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ALTITUDINAL VARIATION OF SKULL SIZE IN DAURIAN PIKA (*OCHOTONA DAURICA* PALLAS, 1868)

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Body size and skull size of animals were usually considered positively correlated with a decrease in temperature. This is known as Bergmann's rule. However, with the increase of altitude other factors besides temperature, such as low oxygen concentration, may affect animals' growth and development. We tested the skull size of Daurian pika (*Ochotona daurica*) that were collected from different altitudinal localities to determine the trend in skull size with altitude. Our study showed that skull size is negatively correlated with altitude. The temperature decreased with altitude, as a result of converse to Bergmann's rule. This confirmed that Bergmann's rule is not universally valid on interpreting for animal body size cline. We contribute this to hypoxia, food shortage caused by short frost-free period and energy distribution. Our study suggests that low oxygen concentration and frost-free period should be considered when animal body size cline is discussed.

Key words: altitudinal variation, Bergmann's rule, Daurian pika, *Ochotona daurica*, frost-free period, oxygen concentration, skull size

INTRODUCTION

Environmental factors are one of the important determinants of postnatal skull ontogeny (HALL 1990) and final size (BURNETT 1983, CALDER 1984, SCHMIDT-NIELSEN 1984, YOM-TOV & NIX 1986, WIGGINTON & DOBSON 1999). As a genetically and epigenetically morphological complex, the mammalian skull can be used to classify taxa. The comparison of skull growth patterns between animals that are subjected to different selection pressures as juveniles and adults will assist in understanding not only geographical variations in population phenotype, but also their life history strategies and evolutionary change (LU 2003).

Bergmann's rule (BERGMANN 1847), which states that warmblooded vertebrate species from cooler climates tend to be larger than congeners from warmer climates, is the most interpreted for animal body size cline. The classic explanation is that larger animals have smaller surface-to-volume ratios, and therefore also have relatively lower costs of thermoregulation in the cold (northern) climates (OCHOCIŃSKA & TAYLOR 2003). As a result, latitude and altitude were usually introduced as surrogates for temperature.

However, the validity of Bergmann's rule has been widely questioned (GEIST 1987, 1990), as a large number of mammals do not conform to it. From a heat transfer perspective, smaller mammals should follow bergmann's rule more strongly than larger ones (PORTER *et al.* 1994, STEUDEL *et al.* 1994). But no evidence was found that smaller mammalian species conform more strongly to the rule than larger species (ASHTON *et al.* 2000). Mammals were found a significantly lower tendency to conform to Bergmann's rule within the 4–50 and 51–500 g body mass categories (MEIRI & DAYAN 2003). Further more, shrews followed the converse to Bergmann's rule (OCHOCIŃSKA & TAYLOR 2003). FRECKLETON *et al.* (2003) found that large-bodied species tend to follow the intraspecific version of the rule more closely than do small-bodied species when body size variation was compared to temperature, but not when it was compared to latitude. In a research on metabolic rates of rodents (REZENDE *et al.* 2004), the result offered no support for Bergmann's rule. Small mammals are thus of a special interest with respect to the Bergmann's rule.

It should be noticed that a series of environmental variations have been largely neglected along with increasing altitude. With increasing altitude, the environmental factors (including temperature) change more rapidly than with latitude. Generally, temperature declines with increasing latitude as well as altitude. But latitude is not always the synonymy of temperature when altitude is also considered. With increasing altitude, temperature drops about 0.6°C per 100 meters (RUNDEL 1994), which decreases more rapidly than with increasing latitude. Moreover, some of the factors only accompany the altitude variation, for example the decline of atmospheric pressure and oxygen concentration.

Body size is one of the most significant features of organisms (CHOWN & KLOK 2003) and body mass is the most common surrogate for size (MEIRI *et al.* 2004). Food availability and fasting endurance are the main determinants of body size (MILLAR & HICKLING 1990) and seasonal changes in body mass have been observed in many rodent species (KORN 1989, ELLISON *et al.* 1993). Reduction in body mass is due to a decrease in total body water and in lean body mass and there is a reduced activity of white adipose tissue lipoprotein lipase (DARK *et al.* 1983). These changes may have caused bias when body mass was evaluated as a surrogate for body size. Thus, unlike body mass, the skeleton of mammals is a comparatively stable feature.

