

## Seasonal variations in thermogenesis and energy requirements of plateau pikas *Ochotona curzoniae* and root voles *Microtus oeconomus*

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The seasonal patterns of nonshivering thermogenesis (NST), resting metabolic rate (RMR) at 15°C and 25°C in plateau pikas *Ochotona curzoniae* (Hodgson, 1858) and root voles *Microtus oeconomus* (Pallas, 1776), from the Qinghai-Tibetan plateau, were determined and thermal conductance was calculated. NST tended to increase during cold season for both species. No significant seasonal variations in NST were found in pikas (mean maximum in winter:  $3.46 \pm 0.19$  ml O<sub>2</sub>/g·h; minimum in spring:  $3.07 \pm 0.16$  ml O<sub>2</sub>/g·h). Voles increased NST significantly as the ambient temperature decreased, from the lowest, mean  $8.00 \pm 0.42$  ml O<sub>2</sub>/g·h, in summer to the peak in winter, mean  $11.29 \pm 0.44$  ml O<sub>2</sub>/g·h. RMR and thermal conductance were lower in winter than those in summer for both species (mean in summer at 25°C:  $4.96 \pm 0.35$  ml O<sub>2</sub>/g·h and  $0.509 \pm 0.027$  ml O<sub>2</sub>/g·h·°C for voles and  $2.11 \pm 0.09$  ml O<sub>2</sub>/g·h and  $0.179 \pm 0.003$  ml O<sub>2</sub>/g·h·°C for pikas, respectively; mean in winter at 25°C:  $4.22 \pm 0.26$  ml O<sub>2</sub>/g·h and  $0.379 \pm 0.012$  ml O<sub>2</sub>/g·h·°C for voles and  $1.55 \pm 0.06$  ml O<sub>2</sub>/g·h and  $0.123 \pm 0.003$  ml O<sub>2</sub>/g·h·°C for pikas, respectively). Voles lost body weights in winter whereas pikas kept their body weights. This suggests that alpine small mammals, which have high levels of metabolism and thermal conductance, mainly depend on increasing thermogenic capacities and insulation, decreasing energy expenditure per individual, augmented by behavioral adjustments to cope with cold temperatures of winter.

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*Key words:* *Ochotona curzoniae*, *Microtus oeconomus*, nonshivering thermogenesis, resting metabolic rate, thermal conductance

### Introduction

Nonhibernating small mammals, which survive in the cold seasons or regions, have presumably developed several anatomical, behavioral and physiological strategies to enhance survivorship. Increased thermogenic capacity and reduced heat loss are important pathways for wintering animals to maintain their constant body temperatures, especially for small mammalian herbivores (Wunder 1985, Merritt 1986).

Nonshivering thermogenesis (NST) is a heat production mechanism which liberates chemical energy due to processes which do not involve muscular contraction, mainly generated from brown adipose tissue (BAT) (Jansky 1973, Foster

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and Frydman 1978). The regulatory role of NST includes additional heat produced at ambient temperatures below the thermal neutral zone (Jansky 1973). The advantage of NST for small mammals is that a great amount of heat can be generated in a short period of time, without interfering with muscular function. Seasonal cycles of BAT and NST have been studied in several small mammal species, including *Peromyscus leucopus* (Lynch 1973, Zegers and Merritt 1988b), *P. maniculatus* (Zegers and Merritt 1988b), *Microtus ochrogaster* (Wunder 1984), *Clethrionomys rutilus* (Feist and Rosenmann 1976), *C. gapperi* (Merritt and Zegers 1991), *Phodopus sungorus* (Heldmaier and Steinlechner 1981), *Blarina brevicauda* (Merritt 1986), and *Sorex cinereus* (Merritt 1995). The controlling factors of NST for seasonally acclimatized small mammals were reported by many researchers (Heldmaier *et al.* 1985, Wunder 1985, Feist and Feist 1986, Zegers and Merritt 1988a, b, and others). The characteristics of NST in arid, semi-arid and subterranean small mammals and the ecological significance of NST were discussed by Haim and Izhaki (1989, 1993).

