



Comparative Study of Thermoregulatory and Thermogenic Characteristics of Three Sympatric Rodent Species: The Impact of High-temperature Acclimation

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ABSTRACT

Background: Ambient temperature is one of the important factors affecting the survival of small mammals in the wild and different animals have different ways of regulating when face the same environmental temperature and different temperatures will also make the same species adjust the energy budget. Therefore, it is helpful to further understand the survival and adaptation patterns of different animals to study the different adjustment modes of animals in the same region in the face of high temperature environment.

Methods: In the present study, three rodents, *Apodemus chevrieri*, *Eothenomys miletus* and *E. olitor*, were exposed to a high temperature (T_a) of 30°C for 28 days. And then body mass, body temperature (T_b), resting metabolic rate (RMR) and thermal conductance (C) were measured at T_a from 5°C to 35°C.

Result: The results showed that T_b of all three mammals increased significantly with the increase of T_a . And thermal neutral zones (TNZ) among three animals were all 25°C-30°C. Moreover, RMR increased with the increase of T_a above the upper critical temperature. Within the range of 30°C to 35°C. C values in three mammals maintained stable within the T_a of 5°C-25°C, which increased with the increase of T_a above 25°C. All of the results suggested that three sympatric rodent species raised their T_b , narrowed their TNZ and changed C values to adapt to the high temperature. Moreover, change amplitudes of thermoregulation characteristics in *E. olitor* were small, indicating that *E. olitor* may have the strong adaptability under high temperature acclimation.

Key words: *Apodemus chevrieri*, *Eothenomys miletus*, *Eothenomys olitor*, Resting metabolic rate, Thermoregulation.

INTRODUCTION

Mammals can enhance their adaptability to natural environmental variations by adaptively regulating physiological characteristics, thereby increasing their survival ability in the field (Jia *et al.*, 2024). Environmental factors such as temperature, food resources and photoperiod can influence the energy balance of mammals in the wild. Among them, temperature is extremely important for their survival and adaptation. Different environmental temperatures force small mammals to choose different thermoregulation modes (Zhang *et al.*, 2012). Thermoregulation is a significant research topic in physiological ecology. Numerous studies have shown that the body temperature of animals is related to the change in the external environment temperature and the heat exchange between the body surface and the surrounding environment takes place in the form of radiation, convection, conduction, or evaporation (Li *et al.*, 2010). Therefore, whether small mammals can maintain a stable body temperature affect their survival adaptations (Zhu *et al.*, 2008).

Thermal neutral zone (TNZ) refers to the temperature range within which metabolic rate does not vary with environmental temperature changes and the metabolic rate is lowest in this temperature range (Kaikaew *et al.*, 2017). It is advantageous for animals' growth and development (Mitchell *et al.*, 2018). Because within the TNZ, animals do not need to expend additional energy to maintain stable body temperature, thereby reducing energy consumption,

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foraging time and lowering the risk of predation (Mitchell *et al.*, 2018). Basic metabolic rate (BMR) is the lowest energy expenditure used by animals to maintain basic physiological functions, which is the metabolic rate in TNZ (Kaikaew *et al.*, 2017; Zhu *et al.*, 2022). Thermal conductance (C) value is closely related to environmental temperature, which is one of the factors that affect animal energy consumption (Naya *et al.*, 2013). Previous researches on energy metabolism in small rodents mainly focus on the effects of cold temperatures. For example, body temperature in *Lasiopodomys brandtii* decreased significantly in the first two hours after cold exposure, while it remained relatively stable under cold acclimation for 28 days (Hou *et al.*, 1999). Thermogenic capacity and self maintenance energy consumption of *Meriones*

unguiculatus increased under low temperature, leading to an increase in energy intake (Li *et al.*, 2004). As global environmental temperatures continue to rise (Qin, 2014; Zhou and Tang, 2023), it is significant to study how small mammals regulate their physiological characteristics to adapt to high-temperature environments (Guo *et al.*, 2020; Khakisahneh *et al.*, 2020).

