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ORIGINAL ARTICLE

Metabolism and thermoregulation in the tree shrew, *Tupaia belangeri*

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Maximum metabolic rate is a physiological limitation that is an important for animals' survival, reproduction and geographic. Basal metabolic rate (BMR), nonshivering thermogenesis (NST), and maximum metabolic rate (MMR) were measured was in a small mammal species, *Tupaia belangeri*, which is a unique species of small-bodied mammals in the Oriental realm. Thermal neutral zone (TNZ) was 30 - 35°C and BMR was 1.38±0.09 ml g^{-1} h^{-1}. NST and MMR were 2.64±0.08 ml g^{-1} h^{-1} and 7.14±0.38 ml g^{-1} $\cdot h^{-1}$ in summer, respectively. The ecophysiological properties of relatively high body temperature, wide TNZ, low BMR and thermogenic capacity enable this species to adapt to its environment.

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The study of phenotypic plasticity has become a central topic in evolutionary ecology (Schlichting and Pigliucci 1998). Theoretically, through phenotypic plasticity, organisms are able to match environmental variability at an ecological scale and can increase their performance under different environmental conditions. In particular, physiological acclimatization or acclimation allows organisms to cope with variations in thermal conditions. Eutherian nonhibernating small mammals display several mechanisms to survive in fluctuating thermal environments (Heldmaier 1993). Thermogenic capacity can be measured as maximum metabolic rate of thermoregulation (MMR), which in eutherian small mammalsmay be deconstructed as the sum of basal metabolic rate (BMR), nonshivering thermogenesis (NST), and shivering thermogenesis (ST; see Heldmaier 1993; Wunder and Gettinger 1996). Therefore, MMR may vary because of changes of any of the former variables.

Based on physiological, modelling and

palaeontological studies, Clarke and Pцrtner (2010) proposed a modification to the aerobic scope hypothesis, this hypothesis is consistent with the research showing that muscle temperatures increase as metabolic rate increases with strenuous exercise (Hodgson et al.1993; Weishaupt et al. 1996); it is the newest evolving endothermy theory that the endothermy originated in smaller, active eurythermal ectotherms living in a cool but variable thermal environment. Rather than an increase in body temperature being a secondary event to the evolution of an enhanced aerobic scope, we suggest that an increase in body temperature was the mechanism by which that increased scope was achieved. An important aspect of thismodified aerobic scope hypothesis is that resting (basal) and sustained (field) metabolic rates are coupled and increase in parallel. A higher body temperature allows a faster rate of ATP generation and higher muscle power output, but it also increases maintenance costs. However an endotherm is not merely a warm ectotherm, and the key development in the evolution of endothermic metabolism was the proliferation and modification of mitochondria. Viewing the evolution of endothermy as a continuous, rather than a two step, process also emphasises that intermediate stages would have been physiologically and ecologically viable.

The tree shrew, *Tupaia belangeri* belongs to Scandentia Tupaiidae. It is a unique species of small mammals in the Oriental realm and widely geographical distribution at Southern China, India, and Southeast Asia. *T. belangeri* is the widest of distribution and lives at the highest of latitude in their family, Yunnan-Kweichow Plateau mostly were its northern limit (Wang et al., 1991) and their habitat always was terrestrial, arboreal, mountainous forest and shrub areas. Early studies in our lab show that the physiological characters of *T. belangeri* show for example resting metabolic rate (RMR), nonshivering thermogenesis (NST) and the metabolism (Wang et al., 1994; 1995; 1999; Zhang et al., 2001) of *T. belangeri* showed robust seasonal cycles. Furthermore, administration of exogenous melatonin at physiological doses induced seasonal cycles of the thermogenesis in *T. belangeri* (Wang et al., 2000) and that thermogenesis in tree shrews was increased during cold exposure (Wang et al., 1995; Li et al., 2001; Zhang et al., 2011; 2012).

Little is known about the physiological characteristics of treeshrews in the wild. Thermogenic and thermoregulatory abilities are critical to the survival and distribution of mammals (Karasov, 1986). The aim of this study is to measure the basal metabolic rate (BMR), nonshivering thermogenesis (NST) and cold-induced maximum metabolic rate (MMRc) in tree shrew from the wild.