Plateau pikas *Ochotona curzoniae* (Hodgson, 1858) and root voles *Microtus oeconomus* (Pallas, 1776) are the dominant species in the alpine meadow on the Qinghai-Tibetan Plateau. Plateau pika is a burrowing steppe-dwelling endemic species to this area. Their social behaviors and life history traits were different from that nonburrowing talus-dwelling species such as *Ochotona princeps* (Smith 1988). Root vole has a wide geographical range, and inhabit vast areas of the northern parts of the Eurasiatic continent (Gębczyńska 1970). The two species are nonhibernating herbivores. Many physiological parameters such as basal metabolic rate (BMR), and the structure and component of BAT have been reported for both species (Jia and Sun 1986, Wang *et al.* 1979, Wang and Wang 1989, Wang *et al.* 1993). The two species showed high levels of metabolism and thermal conductance. There were seasonal variations in structure and components in BAT such as mitochondrial numbers and sizes, cristae numbers, lipid contents, and contents of tissue and mitochondrial protein. These results suggested that plateau pikas and root voles have high thermoregulatory and living costs, and the adjustments of thermogenic ability play important roles in adaptations to their environments.

In order to understand their adaptive strategies to the alpine environment, our objectives in the study were to examine the seasonal changes in NST, resting metabolic rate (RMR), and thermal conductance in plateau pikas and root voles. This is the first report on seasonal patterns of NST, combined with RMR and conductance to describe the survival tactics for representative of the genus *Ochotona*.

## Materials and methods

### Animals

Animals were live-trapped monthly at the Haibei Alpine Meadow Ecosystem Research Station, the Chinese Academy of Sciences (37°29'–37°45'N, 101°12'–101°33'E), located within the Menyuan County, Qinghai Province, with an altitude of about 3200–3500 m a.s.l., from May 1987 through April 1988.



Table 1. Average ambient, surface of ground, and subsurface below ground temperatures (in °C) on the alpine meadow from 1980 to 1990.

	Spring	Summer	Fall	Winter
Ambient				
Mean	-0.9	8.7	-1.3	-13.2
Mean Maximum	6.8	15.6	7.5	-2.2
Mean Minimum	-7.4	2.5	-8.0	-22.1
Surface				
Mean	4.0	13.6	2.0	-11.4
Mean Maximum	27.0	34.9	22.8	14.8
Mean Minimum	-7.6	1.8	-8.7	-25.5
Subsurface - mean at:				
15 cm	0.7	10.7	3.8	-8.5
20 cm	0.2	10.0	3.8	-7.8

The range of daily temperature between day and night is great and that within a year is relatively small. The plant growing period was about 130–140 days. Annual precipitation was 579.6 mm, and solar radiation was about 2523.0 h/year. Mean wind speed was 3.1 m/s. Most snowfall occurred from September to June. The main vegetation were alpine shrub and alpine meadow in the research station. *O. curzoniae* and *M. oeconomus* were trapped at the *Kobresia humillis* meadow and *Potentilla fruticosa* shrub, respectively. The temperatures (ambient, surface, and subsurface) were recorded at the meteorological station (the probes for ambient temperatures were about one meter above the ground and subsurface at the level of 15 cm and 20 cm below ground) of the research station. The temperatures of the study site were presented in Table 1 for comparisons with thermoregulatory parameters.

#### Measurement procedure

Body mass (Mb), sex and reproductive status of the captured animals were examined and recorded in the laboratory. Animals were weighed to the nearest 0.1 g. The metabolic rates (RMR and NST) of the captured pikas and voles were measured on the day of capture after at least 2 hours of stabilizing in laboratory (room temperature about 13°C).

Oxygen consumption was measured using the Kalabukhov-Skovortsov closed circuit respirometer (Górecki 1975). The chamber volume was 3 liters. Temperatures inside the animal chambers were measured and maintained with constant water bath ( $\pm 1^\circ\text{C}$ ). Mb and rectal temperatures (Tb) of animals were recorded before and after each experiment. Tb were measured by insertion of a thermistor (Model 95, Shanghai Medical Instruments Co.) to the rectum at the deep of about 1 cm.