Hengduan Mountain is a typical north-south mountain peak in China, with unique geological features and rich biodiversity (Jia *et al.*, 2024). Yunnan Red-backed Vole (*Eothenomys miletus* and *E. olitor*) were native species of this regions, belonging to the Cricetidae. *Eothenomys* species lives in camp caves and mainly feeds on plants in the families of Poaceae, Asteraceae and Leguminosae (Yan and Zhu, 2023; Zhu and Wang, 2015; Zhu *et al.*, 2014a). *Apodemus chevrieri* (Chevrier's Field Mouse), a typical Palearctic realm species, belongs to the Murinae. *Apodemus* species prefers to eat seeds (Zhu *et al.*, 2014b). Our previous results showed that there were species differences in thermoregulation and thermogenic characteristics among the three rodents. Body temperature and BMR of the two *Eothenomys* species were found to be lower than those of in *A. chevrieri*, while the TNZ exhibited narrow ranges in all three animals (Zhu *et al.*, 2008; Zhu *et al.*, 2013). However, there have been no reports on the thermoregulation of three sympatric rodent species under high-temperature acclimation. Therefore, the objective of this study was to investigate the physiological temperature regulation mechanisms employed by *A. chevrieri*, *E. miletus* and *E. olitor* in order to adapt to high temperature conditions, as well as determine which rodent species exhibits a stronger capacity for thermal adaptation.

MATERIALS AND METHODS

Animal collection

All three species of animals were captured in Yunlong County (98°52'-99°46'E, 25°28'-26°23'N, 2335 m, the annual precipitation is 849.4 mm and the average annual temperature is 16°C) in 2023 within some sampling areas of (20 m×20 m), using rat cages to capture the animals (Yang and Zhu., 2023). After disinfecting and killing fleas, they were brought back to the animal room of Yunnan Normal University and single cage feeding, temperature 25±1°C, photoperio12L:12D. Food (standard mice chow pellets, produced by Kunming Medical University, Kunming, China) and water were provided *ad libitum*. Rodents used in the present experiment were not pregnant, lactating, or young individuals. This experiment was conducted at Yunnan Normal University, starting in 2023 and lasting for three months. *A. chevrieri* (n = 15, ♀:♂ = 10:5, average body mass is 30.38 g), *E. miletus* (n = 14, ♀:♂ = 9:5, average body mass is 39.00 g) and *E. olitor* (n = 12, ♀:♂ = 6:6, average body mass is 34.74 g) were adapted in the animal room for one month and then acclimated for 28 days under the conditions of 30°C and 12L: 12D. After high temperature

acclimation, body mass, body temperature (T_b) and resting metabolic rate (RMR) of the three animals were measured and the thermal conductance was calculated (McNab, 2009). After the experiment, all animals were returned to normal ambient temperature (25°C) for feeding. All animal procedures were within the rules of Animals Care and Use Committee of School of Life Sciences, Yunnan Normal University. This study was approved by the committee (13-0901-011).

Determination of T_b , RMR and C

Randomly select 7-8 animals of each species on 08:00 am, body mass, T_b and RMR were measured in ambient temperature (T_a) of 5°C, 10°C, 15°C, 20°C, 25°C, 27.5°C, 30°C, 32.5°C and 35°C, respectively. Body mass was measured using an analytical balance (AB204-S, Switcherland, accuracy of 0.01 g). T_b was measured using a digital thermometer (XGN-1000T, Beijing Yezhiheng Technology Co. Ltd., accuracy of 0.1°C). RMR was measured by an 8 channel FMS portable respiratory (Sable Systems International, Inc., USA). And the animals were fasted for 2-4 hours before the measurement, place the animal in a metabolic chamber (1.5 L), air flow was 200 mL/min, the experimental temperature was controlled at 25±0.5°C using an artificial climate box (SPX-300 type, Shanghai Boxun Medical Equipment Factory, China), animals adapt to a resting state in the metabolic chamber for 30 minutes, open the Expe Data software to measure metabolic rate for 4 rounds, with each round lasting 15 minutes. Data was recorded every 5 minutes for a total of 60 minutes. After the experiment, export the experimental data and select the lowest oxygen consumption as its RMR, then using Expe Data analysis software for data conversion and analysis. C value was calculated according to the McNab formula:

$$C = \frac{\text{RMR}}{(T_b - T_a)} \quad (\text{McNab, 2009}).$$

Statistical analysis

Data were analyzed using SPSS 26.0 software (SPSS Inc., Chicago, IL, United States). Before all statistical analyses, data were examined for normality and homogeneity of variance using Kolmogorov-Smirnov and Levene tests, respectively. Differences in physiological indicators between the different sexes of three animals were not significant, so all data were combined and counted. RMR and C were all analyzed using one-way ANOVA. And the relationship between T_b , RMR, C and T_a was analyzed simple linear regression analysis. Results were presented as means ± SEM and P<0.05 was considered statistically significant.

RESULTS AND DISCUSSION

Body temperature

T_b of three animals increased with the increase of T_a and showed significantly positive correlations with T_a . The linear

regression equation for *A. chevrieri* was $T_b = 33.830 + 0.110 T_a$ ($F = 185.075$, $P < 0.01$, Fig 1A) and for *E. miletus* was $T_b = 32.236 + 0.164 T_a$ ($F = 361.916$, $P < 0.01$, Fig 1B); and for *E. olitor* was $T_b = 33.625 + 0.094 T_a$ ($F = 90.939$, $P < 0.01$, Fig 1C). Within the TNZ, T_b of *A. chevrieri*, *E. miletus* and *E. olitor* were $36.90 \pm 0.10^\circ\text{C}$, $36.49 \pm 0.17^\circ\text{C}$ and $36.44 \pm 0.13^\circ\text{C}$, respectively (Fig 1).

Thermogenic effect of T_a is considered to be the most influential and direct factor in inducing significant physiological changes in animal behavior and energy balance, particularly in animals exposed to cold or high temperatures (Scholander *et al.*, 1950). Maintenance of mammalian body temperature depends on the metabolic rate levels and thermal conductance (McNab, 2009). Under high temperature acclimation, *Tupaia belangeri* adapts to its environment by increasing T_b (Feng *et al.*, 2022). When mice were acutely exposed to an environment of 42°C , their T_b raised sharply (Miova *et al.*, 2008). In our previously

study, T_b in *E. miletus*, *A. chevrieri* and *E. olitor* decreased under cold exposure or in winter (Zhu *et al.*, 2009; Zhu *et al.*, 2008; Zhu and Wang, 2015). In this study, high temperature acclimation increased T_b of the three animals, which may be an adaptation strategy for high temperature, increasing T_b was beneficial for narrowing the difference with T_a while increasing heat dissipation and reducing metabolic rate (Yang *et al.*, 2008; Vejmlík *et al.*, 2021). Moreover, all three species increased their T_b under high temperature conditions, reflecting convergent adaptation (Table 1). Comparing the amplitude of T_b changes of three animals based on the slope of the linear regression equation, *E. olitor* was less affected by high temperature, which may be related to the thicker fur, which increased its heat insulation effect (Yang *et al.*, 2021). Although *E. olitor* and *E. miletus* belong to the same genus, however, the range of T_b change of *E. olitor* was lower than that of *E. miletus*, which may be related to the habitat environmental temperature

