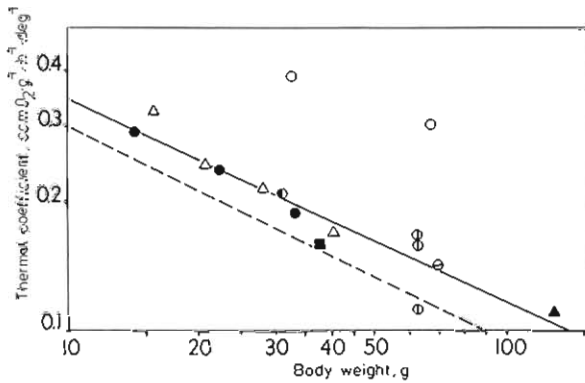
Fig. 6. A comparison of the thermal coefficients ($C = mlO_2 \, g^{-1} h^{-1}$ $°C^{-1}$) of Mongolian rodents with the general prediction (Hart 1971), and data from laboratory animals. $\triangle$, *Microtus brandti*; $\blacksquare$, *Alticola argentatus*; $\bullet$, *Phodopus sungorus*; $\circ$, *Meriones unguiculatus*; $\blacktriangle$, *Ochotona daurica*; (all data, this study) $\ominus$ Mongolian gerbil (Robinson 1959); Φ, Mongolian gerbil (Luebbert et al. 1979); $\mathbf{o}$, Djungarian hamster (Heldmaier 1975). ——, regression line for $C = 1.02 \, W^{-0.47}$, this study, gerbils excluded; ---, regression line for $C = 0.95 \, W^{-0.5}$ (Hart 1971)

Table 2. A comparison of the measured and predicted (Hart 1971) values of basal metabolic rates of Mongolian small mammals. Observed values are means $\pm$ S.E. (n)

Species	Body weight (g)	Basal metabolic rate ($mlO_2 \, g^{-1} h^{-1}$)	
		Observed	Predicted
Microtus brandti	40.3	1.91 ± 0.24 (3)	1.41
Alticola argentatus	37.7	3.21 ± 0.094 (9)	1.44
Phodopus sungorus	33.2	1.60 (2)	1.48
Meriones unguiculatus	66.9	1.15 ± 0.13 (5)	1.22
Ochotona daurica	127.7	1.95 ± 0.14 (7)	1.03

climatic zones could have been observed in the small mammals studied by us.

Our results are based on a rather small number of animals, and therefore the conclusions should be assessed accordingly. Nevertheless, our findings permit some suggestions concerning the metabolic responses of Mongolian small mammals to climatic conditions.

According to Scholander et al. (1950a, b), McNab (1968), Dawson (1955), Bradley and Yousef (1972), Hooper and El Hilahi (1972), Chaffee and Roberts (1971), and others, one can predict the following characteristics as typical for desert animals: (1) a relatively low BMR, (2) a steep thermoregulatory curve, (3) a narrow and hardly definable thermoneutral zone, and (4) a poor tolerance for high ambient temperatures. Arctic and alpine forms, on the other hand, will show the following adaptations: (1) a broad thermoneutral zone, (2) a basal metabolism higher than in the species of a temperature zone.

When comparing the metabolic rates of the five

species studied in Mongolia with the values predicted for small mammals from the general formula (Hart 1971), we find that *Microtus brandti, Ochotona daurica* and particularly *Alticola argentatus* show an increased basal metabolism (Table 2).

Figure 6 presents a comparison of the thermal coefficients of regression equations for metabolism vs temperature, in relation to body weight of the five species studied, and general formula for small mammals (Hart 1971). Brandt's voles, hamsters and pikas have slightly higher thermal coefficients than predicted ($C = 0.998 \, W^{-0.463}$ as compared to Hart's 1971, $C = 0.95 \, W^{-0.50}$, Fig. 6); only *Alticola argentatus* exhibits a heat transfer coefficient close to that predicted from Hart's formula.

This last species is an alpine form (Pokrovski and Bolshakov 1968), and in the steppes of eastern Mongolia it reaches probably its most southern and its lower limits of occurrence. *Alticola* shows very marked adaptations to a cold climate: a relativaly low critical temperature and a broad thermoneutral zone, elevated BMR and a low thermal coefficient (Tables 1 and 2, Fig. 6).