RMR measured at 15°C and 25°C. Each measurement lasted for approximately 40 min after the animals adapted for about 1 h in the metabolic chamber. Following the RMR measurements at 25°C, the animals were immediately taken out of the chambers and injected with a mass-dependent dosage of norepinephrine (NE) subcutaneously (Heldmaier 1971), and placed back into the chamber. The test were lasted for further 45 min to 1 h. The maximum metabolic responses to NE were measured as the highest oxygen consumption (NST) in unanesthetized quiescent animals.

All measurements were made between 08.00 and 18.00 o'clock. RMR and NST were expressed as the unit of ml O<sub>2</sub>/g·h and corrected to STP conditions. For the seasonal variations in body weight, BMR and NST were corrected with the 2/3 power of body weight. Pregnant or lactating animals and young individuals (< 100 g for pikas and < 16 g for voles in summer and fall) were excluded in the experiments.

### Thermal conductance

The thermal conductance (C, ml O<sub>2</sub>/g·h·°C) were calculated as:

$$\text{Conductance} = \text{MR} / (\text{Tb} - \text{Ta})$$

where MR is metabolic rate (ml O<sub>2</sub>/g·h), Tb is body temperature (°C), and Ta is ambient temperature (°C) (McNab 1980).

### Statistics

The results of experiments conducted from June to August were pooled as summer data, September to November as fall, December to February as winter, and March to May as spring. Data were analyzed with one-way ANOVA and  $p < 0.05$  was taken to be statistically significantly different.

## Results

### Body weight

In plateau pikas, the mean body weight was significantly lower in summer than that in spring ( $p < 0.01$ ), and no significant differences existed among those in summer, fall and winter ( $p > 0.05$ ; Table 2). Root voles showed significant seasonal variations in body weight ( $p < 0.01$ ), declining from fall, to the lowest in winter ( $p < 0.01$ ; Table 3). In winter, their body weight was reduced to about 21% of that in summer.

Table 2. Average body weight (Mb), resting metabolic rate (RMR), nonshivering thermogenesis (NST), and thermal conductance in plateau pika *Ochotona curzoniae* at different seasons (mean ± SE). \* % predicted =  $(\text{NST}/30\text{Mb}^{-0.454}) \times 100$ .

Parameters	Spring	Summer	Fall	Winter
Mb (g)	137.4 ± 3.5	118.8 ± 4.7	128.7 ± 4.4	125.7 ± 3.5
RMR				
15°C ml O <sub>2</sub> /g·h	2.38 ± 0.11	2.67 ± 0.17	2.45 ± 0.17	2.37 ± 0.11
ml O <sub>2</sub> /g <sup>2/3</sup> ·h	12.78 ± 0.42	12.91 ± 0.86	12.36 ± 1.00	11.84 ± 0.57
ml O <sub>2</sub> /h	327.4 ± 8.2	316.9 ± 11.8	315.7 ± 21.2	297.6 ± 12.2
25°C ml O <sub>2</sub> /g·h	1.77 ± 0.08	2.11 ± 0.09	1.98 ± 0.08	1.55 ± 0.06
ml O <sub>2</sub> /g <sup>2/3</sup> ·h	9.12 ± 0.55	10.36 ± 0.50	9.98 ± 1.14	7.75 ± 0.49
ml O <sub>2</sub> /h	243.2 ± 21.1	250.7 ± 6.9	254.8 ± 16.0	194.8 ± 16.9
NST				
ml O <sub>2</sub> /g·h	3.07 ± 0.16	3.25 ± 0.11	3.38 ± 0.18	3.46 ± 0.19
ml O <sub>2</sub> /g <sup>2/3</sup> ·h	15.83 ± 1.20	15.95 ± 0.50	17.04 ± 0.40	17.30 ± 0.44
ml O <sub>2</sub> /h	422.1 ± 27.2	386.1 ± 16.2	435.0 ± 10.5	434.9 ± 20.7
% predicted*	95.6	94.8	102.2	103.5
Conductance				
15°C ml O <sub>2</sub> /g·h·°C	0.107 ± 0.005	0.114 ± 0.012	0.109 ± 0.008	0.106 ± 0.006
25°C ml O <sub>2</sub> /g·h·°C	0.148 ± 0.002	0.179 ± 0.003	0.153 ± 0.008	0.123 ± 0.003
Tb (°C)	37.1 ± 0.2	37.3 ± 0.2	37.7 ± 0.2	37.5 ± 0.2
Sample size	53	44	41	45