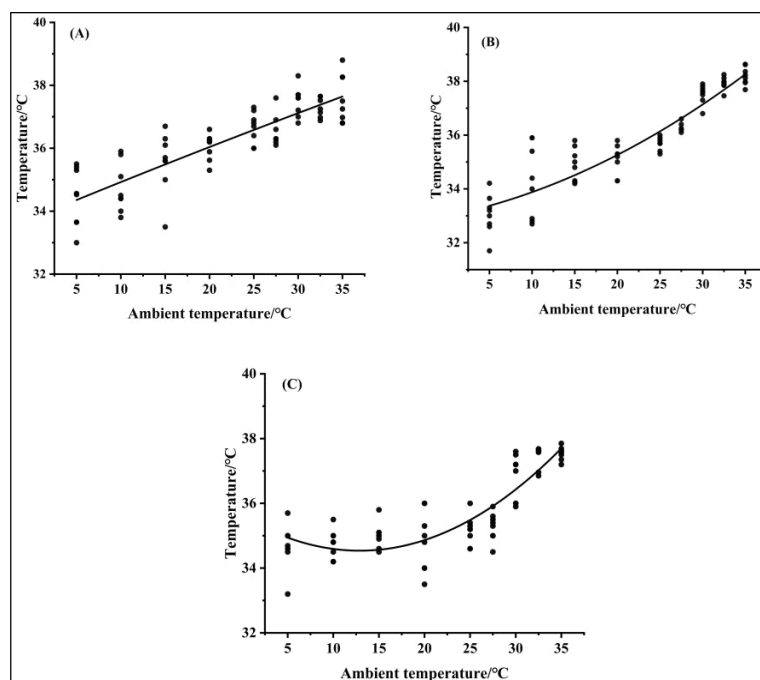


Fig 1: Changes of body temperature in *Apodemus chevrieri* (A), *Eothenomys miletus* (B), *Eothenomys olitor* (C).

Table 1: Comparison of physiological indexes of *Eothenomys miletus*, *Eothenomys olitor* and *Apodemus chevrieri* between normal temperature and high temperature acclimation.

Species	<i>Eothenomys olitor</i>		<i>Eothenomys miletus</i>		<i>Apodemus chevrieri</i>	
	Normal temperature 25°C	High temperature 30°C	Normal temperature 25°C	High temperature 30°C	Normal temperature 25°C	High temperature 30°C
T_b (°C)	35.55±0.46	36.44±0.13	35.75±0.50	36.49±0.17	36.54±0.61	36.90±0.10
RMR (ml O_2 /g.h)	2.84±0.12	2.21±0.45	3.03±0.22	1.93±0.33	3.31±0.14	2.58±0.57
TNZ (°C)	20-27.5	25-30	22.5-27.5	25-30	20.0-27.5	25-30
C (ml O_2 /g.h.°C)	0.18±0.01	0.28±0.08	0.23±0.08	0.22±0.06	0.25±0.06	0.29±0.11
References	Yang <i>et al.</i> 2021	The present study	Zhu <i>et al.</i> 2016	The present study	Zhu <i>et al.</i> 2008	The present study

Data were expressed as mean±SEM.

of its field distribution, the ambient temperature of the habitat in *E. miletus* was higher than that of *E. olitor*. T_b in *A. chevrieri* was higher than that of the two species of *Eothenomys*, which may be related to its higher RMR (Wang *et al.*, 2006; Yang *et al.*, 2021).

Resting metabolic rate and thermal neutral zone

RMR of *A. chevrieri* showed significant differences in different T_a ($F = 27.850$, $P < 0.01$). According to the definition

of TNZ, there was no significant difference in RMR between temperatures of 25°C and 30°C during high temperature acclimation, indicating that TNZ for this species is estimated to be within the range of 25-30°C. The regression equation for lower critical temperature was $RMR = 7.930 - 0.231 T_a$ and the regression equation for the upper critical temperature was $RMR = -4.604 + 0.255 T_a$ (Fig 2A). RMR of *E. miletus* was significantly affected by T_a ($F = 65.770$, $P < 0.01$). Differences in RMR between 25°C