MATERIALS AND METHODS

Animals

The tree shrew, *T. belangeri* were livetrapped (25°25'~26°22' N, 102°13'~102°57' E, 1 679 m in altitude) around boscage at Luquan County, Yunnan Province, China, in August 2009. The area is located in the northern Yunnan-Kweichow Plateau, the climate belong to the north subtropical plateau climate. Average temperature was 15.6 °C each year, maximal average temperature was 19.8 °C in July, minimum average temperature was 7.8°C in January, and uttermost minimum temperature was -9.5°C. After capture, tree shrew was transported to the School of Life Science of Yunnan Normal University, Kunming, China (1910 m in altitude). Animals (5 ♂, 5 ♀), all healthy adults, each tree shrew was housed individually in a wire cages (40 cm x 40 cm x 40 cm) with no bedding, and were provided with natural illumination and 85%~92% relative humidity for 3 days, then experiment, metabolic determinations were carriedout in September 2009. All pregnant, lactating or young individuals were excluded. They were fed the mixed food; the food mixture contained the following ingredients in proportion (by weight): 90 parts cornmeal, 5 parts milk, and 5 parts sugar, add a little water. The tree shrews were fed once daily at 12:00 h., additionally, once two days, the tree shrews were provided with appropriate apples, pears and other fruits.

Measurement of metabolic rates

The level of BMR of *T. belangeri*, were determined in every experimental using AD ML870 open respirometer in every experimental week. All the experimental animals' sets were incubated in breath chamber with volume of 500ml with flow rate 200ml/min. The temperature was maintained 30°C (The thermal neutral zone of *T. belangeri* was 30 - 35°C, Wang et al., 1994) by SPX-300 artificial climatic engine (±0.5°C) for 1.5 hrs and the metabolic rates were measured using ML206 gas analyzer. The animal's body mass was measured by weight loss method and temperature was determined by portable-thermometer before and after the experiment. The method used for calculating the metabolic rate is detailed in Hill (1972).

Maximum NST was defined as the maximum metabolic response to norepinephrine (NE) and was induced by a subcutaneous injection of NE at 30°C(TNZ, thermal neutral zone). The mass-dependent dosage of NE (Shanghai Harvest Pharmaceutical Co. Ltd.) was calculated according to body weight (0.8 mg/Kg). Two continuous stable maximal recordings were used to calculate maximum NST. Oxygen consumption reached peak values within 15–30min after NE injection.

The methods used for our measurements of MMRc in animals are given in Wiersma et al. (2007). Briefly, we used heliox (79% He, 21% O_2) in a flow-through respirometry system. Since helium conducts heat four times faster than that of nitrogen, heat loss in the mixture is considerably higher than air. Maximum oxygen consumption can, therefore, be elicitedat relatively high temperatures (Rosenmann and Morrison, 1974). The temperature of the chamber was gradually lowered until the animals' oxygen consumption did not increase or start to decrease. The cold-induced MMR was defined as the highest oxygen consumption that Inlet and outlet O_2 concentration was recorded at 1-sec intervals. Instantaneous VO_2 (VO_2 inst) was calculated by using equations from Hill (1972), based on 30-min running averages of O_2 concentrations. The effective volume of the system was estimated as 760 ml from washout curves, gas streams were forced through individual metabolic chambers at 200ml/min during measurement of cold-induced maximum metabolic rates. We defined VO_2 inst as the highest O_2 averaged over 2 min of the last 5 min of 15 min Helox exposure.

Thermal conductance (C)

Thermal conductance (ml $O_2 \cdot g^{-1} \cdot h^{-1} \cdot {}^{\circ}C^{-1}$) was evaluated as $C = RMR / (T_a - T_b)$ (McNab, 1980), where RMR is the basal metabolic rate (BMR) (ml $O_2 \cdot g^{-1} \cdot h^{-1}$), Tb is the body temperature (°C), and Ta is the ambient temperature (°C). This formula was suggested by McNab (1980) as well as Bradley and Deavers (1980) for calculating conductance at any given ambient temperature.

Statistical analysis

Statistical analyses were performed using sigmaplot10.0, SPSS for Windows15.0 statistical package. Statistical analyses among groups were determined by one-way ANOVA; to compare body mass with metabolic rates, we used AOCOVA. All data are expressed as the means ± SE, $P < 0.01$ and $P < 0.05$ were considered to be statistically significant. The research complied with protocols approved by China Wildlife Conservation Association, adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates, and also adhered to the legal requirements of China.

RESULTS

Tb's were fairly constant between -5 and 37.5°C mean Tb was 39.4°C. The relationship between the body temperature (Tb) in *T. belangeri* and Ta is shown in Fig.1, and is represented by the following equation: Tb (°C) =38.67+0.37T_a (r^2=0.87, $P<0.001$, n=10).