**Resting metabolic rate (RMR)**

There were no significant seasonal changes in RMR in pikas and voles at 15°C (Tables 2 and 3). At 25°C, the RMR showed significant seasonal variations for both pikas and voles ( $p < 0.01$ ; Tables 2 and 3). For pikas the trend was summer > fall > spring > winter, and for voles it was fall > summer > spring > winter. The RMR was reduced in winter by 36% and 18% for pikas and voles respectively, when compared with summer data. After removing the effect of body weight, the similar variational trend were seen for both voles and pikas.

The RMR per individual (mlO<sub>2</sub>/h) for both species reached the lowest point in winter. RMR for pikas at 15°C and 25°C in winter was only 94% and 77% of the summer values respectively, and 84% and 70% for voles.

**Nonshivering thermogenesis (NST)**

Although the NST of pikas increased in winter 6% from summer to winter, but the difference was not significant ( $p > 0.05$ ; Table 2). The voles showed significant seasonal changes in NST ( $p < 0.01$ ), the trend was winter > fall > spring > summer. After removing the effect of body weight, the variational patterns were not changed for both species. The NST (expressed as ml O<sub>2</sub>/h) increased 41% from summer to winter in voles and 13% in pikas (Tables 2 and 3).

Table 3. Average body weight (Mb), resting metabolic rate (RMR), nonshivering thermogenesis (NST), and thermal conductance in root vole *Microtus oeconomus* at different seasons (mean ± SE). \* % predicted =  $(\text{NST}/30\text{Mb}^{-0.454}) \times 100$ .

Parameters	Spring	Summer	Fall	Winter
Mb (g)	24.5 ± 1.2	23.7 ± 1.3	20.2 ± 0.8	19.6 ± 0.8
<b>RMR</b>				
15°C ml O <sub>2</sub> /g · h	6.51 ± 0.36	6.15 ± 0.25	6.70 ± 0.57	6.70 ± 0.41
ml O <sub>2</sub> /g <sup>2/3</sup> · h	18.89 ± 2.49	17.65 ± 1.13	18.22 ± 0.88	18.05 ± 1.18
ml O <sub>2</sub> /h	159.5 ± 12.4	156.8 ± 4.1	135.3 ± 8.5	131.3 ± 8.7
25°C ml O <sub>2</sub> /g · h	4.50 ± 0.28	4.96 ± 0.35	5.18 ± 0.25	4.22 ± 0.26
ml O <sub>2</sub> /g <sup>2/3</sup> · h	13.06 ± 0.45	14.23 ± 0.15	14.09 ± 1.01	11.37 ± 0.53
ml O <sub>2</sub> /h	110.3 ± 14.3	117.6 ± 8.8	104.6 ± 10.3	82.7 ± 6.3
<b>NST</b>				
ml O <sub>2</sub> /g · h	9.89 ± 0.59	8.00 ± 0.42	10.05 ± 0.56	11.29 ± 0.44
ml O <sub>2</sub> /g <sup>2/3</sup> · h	28.73 ± 1.18	22.96 ± 0.53	27.37 ± 0.29	30.44 ± 1.14
ml O <sub>2</sub> /h	242.4 ± 17.8	189.6 ± 11.8	202.9 ± 9.1	231.3 ± 8.5
% predicted*	140.9	112.2	131.1	145.3
<b>Conductance</b>				
15°C ml O <sub>2</sub> /g · h · °C	0.326 ± 0.030	0.305 ± 0.025	0.321 ± 0.025	0.331 ± 0.032
25°C ml O <sub>2</sub> /g · h · °C	0.481 ± 0.011	0.509 ± 0.027	0.482 ± 0.035	0.379 ± 0.012
Tb (°C)	35.0 ± 0.3	35.1 ± 0.4	35.8 ± 0.1	35.7 ± 0.3
Sample size	45	49	41	36