The extant pikas (number of recorded species vary from 18 to 29) are endemic to the Holarctic realm and consist of a monotypic genus, *Ochotona* (NIU *et al.* 2004). Most of the species can be found in the Tibetan Plateau or in the vicinity. They are distributed in broad areas and occur almost exclusively in remote settings. Most pikas live at high altitudes (over 3000 meters above sea level (a.s.l)), some at heights of up to 6000 meters (FENG *et al.* 1986).

Environmental changes can often produce strong selective pressures that can result in rapid morphological diversification (HUNTLEY & WEBB 1989). Uplift of the Tibetan Plateau began about 50 mya, and further significant increases in altitude are thought to have occurred about 10–8 mya, or more recently (ZHISHENG *et al.* 2001). It largely influenced the climate and surroundings and provided the basis for animal evolution. Differentiations of species that distributed in the Tibetan Plateau and adjacent mountains are closely related to the uplifting of the Tibetan Plateau and subsequent climatic changes (NIU *et al.* 2004). Pikas have undergone a rapid radiation since the early Pleistocene (about 2.2 mya) (NIU *et al.* 2004).

The Daurian pika (*Ochotona daurica*) is considered to be an earlier split among species of subgenus *Ochotona*. It mainly inhabits the arid, open grasslands of lower altitudes (YU *et al.* 1992) and can be found in most northern areas in China as well as the Tibetan Plateau. As an earlier split species, Daurian pika was affected by the rapid uplift of the Tibetan Plateau. The changes caused by the different altitude lead to adaptations in the anatomy, physiology and behaviour of the Daurian pika. Occurring at varying altitudes (from 400 to 4000 m a.s.l in our study), the Daurian pika is an ideal species for our study. In this paper, we pay close attention to whether or not the skull size of the Daurian pika was affected by the change of altitude and, if so, the possible interpretation of it, for example, the Bergmann's rule.

MATERIALS AND METHODS

This study is based on specimens from The Institute of Zoology, Chinese Academy of Sciences (CAS) and Northwest Institute of Plateau Biology, CAS. The specimens were collected from localities in the north of China and the Tibetan Plateau (Table 1). Measurements were taken using vernier calipers. All measurements were recorded to the nearest 0.1 mm. 131 adult Daurian pikas' skulls were measured. Three measurements were taken: greatest length of skull (GLC), mastoid breadth (MB) and nasal length (NL). To get the size of the skull, we treated pikas skulls as cone shaped so that the skull size was achieved by $\pi\ (MB/2)^2 \times GLC/2$. We took no sexual division, as the pika is sexually monomorphic the correlation coefficient of the items was usually very similar for males and females. We confirmed this by testing the skull size and the relative skull size with ANOVA for males and females of Daurian pika. There is no significant difference between them (for skull size, $F = 2.523$, $P = 0.115$, $n = 121$ (female: 45, male: 76); for relative skull size, $F = 0.219$, $P = 0.158$, $n = 121$ (female: 45, male: 76)).

With bivariate correlation analysis, we tested the relationships between altitude, skull size, greatest length of skull, mastoid breadth and nasal length. Although we paid close attention to the skull size and the altitude, we also noticed that the skull size could be affected by latitude as mentioned as Bergmann's rule. We used partial correlation analysis to test this possible influence.