The relationship between metabolic rates and Ta's are shown in Fig. 2. There was no significant difference in metabolic rates between 30 ºC and 35 ºC. Metabolic rates between 25 °C and 30 °C showed a significant difference, and the difference between 35 °C and 37.5°C was also significant. Above 35°C, the metabolic rate significantly increased and thus was regarded as the upper critical temperature. The thermal neutral zone (TNZ) of tree shrew was from 30°C to 35°C. The mean RMR within the TNZ is 1.38±0.09 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ (n =10), which is 150.33% (Fig. 4) predicted values by McNab (1988) (RMR (ml $O_2 \cdot g^{-1} \cdot h^{-1}$) =$3.45M_b^{-0.287}$ (g)). Between -5 - 37.5℃, the relation between oxygen consumption in *T. Belangeri* and Ta is represented by the following equation: BMR (ml $O_2 \cdot g^{-1} \cdot h^{-1}$) =4.05 - 0.26$T_a$ (r^2=0.64, $P<0.001$, df=10).

The maximum NST of the treeshrews is 2.64±0.08 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ (n =10), which is 70.03% predicted value based on body mass by Heldmaier (1971) (NST (ml $O_2 \cdot g^{-1} \cdot h^{-1}$) =$30M_b^{-0.454}$ (g)) (Fig. 4). The metabolic rate in the gas mixture of He-O_2 was measured at four temperatures, -10°C, -5°C, 0°C and 5 °C. With the decrease in Ta; the metabolic rate in the gas mixture increased (Fig. 3). The metabolic rates at -10°C, 0°C and 5°C are significantly lower than at -5°C, so it is regarded as the MMR. The mean MMR is 7.14±0.38 ml·$g^{-1} \cdot h^{-1}$, which is 1.18 times the predicted values by Bozinovic and Rosenmann (1989) (MMR (ml·$g^{-1} \cdot h^{-1}$) =$28.3M_b^{-0.338}$ (g)) (Fig. 4). The ratio of MMR to BMR is 5.17.

The variations of overall thermal conductance with Ta for the treeshrew are shown in Fig. 5. At temperatures below TNZ, the over all thermal conductances showed no significant difference. The minimum thermal conduction (Cm) was calculated as 0.112±0.0055 ml $O_2 \cdot g^{-1} \cdot h^{-1} \cdot {}^{o}C^{-1}$, which is 104.67% predicted value by Bradley and Deavers (1980), (Cm (ml$O_2 \cdot g^{-1} \cdot h^{-1} \cdot {}^{o}C^{-1}$) =$0.76M_b^{-0.426}$(g)), based on body mass. Within and above the TNZ, C increased significantly with Ta; thermal conductance increased when the ambient temperature increased. Between -5 and 35°C, the relation between the thermal conductance of *T. belangeri* and Ta was C=0.04T_a -0.06(r^2=0.41, $P<0.001$, df=9).

Table 1 Basal metabolic rates (BMR) for some relative species

Species	Body mass(g)	BMR (ml O_2/g·h)	Predicted* (ml O_2/g·h)	% of predicted	Reference
Apodemus chevrieri	32.6	4.24	1.43	296.6	Zhu et al., 2008
Apodemus draco	23	3.17	1.57	202	Li et al., 2009
Eothenomys miletus	44.9	2.99	1.33	226.77	Zhu et al., 2008
Tupaia belangeri	100.86	1.381	1.073	128.62	This study
Tupaia glis	116.8	0.76	0.92	83.3	Bradly et al., 1974
Urogale everetti	264	0.87	1.032	84.3	Lovegrove et al., 1991
Ptilocercus lowii	57.5	0.936	0.98	95.5	Whittow et al., 1976

*BMR= $3.42W^{-0.25}$ (Kleiber, 1961)