According to the allometric equation between body mass and NST,  $NST = 30Mb^{-0.454}$ , described by Heldmaier (1971), the NST of pikas was close to the predicted value, and the NST in voles was significantly higher than the theoretical value (Tables 2 and 3).

#### Thermal conductance

The thermal conductance showed no significant seasonal changes at 15°C in both pikas and voles ( $p > 0.05$ ; Tables 2 and 3), but changed significantly at 25°C ( $p < 0.01$ ). The trend was summer > fall > spring > winter for both species (Tables 2 and 3). From summer to winter, the conductance was reduced 46% in pikas and 34% in vole.

#### Body temperature (Tb)

No significant seasonal variations of Tb were recorded in both species ( $p > 0.05$ , Tables 2 and 3) and the Tb in voles was relatively lower (Table 3).

### Discussion

Winter survival of small nonhibernating mammals is affected by their feeding activity and the microclimates in their burrow systems. For voles and pikas, although the ambient temperatures were very low during winter, both species lived in their burrows and reduced their foraging activities. The temperatures of surface of ground and subsurface below ground were higher (Table 1). Animals lived in cold regions could reduce body weight and adjust their metabolism for their wintering (Wunder 1985, Merritt 1986).

Our results indicated that RMR showed no significantly seasonal changes at 15°C, however, the RMR was lower at 25°C in winter, and the energy expenditure per individual was decreased during the winter, for both pikas and voles. This suggested that small mammals on alpine meadows do not depend on increasing the RMR in winter for their wintering, but reduce the individual energy expenditure to resist the cold. Similar results were reported for *Peromyscus leucopus* and *P. maniculatus* (Zegers and Merritt 1988a), and *Clethrionomys gapperi* (Merritt and Zegers 1991).

It was interesting that RMR of root voles in Poland was lower in winter than that in any other seasons (Gębczyńska 1970). The RMR in our voles were similar to that reported by Gębczyńska (1970) in summer, but higher in winter. The difference might be due to the difference in environmental characteristics, such as lower ambient temperatures of our research site, higher altitude (3200 m vs 120 m a.s.l.), and open meadow habitat vs woods. Gębczyńska (1970) compared the energy requirements of root voles in Alaska taiga and Poland and suggested that root voles have similar physiological characteristics over their entire range. Our results of RMR in root voles of the alpine meadow did not support this hypothesis.

Nonshivering thermogenesis enables small mammals to increase heat production rapidly during cold exposure (Wunder 1984, 1992). The ability for NST is