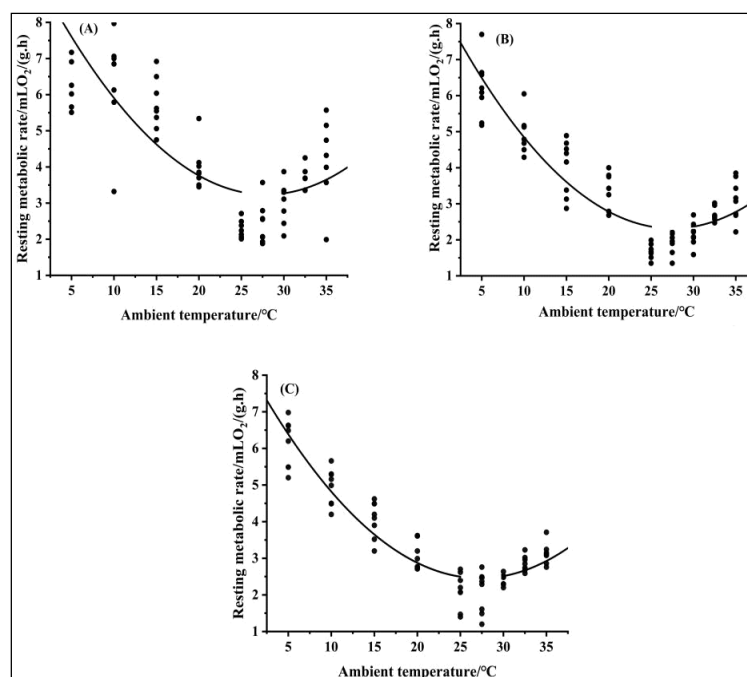


Fig 2: Changes of RMR in *Apodemus chevrieri* (A), *Eothenomys miletus* (B), *Eothenomys olitor* (C).

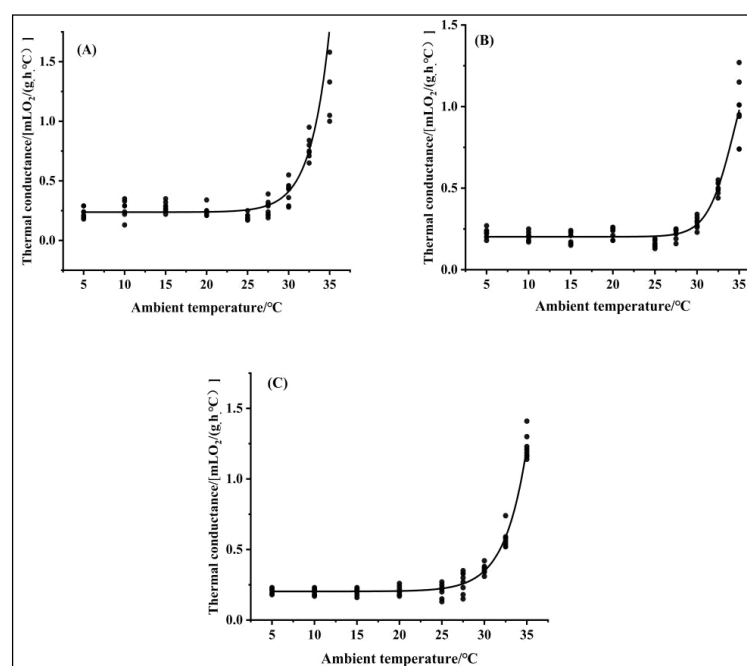


Fig 3: Changes of C in *Apodemus chevrieri* (A), *Eothenomys miletus* (B), *Eothenomys olitor* (C).

and 30°C were not significant, so the TNZ of *E. miletus* was 25–30°C. The regression equation for the lower critical temperature was $RMR = 7.238 - 0.214 T_a$ and the regression equation for the upper critical temperature was $RMR = -3.549 + 0.191 T_a$ (Fig 2B). RMR of *E. olitor* showed similar trends to *A. chevrieri* and *E. miletus* ($F = 80.214$, $P < 0.01$). TNZ in *E. olitor* was 25–30°C. The regression equation for lower critical temperature and upper critical temperature were $RMR = 7.045 - 0.199 T_a$ and $RMR = -1.755 + 0.140 T_a$, respectively (Fig 2C).

RMR represents the minimal energy expenditure necessary for an animal's survival (Janelle and Ayres, 2020). It plays an important regulatory role in animals facing different environments (Feierabend *et al.*, 2015). Temperature is an important environmental factor affecting RMR (Chen *et al.*, 2020). RMR in *C. barabensis* acclimated at high temperature was significantly lower than that acclimated at low temperature (Xu *et al.*, 2014). High temperature reduced RMR and non-shivering thermogenesis in *M. unguiculatus* (Guo *et al.*, 2020). In present study, RMR of all three animals decreased with increasing T_a within the temperature range of 5 to 25°C, which increased above 30°C. RMR of the three animals in our study were lower than that of in normal temperature, when facing high temperature environments, the three species in this study chose the similar adaptation strategy (Table 1) (Zhu *et al.*, 2009; Zhu *et al.*, 2008; Zhu and Wang, 2015). Through comparison, it was found that three species all decreased RMR under high temperature, indicating that high temperature can reduce heat production to regulate body temperature.