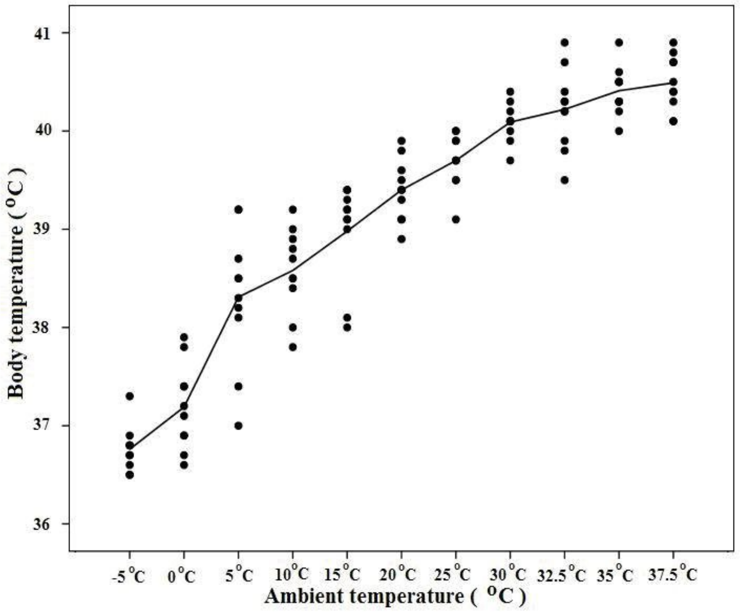

Figure 1 The body temperature in different temperature in *T. Belangeri*

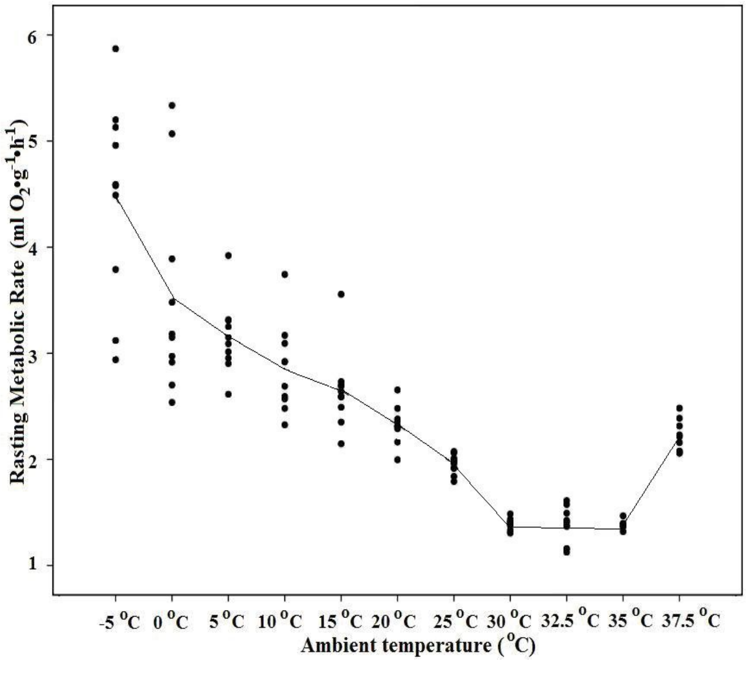

Figure 2 The Rasting Metabolic Rate (RMR) in different temperature in *T. Belangeri*

DISCUSSION

McNab (1970) considered that the small mammals located in the tropical area have a low metabolic rate, high thermal conductivity, it's the beneficial to prevent overheating; however, in the high latitudes area, the species have a high metabolic rate and low thermal conductivity, it's the beneficial to reduce heat loss at low temperatures. The tree shrew was a unique species of small mammals in the Oriental realm, BMR values in *T. belangeri* was 1.38 ml $O_2 \cdot g^{-1} \cdot h^{-1}$, BMR values was Kleiber's (1961) body mass predicted values 128.62%; 150.33% (Fig. 4) that predicted by McNab (1988).

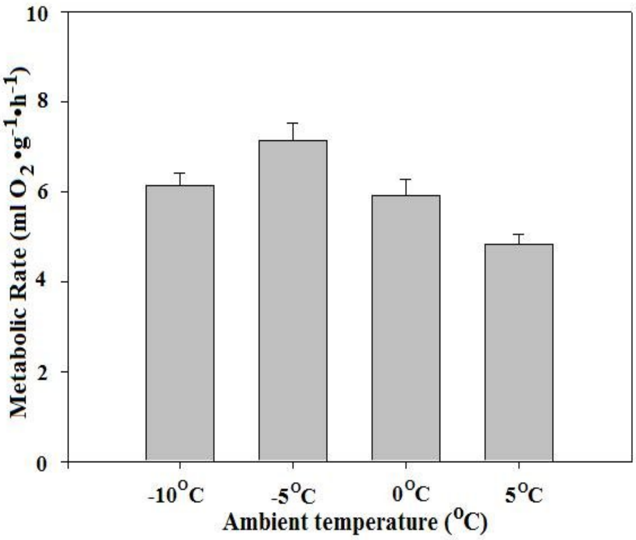

Figure 3. Metabolic rates measured in He-O_2 mixture (79%: 21%) at different ambient temperatures in the tree shrew *T. belangeri*. Values are mean±S.E. *N*=10