generally considered to be an evolutionary adaptation, because it allows small mammals to remain normothermic while active in the cold (Bartholomew 1982, Richardson *et al.* 1994). Increase of NST capacity (NST-BMR) in winter was an important adaptational strategy for rapid heat production and was documented in some species of small mammals (Table 4). Lynch (1973) showed that *Peromyscus leucopus* caught in fall and winter exhibited an average increase of 8.0 ml O<sub>2</sub>/g·h above BMR after NE injection, NST capacity in January increased by about 100% relative to July. Feist and Rosenmann (1976) revealed that NST capacity in *Clethrionomys rutilus* increased greatly from summer to winter – in the coldest winter NST was about 10 times the BMR. Wunder (1984) found that in *M. ochrogaster* a 35% increase in NST capacity during winter as compared to summer rates. Heldmaier *et al.* (1982) showed that in *Phodopus sungorus* NST capacity for winter represented a 71% increase over the low value in summer. Merritt (1986) tested wild acclimatized *Blarina brevicauda* on a year-round basis and showed a 54% increase in NST capacity in January relative to August. NST increase in winter were also reported for *Peromyscus maniculatus* (Zegers and Merritt 1988a, b), *C. glareolus* (Klaus *et al.* 1988), *C. gapperi* (Merritt and Zegers 1991), *Sorex cinereus* (Merritt 1995), and other species. The results of our study in pikas and voles revealed similar variational patterns to the temperate zone and northern region species. In *O. curzoniae* mean NST capacity increased by 88% in winter relative to summer values and NST in January, the coldest month, was about 2.8 times of the BMR (BMR value according Wang *et al.* 1979). In *M. oeconomus* mean NST capacity in winter represented 101% higher than that recorded in summer and NST was about 3.7 times the BMR in January (BMR value according to Jia and Sun 1986). Previous studies indicated that numbers of mitochondrial cristae and weight of BAT, the dominant site for NST, of pikas and voles increased during the winter (Wang and Wang 1989). Tissue and mitochondrial protein contents also increased in the cold season (Wang *et al.* 1993), in accordance with the NST changes.

Increased insulation coupled with reduced body weight could cause animals to decline their total energy requirements during the cold season (Bozinovic *et al.* 1990, Merritt and Zegers 1991, Wunder 1984). However, plateau pikas showed no reduction in body weight in winter, indicating that declining body weight is not the only means to save heat for this species in the cold season. The thermal conductance at 25°C reduced to a lower level in winter caused by increasing the insulation for both species. Thus plateau pikas perhaps depend mainly on increasing the insulation to reduce heat loss. The root voles, however, combine insulation and declined body weight to reduce the energy expenditure. From the perspective of seasonal changes of energy expenditure per individual, both species reduced the energy requirements and increased the NST capacities in winter (Table 2 and 3). This suggested that increasing in thermogenic abilities is an important aspect to compensate the higher levels of thermoregulatory cost for alpine small mammals. It should be pointed out that the body weights for voles and pikas were adult mean values. The best way to track body weight changes is

Table 4. The maximum and minimum NST in some small mammals. Sources of data: *B. brevicauda* (Pennsylvania, USA) and *S. cinereus* (Pennsylvania, USA) from Merritt (1986, 1995); *C. rutilus* (Alaska, USA) from Feist and Rosenmann (1976); *C. gapperi* (Pennsylvania, USA) from Merritt and Zegers (1991); *P. leucopus* (Iowa, USA) from Lynch (1973); *M. ochrogaster* (Colorado, USA) from Wunder (1984); *P. sungorus* (Siberian species, bred and raised in Germany) from Heldmaier *et al.* (1982); the arid and semiarid species of *O. irroratus* from Haim and Fairall (1987); *Spalax ehrenbergi* from Haim *et al.* (1984); *Gerbillus pyramidum*, *Gerbillus gerbillus*, *Sekeetamys calurus*, *Rhabdomys pumilio* and *Acomys russatus* quoted from Haim and Izhaki (1993); alpine meadow species of *M. baileyi* from Su *et al.* (1991); *O. cansus* from Wang *et al.* (1991b); *M. oeconomus* and *O. curzoniae* from the present studies (August value for summer minimum NST and January value for winter maximum NST). <sup>a</sup> Percent =  $\text{NST} \times 100/30 \text{ Mb}^{-0.454}$ , <sup>b</sup> Percent =  $(\text{NST/BMR}) \times 100/13.9 \text{ Mb}^{-0.312}$