Table 1. Locations where specimens of Daurian pikas (*Ochotona daurica*) were collected

Location	n	Latitude (N)	Longitude (E)	Altitude (m)
Yichun	2	47°40’	129°12’	400
Hulun Buir	1	50°13’	120°63’	500
Dong Ujimqi Qi	16	45°31’	116°58’	839
Luliang	5	37°43’	111°21’	950
Hilinhot	1	43°57’	116°04’	990
Xi Ujimqi Qi	5	44°35’	117°36’	996
Sonid Youqi	1	42°37’	112°50’	1102
Abag Qi	1	44°01’	114°57’	1126
Tongliao	1	43°36’	122°16’	1200
Duolun	18	42°11’	116°28’	1245
Taibus Qi	2	41°53’	115°26’	1300
Xianghuang Qi	2	42°14’	113°50’	1322
Kangbao	2	41°51’	114°37’	1370
Shenchi	1	39°14’	112°19’	1600
Haiyuan	5	36°20’	105°20’	2500
Tongde	4	35°16’	100°39’	3100
Guinan	51	35°34’	100°46’	3290
Dege	13	31°44’	98°34’	4000
Total	131			

Although latitude is a useful proxy for a number of environmental variables, it alone is unlikely to influence body size (HAWKINS & DINIZ-FILHO 2004). Thus evaluation causes of size-latitude trends will require examination of how body size responds to specific environmental variables (ASHTON 2004). Temperature was considered the main cause for animal body cline and a frost-free period can be used as index of vegetable growth. We collected temperature and frost-free period data of the localities where the Daurian pikas inhabited and dealt with bivariate correlations analysis. The weather data (varying from 10 to 30 years) of the localities where the specimens were collected were gained from National Climatic Data Center. We did not deal with air pressure or oxygen concentration for it has a decreasing gradient along with increasing altitude (LIST 1984) so the same ratio of negative tendency compared to the result of relationship between altitude and skull size could be expected.

All statistical analyses were performed using SPSS 12.0.1 for Windows software.

RESULTS

The measurements of the collected Daurian pikas from different altitudes are given in Figure 1. It indicated that skull size was negatively correlated with altitude. Greatest length of skull and nasal length tended to shorten with increasing altitude and mastoid breadth became narrower. The results of partial correlation analysis indicated the same trend when latitude treated as controlled variables (Table 2).