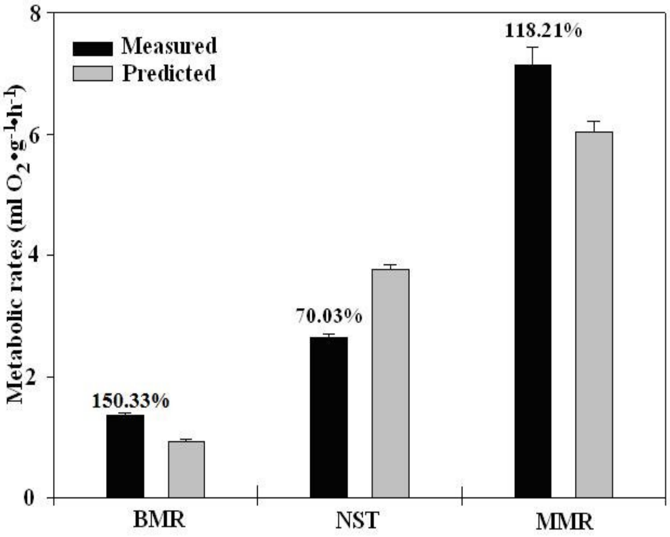

Figure 4. BMR, NST and MMR of *T. belangeri* and percent ages of predicted values by McNab (1988) BMR (ml $O_2 \cdot g^{-1} \cdot h^{-1}$) $=3.45M_b^{-0.287}$ (g), by Heldmaier (1971) NST (ml $O_2 \cdot g^{-1} \cdot h^{-1}$) $=30M_b^{-0.454}$ (g) and by Bozinovic and Rosenmann (1989) MMR (ml $O_2 \cdot g^{-1} \cdot h^{-1}$) $=28.3M_b^{-0.338}$ (g). Values are mean±S.E.

Compared with other rodents, the BMR values in *T. belangeri* was between the tropical and the Hengduan mountain region species (Table 1), BMR values in *T. belangeri* was higher than the tropical species maybe related to distribute in the high-altitude areas, lower than the Hengduan mountain region species maybe related to their adaptive mechanisms. Most of the variation in the basal rate of metabolism in eutherians can be accounted for by the combined influences of body mass, food habits, behavior and climate (McNab, 1986).