Species	Season	Mb (g)	NST (ml O <sub>2</sub> /g·h)	Percent <sup>a</sup>	NST/BMR	Percent <sup>b</sup>
<i>Blarina brevicauda</i>	summer	18	6.4	79.2	2.3	40.7
	winter	19	9.9	125.6	2.7	48.6
<i>Sorex cinereus</i>	summer	3.4	10.7	62.3	1.8	18.6
	winter	3.0	14.6	80.6	2.1	21.2
<i>Clethrionomys rutilus</i>	summer	27.8	6.8	102.6	4.4	89.2
	winter	14.4	18.7	209.2	10.1	166.8
<i>Clethrionomys gapperi</i>	summer	31	5.1	80.8	1.8	38.7
	winter	22	9.5	128.4	2.8	52.7
<i>Peromyscus leucopus</i>	summer	23.5	6.5	90.8	2.6	50.0
	winter	22.5	11.0	150.7	3.7	70.2
<i>Microtus oeconomus</i>	summer	25.4	7.0	101.3	2.0	39.4
	winter	20.9	12.5	165.6	3.7	68.6
<i>Microtus ochrogaster</i>	summer	47.4	2.6	50.0	1.5	34.0
	winter	38.5	3.5	61.2	1.6	36.0
<i>Phodopus sungorus</i>	summer	40.5	7.0	125.2	4.2	95.7
	winter	26.2	12.0	176.2	8.2	163.2
<i>Ochotona curzoniae</i>	summer	114.3	3.4	97.4	1.6	50.4
	winter	126.7	4.1	123.1	2.8	91.1
<i>Ochotona cansus</i>	summer	56.2	4.4	92	1.5	28
<i>Myospalax baileyi</i>	summer	225.3	1.6	61.6	1.2	45.6
<i>Otomys irroratus</i>	summer	102.4	2.4	65.4	3.1	94.4
<i>Spalax ehrenbergi</i> (2n = 60)	-	133.6	0.92	28	3.3	109
<i>Gerbillus pyramidum</i>	-	53	3.26	66	2.6	64
<i>Gerbillus gerbillus</i>	-	29.7	4.15	64	2.9	60
<i>Sekeetamys calurus</i>	-	56.9	2.26	47	2.9	74
<i>Rhabdomys pumilio</i>	-	39.6	4.00	71	5.2	118
<i>Acomys russatus</i>	-	60	4.10	88	5.8	149

to follow individuals through consecutive trapping periods for the life of the individuals (Merritt 1995). The phenomena of overwinter weight decline has been well studied in micotine rodents and shrews and is referred to as Dehnel's phenomena. Merritt (1986, 1995) and Merritt and Zegers (1991) have provided a thorough review of overwinter weight decline in small mammals.



Environmental temperature at alpine meadow was low (minimum about  $-35^{\circ}\text{C}$ , annual mean  $-2^{\circ}\text{C}$ ). Animals lived there exposed to cold stress everyday. Hence, both pikas and voles deposited BAT whole year (Wang and Wang 1989) and maintained NST at a relatively high level throughout the whole year, even in the relatively warm summer. This is different from *O. princeps* which lived in cold macro-environments and at about 3660 m elevation in Colorado, USA and some other species that no BAT deposited in summer and/or in winter when there is long-time snow cover (Wunder 1992). In fall, when it is cold, *O. princeps* may use BAT, but once snow accumulated and insulates their habitat and dens they lose the BAT as they lived in an effectively warm environment. And they are well insulated and have increased BMR (Wunder 1992). Alpine meadow rarely covered by snow. However, snow cover may last for a long period, *O. curzoniae* starved to death because they do not cache food, not like *O. princeps* which storing hay and feeding under snow cover in winter, must forage on the snow surface. The temperature difference between day and night in alpine meadow was also constraint for the animal's survival. Previous studies indicated that pikas and voles have high levels of BMR (Jia and Sun 1986, Wang *et al.* 1979), 144–208% and 205–235% of expected values based on Kleiber (1961;  $3.4\text{Mb}^{-0.25}$ ), respectively. To maintain a high BMR level at the relatively high daily temperature, especially in summer, it is no benefit for their surviving. So animals developed the forms of higher levels of thermal conductance (135–193% for pikas and 126–158% for voles of expected values,  $1.0\text{Mb}^{-0.5}$ , Herreid and Kessel 1967; see Jia and Sun 1986, Wang *et al.* 1979), to cope with the occasionally high temperature at day time even in winter, during their thermoregulatory evolution. Thus, animals could reduce the double pressure of severe cold at night and relatively hot times at day.