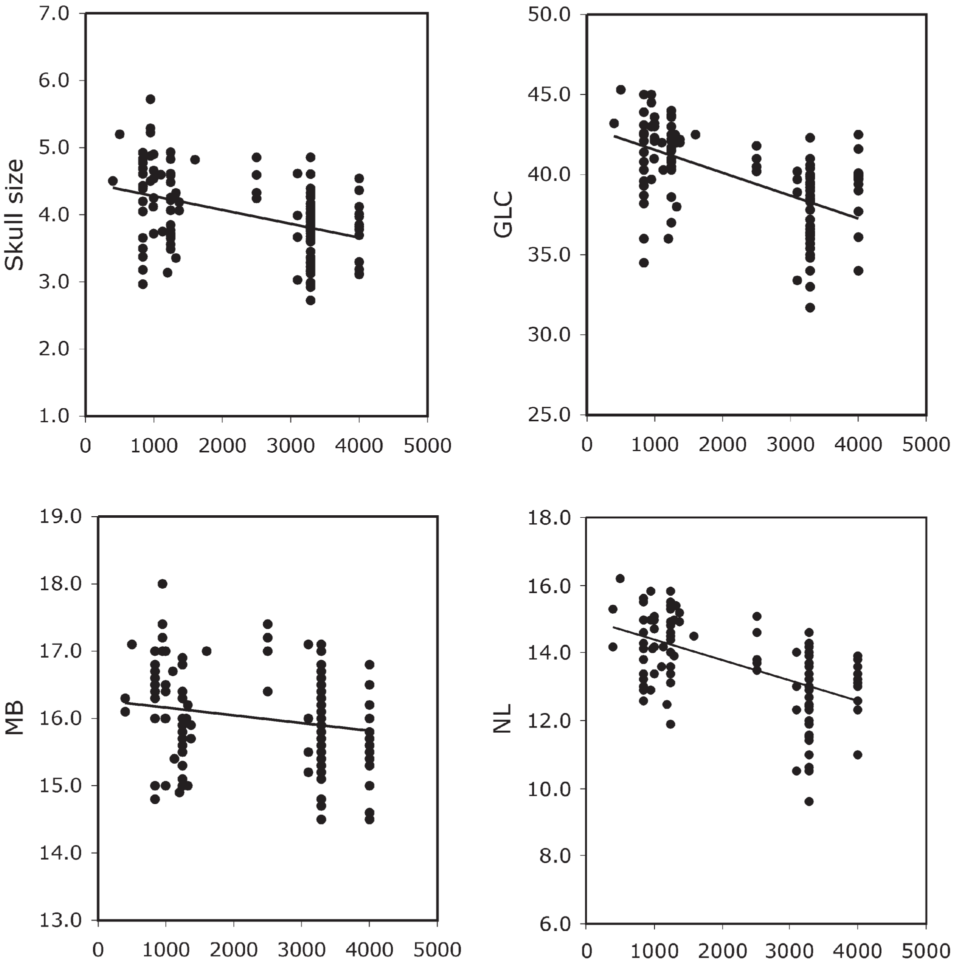

Fig. 1. Skull measurements of Daurian pika (*Ochotona daurica*) vary with altitude, where GLC stands for greatest length of skull, MB for mastoid breadth and NL for nasal length. The entire measurement unit was millimetre (mm) except the skull size, which was centimeter cube (cm^3). The results indicate that all of the measurements are negatively correlated with altitude, for skull size: $r = -0.420$, $P < 0.001$, $n = 123$; for GLC: $r = -0.565$, $P < 0.001$, $n = 123$; for MB: $r = -0.191$, $P = 0.031$, $n = 128$ and for NL: $r = -0.557$, $P < 0.001$, $n = 118$.

Table 2. Partial correlations of Daurian pika (*Ochotona daurica*) skull size to altitude. The correlation coefficient indicated the relationship of skull measurements to altitude when latitude was controlled. The df stands for degree of freedom, GLC for greatest length of skull, MB for mastoid breadth and NL for nasal length.

	Correlation coefficient	df	Sig. (2-tailed)
Skull size	–0.437	120	<0.001
GLC	–0.434	120	<0.001
MB	–0.330	125	<0.001
NL	–0.382	115	<0.001

As to the climate factors, the frost-free period negatively correlated to altitude ($r = -0.800$, $P < 0.001$, $n = 131$). Skull size was positively correlated with the frost-free period ($r = 0.449$, $P < 0.001$, $n = 123$). Unexpectedly, skull size had a positive tendency of correlation with temperature ($r = 0.411$, $P < 0.001$, $n = 123$).

DISCUSSION

In our study, it is a coincidence that altitude declined with increasing latitude. Skull size and measurements of greatest length of skull, mastoid breadth and nasal length were all negatively correlated with altitude. The result of partial correlation analysis indicated the same trend for skull size when latitude was treated as a controlled variable. Therefore latitude effect could be excluded. The result that skull size positively correlated with temperature obviously conversely to Bergmann's rule and so it would be improper to interpret the skull size decline by Bergmann's rule. Whether work was done in the field or laboratory to evaluate a cline, it's incomprehensive to account for Bergmann's rule by temperature only. Considering the unique environment of the Tibetan Plateau, which holds the uplift to an average elevation exceeding 5000 m a.s.l, we contribute the decline of skull size to three main causes: hypoxia (or low oxygen pressure), food shortage caused by short frost-free period and energy distribution.

Generally, in response to stressful environmental conditions, some organisms have metabolic rates below normal resting level for body size (GILLOOLY *et al.* 2001). Organisms at high altitude must adapt to the stress of limited oxygen availability relative to sea level and still sustain aerobic metabolic processes. For example, at an altitude of 4000 m (13,200 ft) the concentration of oxygen in 1 liter of inspired air is 21% oxygen, just as at sea level, but because of the lower barometric pressure, 1 liter of air at 4000 m contains just 63% of the number of oxygen molecules at sea level (BEALL 2000), which leads to hypoxia in animals. Hypoxia is the most prominent stress that populations living at high altitudes must deal with (HAMMOND *et al.* 2001). The oxygen consumption of animals will show a drop under hypoxia conditions (VAN DEN THILLART *et al.* 1992) and this reduces the amount of oxygen available to the tissue (MORAN 1982). In this condition, the same quantity food that a pika consumes will produce less energy than in normal conditions. Animals living at high altitudes generally have increased energy demands and energy intake for colder surroundings and may experience limitations to aerobic activities such as exercise and heat production for lower oxygen concentration (SNYDER 1981, CHAPPELL *et al.* 1988). There comes a dilemma that the maximum metabolic rates of mammals will decrease when they are under low oxygen pressure and increase when they are stressed by low environmental temperature (CERRETELLI 1976, WIKLER 1980, REZENDE *et al.* 2004). This is the case with the Daurian pikas that inhabit the Tibetan Plateau. Daurian pikas have to balance the conflict of low oxygen pressure and low environmental temperature for maintaining physical activity. Smaller skull size appears as one such adaptation to achieve this balance.