TNZ is a crucial concept in the study of energy strategies in physiological ecology, primarily referring to a range of environmental temperature fluctuations within which mammals can maintain their lowest metabolic rate (Bligh and Johnson, 1973). Although there are many factors that affect TNZ, T_a is one of the most important factors that cannot be ignored (Yang *et al.*, 2021). For same species, TNZ can change with T_a , it showed that there had a decrease in the lower critical point and an increase in TNZ width under cold temperature, while increasing the lower critical point and decreasing the width of TNZ under high temperature (Zhu *et al.*, 2016). For example, *Dipus sagitta* had a narrower TNZ in summer and it had a wider TNZ in winter (Bao *et al.*, 2000). For different species, TNZ is closely related to altitude or temperature (Zhu *et al.*, 2022). Based on our previous researches, it found that high temperature acclimation narrowed the TNZ and the lower critical temperature point increased in three rodents (Yang *et al.*, 2021; Zhu *et al.*, 2008; Zhu and Wang, 2012). Narrowing TNZ might be beneficial for reducing energy consumption and is an adaptation method for high temperature acclimation (Table 1) (Zhang *et al.*, 2007).

Thermal conductance

C values in three animals showed significant differences under different T_a (*E. miletus*: $F = 117.764$, $P < 0.01$; *A. chevrieri*:

$F = 35.533$, $P < 0.01$; *E. olitor*: $F = 346.111$, $P < 0.01$; Fig 3A, B, C). All of them remained C values stable within the range of 5 to 25°C, which increased with increasing temperature within the range of 25 to 35°C, the linear regression equations were $C = -3.171 + 0.123 T_a$ (*E. miletus*: $F = 155.516$, $P < 0.01$); $C = -3.116 + 0.121 T_a$ (*A. chevrieri*: $F = 148.715$, $P < 0.01$); $C = -0.398 + 0.120 T_a$ (*E. olitor*: $F = 146.419$, $P < 0.01$), respectively.

Thermal conductance affects the energy balance and is one of the important factors affecting animal's energy consumption in small mammals (Naya *et al.*, 2013; Meyer *et al.*, 2010). The limited size of small mammals makes it difficult for them to change the thickness of their fur to adapt to different environmental temperatures; it is therefore particularly important to change the C value (Yang *et al.*, 2021). In our study, it was found that the C values of three animals remained stable below the TNZ, while it increased with the increase of T_a above 25°C, showing that three animals need to enhance their heat dissipation ability under high temperature (XuanYuan *et al.*, 2023). Moreover, according to the slope of the correlation linear regression, the change ranges of C from large to small is *E. miletus*, *A. chevrieri* and *E. olitor*, suggesting that the C value may be related to the cave depth. The cave depth of *A. chevrieri* was deeper and the temperature in the cave is lower. Therefore, the C value of *A. chevrieri* was small, which is beneficial for reducing energy loss (Luo *et al.*, 2000). Because the living environment temperature of *E. olitor* is lower than that of *E. miletus* and *A. chevrieri* and its fur was thick and its heat insulation effect was strong. Therefore, C value of *E. olitor* was lower than that of *E. miletus* and *A. chevrieri* (Luo *et al.*, 2000; Li *et al.*, 2012).

CONCLUSION

Our data confirmed high temperature acclimation increased T_b , reduced RMR and changed C value of *E. olitor*, *A. chevrieri* and *E. miletus*. By comparing the thermogenic characteristics of three animals, it can be inferred that the variation ranges of the thermogenic indexes from large to small were *E. miletus*, *A. chevrieri* and *E. olitor*, which may be related to its classification status or habitat temperature. Based on the lower sensitivity of *E. olitor* under high temperature acclimation, which was suggested that *E. olitor* might be a more adaptable species under high temperature.

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Conflict of interest

The authors declare no conflicts of interest.

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