Although the thermal conductance at  $15^{\circ}\text{C}$  did not change significantly in winter for both pikas and voles, their total energy expenditure declined (Tables 2 and 3), therefore increased the insulation, and elevated in NST capacity further enhanced cold resist ability in both species. The vole reduced the body weight in winter, and kept high thermogenic level to maintain a relative small body, thus the cold endurance ability was increased. Bozinovic and Merritt (1992) studied the thermal conductance of *Blarina brevicauda* and found that the shrews increased insulation probably by increasing hair density and/or length during winter, and concluded that these mechanisms may be useful in energy conservation and compensate for the large difference between body and ambient temperatures during winter. Heldmaier and Steinlechner (1981) suggested that the combined strategy of small body weights in winter and improvement of fur thermal insulation may indeed be a widely used concept for seasonal acclimatization in small mammals. Gębczyńska (1970) found that root voles in Poland increased their body weights in winter, contrasting to our results. No available data of NST and thermal conductance in root vole of other places were compared.

Haim and Izhaki (1989, 1993) analyzed the ecological significance of NST in rodents and indicated that besides body weight, habitat, habits and phylogeny also played important roles in producing heat by NST, and also concluded that rodents

with low BMR levels or with high conductance values are expected to have a high regulatory NST magnitude (NST/BMR), while rodents with high BMR values or low conductance values are expected to have a low regulatory NST magnitude. According to this point of view, it was difficult to expect the NST levels of the alpine small mammals, which have both high levels in BMR and conductance. Our results showed that plateau pikas and root voles have relatively higher levels of NST compared with other species listed in Table 4 except the ones distributed in extreme cold regions such as *C. rutilus* (Alaska) and *P. sungorus* (Siberian steppe). Compared with that of arid and semi-arid species, pikas and voles had higher levels of NST and relative lower values of NST/BMR, because pikas and voles had higher levels of BMR than arid and semi-arid species. The fossorial mammals possess lower levels of NST, even in alpine meadow, eg *Myospalax baileyi* (Table 4), undependently whether they had lower values of BMR or not. The conclusion was the same when compared *Myospalax baileyi* in alpine meadow and *Spalax chrenbergi* in arid and semi-arid habitats and was further confirmed by comparing the percentage of expected values based on their body weight (Table 4). Northern temperate zone and arctic small mammals have higher percentages of expected values in NST than arid and semi-arid species. *M. oeconomus* have higher levels of NST and NST/BMR and percentages of their expected values than *M. ochrogaster*. It was also showed that alpine small mammals (*M. oeconomus*, *O. curzoniae*, *O. cansus*, and *Myospalax baileyi*) have lower NST/BMR ratio and percentages of expected values because of their high levels of BMR, compared with arid and semi-arid species. This phenomena were also found in shrew species which have high levels of BMR such as *B. brevicauda* and *S. cinereus* (Table 4).

In winter, huddling and nest building were also an important means to reduce the energy expenditure in root voles (Wang *et al.* 1991a, b). For instance, four voles huddling could reduced energy expenditure by 43% compared with single individual at 10°C in October and five individuals huddling could reduced energy expenditure by 32% at 5°C in December. The social thermoregulation in root voles was also recorded in Poland (Gębczyńska 1970). Reduction of the activity time during cold season and living in the relatively warmer burrow could decline the cold stress for both species. We have no data about social thermoregulation in pikas. We do observed that pikas in cages huddled and built simple "nest" and "burrow system" by using dried hay during winter in the cold room (room temperature as same as outside). Pikas's huddling seemed relative "loosing", usually three to five individuals distributed in the four corners of the cages, differing from voles which all individuals huddled in a communal nest.

In conclusion, alpine small mammals mainly depend on increasing thermogenic capacities and insulation, adjusting energy requirements, and accompanying by behavioral adjustments to survive the cold winter. Overwinter body decline may be an important adaptive strategy for root voles to enhance their winter survival.

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