In *Ochotona daurica* the pattern of thermoregulation as well as a relatively high BMR (Fig. 5, Table 1) could lead to similar conclusions. However, comparing the metabolism of different species of *Lagomorpha*, one finds that an increased BMR is characteristic for the whole group (MacArthur et al. 1972; Wang et al. 1973). The BMR predicted for the Dahurian pika from the allometric regression calculated for lagomorphs ($BMR = 9.16 \, W^{-0.36}$, $r = -0.97$; 11 species with a body weight range 109–1,340 g; Weiner, unpublished) equals $1.59 \, mlO_2 \, g^{-1} h^{-1}$, close to our experimental findings (Table 1).

The BMR of Djungarian hamsters was found to be only slightly higher than predicted from Hart's (1971) formula, and somewhat lower than reported by Heldmaier (1975) for laboratory animals ($1.7 \, mlO_2 \, g^{-1} h^{-1}$). In addition the slope of the thermoregulatory line does not differ substantially from Heldmaier's (1975) estimate. This author has demonstrated an extreme cold tolerance in *Phodopus*, and has also established that the thermoneutral zone in this species falls at about 25 °C.

Also in Brandt's vole the BMR is slightly higher than the predicted value (Table 2), but since the zone of thermoneutrality has not been established for this species in the range of temperatures studied, it must be considered that the lowest level of metabolism in our experiments does not represent the true BMR. The slope of the thermoregulatory line in this species does not differ significantly from the general prediction (Fig. 6).

The results obtained for the Mongolian gerbils are uncertain. A steep thermoregulatory line and a

narrow thermoneutral zone might be indicative of desert adaptation in this species. However, the reaction of gerbils to changes in T_a in our experiments seems excessive. It is possible that it was influenced by the inability of gerbils to employ behavioral mechanisms of thermoregulation due to the small size of the experimental cages.

Our results differ considerably from those obtained by Robinson (1959) and Luebbert et al. (1979). Their gerbils had rather high BMR's when compared to other rodents of similar body weight (1.4 mlO_2 $g^{-1}h^{-1}$; Robinson 1959), a moderate slope of the thermoregulatory line (1.112–1.166 mlO_2 $g^{-1}h^{-1}$ $°C^{-1}$), and a lower critical temperature of about 25 °C (Luebbert et al. 1979; Martin et al. 1980). The laboratory gerbils could resist ambient temperatures as high as 40 °C (Robinson 1959) or 38 °C (Luebbert et al. 1979). McManus and Mele (1969) have also shown the ability of Mongolian gerbils kept in the laboratory, to tolerate both low (-20 °C) and high (up to $+35$ °C) ambient temperatures. Robinson (1969) did not describe his respirometric chambers, but the 770 ml jars used by Luebbert et al. (1979) probably provided the animals with space comparable to that of our chambers.

The results obtained by Robinson (1959) led him to the conclusion that *Meriones unguiculatus* is not a true desert form, and that gerbils might be active even during summer days. Our direct observations in the field do not support the conclusion concerning the possible diurnal activity of this species.

One of the possible reasons for the difference in the metabolic response of wild gerbils compared with laboratory animals, is that the whole population of laboratory gerbils was raised from only 11 pairs, imported to the USA in 1954. Since that time, these animals have been inbred (Schwentker 1964; Mele 1972), and there is no doubt that they differ substantially in their climatic adaptations from the wild population. Luebbert et al. (1979) have also demonstrated efficient temperature acclimation in this species. On the other hand, the narrow thermoneutral zone (13–18 °C) of wild Mongolian gerbils corresponds neatly with the summer night temperatures above ground, and to the average temperature at approximately 0.5 m below ground surface, which is probably the normal temperature of the burrow (Kowanetz and Olecki 1980).

It appears, that even in a small area in the arid steppe zone of continental Asia, a variety of climatic adaptations may exist among sympatric species of small mammals: alpine adaptations in *Alticola*, intermediate in *Phodopus*, and perhaps also some desert features in *Meriones*.

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