Body size is the major determinant of daily energy and food requirements, accounting for approximately 95% of the variation present in currently available results (NAGY 2005). Daily food needs of free-ranging vertebrates, within taxonomic classes, are determined primarily by body size (mass). Food quality and abundance have a strong positive association with body size for some mammals (LANGVATN & ALBON 1986, LINDSAY 1986, ERLINGE 1987). CHOWN and KLOK (2003) stated that availability of resources is likely to constrain body size irrespective of the influence of temperature on growth and development above the lower development threshold. Compared with populations inhabiting lower altitude regions, pikas inhabiting higher altitude regions will experience food shortages. This could be inferred by evaluating the frost-free period as showed in the results. As herbivorous species, Daurian pika directly relies on primary productivity. Since the frost-free period negatively correlated to altitude, the higher the altitude, the shorter the frost-free period. It brings on a shorter growth period of grass, which is the main food resource of the Daurian pika. In addition, the pikas build “haypile” caches from which they feed during long winters (DEARING 1997) as they show no torpor or hibernation during the winter months. Thus they spend more time and energy collecting hay for warm bedding and food storage than those living in lower altitude regions.

Adjustment of metabolic enzyme activities may be of particular importance to mammals that inhabit high altitudes (SHEAFOR 2003). Not only are these animals continuously subjected to low partial pressures of oxygen but they also have the added metabolic cost of maintaining body temperature while being exposed to extremely low ambient temperatures. The phenotypic changes in deer mice were widespread across the cardiac, hematological, respiratory and digestive systems (HAMMOND *et al.* 2001). In deer mice it was found that the masses of both small intestine and kidney were negatively correlated with altitude, while lung mass and hematocrit were positively correlated with altitude. Such adjustments and changes demand Daurian pika in higher altitudes to deal with energy in different ways to those in lower altitudes.

Evidence on paleontology and the results of mitochondrial DNA restriction site analysis indicated that the Tibetan Plateau and adjacent area could be considered as the centre responsible for the abundance of recent *Ochtona* species (YU *et al.* 1992, YU *et al.* 1998, NIU *et al.* 2004). Some closely related species that inhabit the same area, e.g. plateau pika (*O. curzoniae*), compete for food resources. Daurian pikas had to use extra energy in protection and alerting activities for keeping from being captured by predators.

In spite of many interpretations, such as heat conservation, seasonality, temperature, moisture, resource availability, exploiting stored food reserves, microclimatic refugia, hibernation or torpor, range restriction, competition and predator, measurement error and so on (SEARCY 1980, DUNBRACK & RAMSAY 1993, STEUDEL *et al.* 1994, ASHTON *et al.* 2000, FRECKLETON *et al.* 2003, ASHTON 2004, BLACKBURN & HAWKINS 2004), Bergmann's rule, at least in small mammals, may be a null hypotheses for small animals.

We conclude that the skull size of Daurian pikas decreased with increasing altitude. As the temperature decreased with altitude, it's a result of converse to Bergmann's rule. This confirmed that Bergmann's rule is not universally valid on interpreting for animal body size cline. We contribute this decline to hypoxia, food shortage caused by short frost-free period and energy distribution. The interaction of environmental factors, especially lower oxygen concentration, forced Daurian pikas inhabiting different altitudinal regions to corresponding selections. We suggest that low oxygen concentration and frost-free period should be considered when animal body size cline is discussed.

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