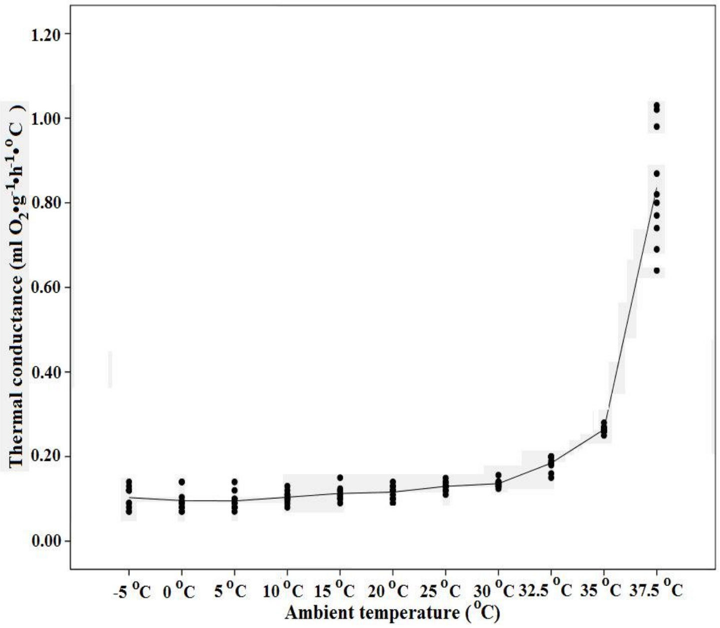

Figure 5 The thermal conductance (C) in different temperature in *T. belangeri*

The character of the environment temperature distributes in time and space variation where Homotherm locates, it includes the habitat of small climate, geographical distribution and seasonal and diurnal temperature changes, and it determines the homeothrem's the minimal thermal conductivity (C_{min}) and endogenous heat capacity, and the higher C_{min}, the higher temperature drop rate (Lovegrove et al., 1991). The study found the average body temperature in *T. belangeri* (39.4°C) was higher than the sympatric species of *E. miletus* (35.9°C), *A. chevrieri* (36.0°C) (Zhu et al., 2008) and *A. draco* (36.7 °C) (Li et al, 2009); the C_{min} value in *T. belangeri* was 104.67% predicted value by Bradley and Deavers (1980), which was related to the habitat of tree shrews, tree shrews live in the climatic transition zone, where gradually changes from the hot and humid into the cold and drought, the average temperature is lower than the tropical area, the seasonal temperature does not change significantly, but it has a larger temperature difference between day and night, it usually range about 20℃, there are high-temperature and low-temperature stress in the whole day, it leads to increase the ability of heat production and the thermal conductance. During the summer, the tree shrew replies to the larger temperature difference in whole day and saves energy, thus its heat loss ability was stronger than *T. glis* locate in the tropical area (Bradly, 1974); it is an important adaptability for subsistence.

Bockler et al. (1982) found that NE-induced heat production was equivalent to that of cold-induced NST. So it can be a measure of NST. In this study, the contribution of NST to MMR is 36.97%, 1.9 times BMR. Degen (1997) reported that the ratio of NST/BMR ranged between 1.0 and 5.8 in desert rodents. In species distributed in northern temperature zones in China, the ratio of NST/BMR in the striped hamster is higher than that of *Microtus brandti* (1.4), *Spermophilus dauricus* (1.6), *Ochotona curzoniae* (1.6), but it is lower than *Meriones unguiculatus* (2.2) (Li et al., 2001) and *Cricetulus barabensis* (3.4) (Song and Wang, 2003).

Haim and Izhaki (1993) proposed that species that have low BMR values show high values of NST. Tree shrew has the characters. It may be inter preted as the effect of habitat and habits on NST. Haim and Izhaki (1993) proposed that diurnal species have a significantly higher NST/BMR ratio (4.2) than nocturnal species (2.5), and the NST/BMR ratios of mesic species (2.5) are significantly lower than those of arid species (3.7). The NST/BMR ratio of the tree shrew (1.9) is under the nocturnal species but close to the mesic species. However, the tree shrew is one of diurnal species. This support a hypothesis which the tree shrew is more adapted to mesic habitats than arid habitats.

The mean MMR is 1.18 times of the predicted value by Bozinovic and Rosenmann (1989). It is lower than Brandt,s voles (1.49, *M. brandti*), Mongolian gerbils (1.47, *M. unguiculatus*) (Song and Wang, 2002) and , however, it is higher than *Eothenomys miletus* (1.06) (Zhu et al. 2010). With this MMR, the tree shrew has a high tolerance to low temperatures and is able to with standan effective minimum temperature of -35°C (Derived from the assumption that Cm and Tb were stable). Maximum factorial aerobic scope (the ratio of maximal to resting metabolic rate), data on maximal oxygen consumption in mammals are few, and come predominantly from just three groups of mammals. Factorial aerobic scopes are lower in rodents (mean~9, N = 12), but higher in carnivores (~27, N = 4) and artiodactyls (~23, N = 7) (Weibel & Hoppeler, 2005; White et al., 2008), the single very highest value was 70 in the pronghorn, *Antilocapra americana* (Lindstedt et al., 1991).The aerobic factorial scope was 5.17 in the tree shrew is near the mean values in eutherians (5.1, Hinds et al., 1993), but it is lower than the mean values in rodents, carnivores and artiodactyls.

In the newest evolving endothermy theory, Clarke and PЦrtner (2010) critical to they understanding of the evolution of endothermy will be further elucidation of the functional links between active and resting metabolism in vertebrates, and the mechanisms underlying physiological flexibility of mitochondria.

Thus, the ecophysiology properties for the tree shrew were (1) the high Tb, low BMR and Cm; (2) an unfitted TNZ and low upper critical temperature, and (3) high NST and MMR. These characteristics were closely related to their living habits. The higher Tb, lower BMR may imply that the tree shrew is more adaptable to warm rather than to cold. The high NST and high MMR can enable the tree shrew to with stand cold and increase the fetching food time and food collection at low temperatures, this is very important for the survival of the tree shrew, which has a high NST and MMR. The ecophysiological characteristics of the tree shrew might constrain their distribution and extension to the Oriental realm, low latitudes and high altitude in China.

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