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CONFORMITY TO BERGMANN'S RULE IN THE PLATEAU PIKA (*OCHOTONA CURZONIAE* HODGSON, 1857) ON THE QINGHAI-TIBETAN PLATEAU

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Interspecific and intraspecific variation in the body sizes of warm-blooded animals is usually correlated with geographical gradients (latitude and/or altitude) according to the well-known Bergmann's rule. However, what determines conformity to Bergmann's rule or even whether this rule is valid has been debated. We tested the relationships between skull size of the plateau pika (*Ochotona curzoniae*) collected from different geographic localities and two geographic variables (latitude and altitude) as well as some environmental factors that usually change with geographical gradients on the Qinghai-Tibetan Plateau. Our results indicated that skull size was positively correlated with both latitude and altitude, and negatively correlated with annual temperature, annual precipitation, and annual net primary production. These results indicated conformity to Bergmann's rule in this species, i.e., the body size of the plateau pika tends to increase with climate severity and food scarcity.

Key words: Bergmann's rule, geographic variables, climatic variables, food resource

INTRODUCTION

The physical size of an animal is an important biological parameter. It has close relationships with rate of diffusion, rate of heat transfer, and other physiological functions (SCHMIDT-NIELSEN 1984). There are distinct geographical patterns of size variation either inter- or intra- warm-blooded species, the best known being Bergmann's rule (MCNAB 1971), which states that body size tends to increase with latitude and altitude. Although Bergmann formulated his rule based on body size variation among different species, an alternative rule or explanation by MAYR (1956) and JAMES (1970) emphasizes intraspecific variation and is also widely accepted (BLACKBURN *et al.* 1999, BLACKBURN & HAWKINS 2004).

Based on their analysis of the relationship between body size and latitude and/or temperature within various species of mammals, ASHTON *et al.* (2000) found broad support for Bergmann's rule. MEIRI and DAYAN (2003) also con-

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cluded that the Bergmann's rule was valid for most mammalian and avian species. Many species, however, do not follow Bergmann's rule or even follow the converse to Bergmann's rule. (ASHTON *et al.* 2000, OCHOCINSKA & TAYLOR 2003, MEIRI *et al.* 2004, LIAO *et al.* 2006).

The current study determined whether Bergman's rule applies to the plateau pika. The extant pikas are endemic to the Holarctic realm and consist of a monotypic genus, *Ochoton*a (NIU *et al.* 2004). Some pika species have broad distributions and can be good candidates for testing Bergmann's rule because species with large geographical ranges are likely to exhibit size clines (MEIRI *et al*. 2007). A previous study (LIAO *et al.* 2006) focused on the Daurian pika (*Ochotona daurica*), which occurs mainly in northern China as well as on the Qinghai-Tibetan Plateau; the authors concluded that this species followed the converse to Bergmann's rule. Another animal on the Qinghai-Tibetan Plateau, the lizard *Phrynocephalus vlangalii*, also followed the converse to Bergmann's rule (JIN *et al.* 2007), although the adaptive patterns for ectotherms may differ from that for endotherms (PINCHEIRA-DONOSO *et al.* 2008).

Whether these two exceptions to Bergmann's rule are caused by the special geographical characteristics of the Qinghai-Tibetan Plateau (extremely high elevation) is unclear because of the scarcity of other relevant data from this region. In this study we analyzed the relationships between the geographic variables (latitude and altitude) and body size variations of another pika species, *Ochotona curzoniae* (the plateau pika), which is a keystone species and is broadly distributed on the Qinghai-Tibetan Plateau (LAI & SMITH 2003). To further our understanding of Bergmann's rule, we also determined whether body size was related to mean annual temperature, annual precipitation, and annual net primary production.

MATERIALS AND METHODS

Individual pikas were caught with spring-loaded bar mousetraps on the Qinghai-Tibetan Plateau in July 2006. Latitude, longitude, and altitude information at each sampling site were recorded using an Etrex GPS (Global Position System) unit (Garmin, Taiwan). The sex of each individual was identified by body dissection. The skulls were collected and cleaned in laboratory. The age stages were determined based on the developmental status of the palatal bridge (SHI *et al*l. 1978), and only adults were used for the analysis. Skulls were measured to 0.01 mm using vernier calipers. So that we could compare our data with the former analysis of Daurian pika, we measured greatest length of skull (GLC) and nasal length (NL) following the methods of LIAO *et al.* (2006). Unfortunately, mastoid breadth (MB) could not be recorded, as was done in LIAO *et al.* (2006), because the mastoid was usually too fragile to measure. As a result, the zygomatic breadth (ZB) was used instead of MB. We tested the deviations of these three variables with ANOVA for males and females.

The data for annual temperature (AT), annual precipitation (AP), and annual net primary production (ANPP) were extracted from three data products using Spatial Analysis Tools in ArcGIS 9.0

(Environmental Systems Research Institute). The AT and AP data products were provided by the Environmental & Ecological Science Data Center for West China, National Natural Science Foundation of China (http://westdc.westgis.ac.cn). The AT and AP data products were the average values from 1960 to 1990. ANPP data products were downloaded from the website of The University of Montana (ftp://ftp.ntsg.umt.edu). We used the average values of seven annual NPP data sets from the years 2000 to 2006.

With Spearman correlation analysis, we analyzed the relationships between latitude and altitude and skull size variables to test whether body size was significantly related with geographic gradient. It should be noted that latitude and altitude values in the study region were negatively correlated with high significance (Spearman correlations, $R = -0.629$, $P < 0.001$). Because latitude and altitude usually have similar effects on local climate and organisms, the highly negative correlation between these two geographic variables might confuse our analysis. Thus, we used partial correlation analysis rather than simple bivariate correlation analysis to indicate the relations between each of the two geographic variables and skull size. We used both Spearman correlation and multiple regression analyses to test the effects of AT, AP, and ANPP on skull size. All statistical analyses were performed using SPSS 15.0 for Windows software.

RESULTS

A total of 183 (95 females and 88 males) adult individuals from 23 sampling sites were measured. Sample size, geographic information, AT, AP, and ANPP are listed in Table 1. There was no significant difference in GLS ($F = 0.884$, $P = 0.348$), ZB ($F = 0.076$, $P = 0.783$), or NL ($F = 0.033$, $P = 0.857$) between the two sexes. Thus, the data for the three measurements of female and male individuals were combined. The partial correlation analysis showed that the three skull size variables were positively and significantly correlated with latitude; however, only GLS was positively and significantly correlated with altitude (Table 2).

Spearman correlation analysis showed that, AT, AP, and ANPP were negatively related on skull size of the plateau pika. AT and AP were significantly correlated with all three skull size variables. ANPP was significantly correlated with GLS and NL (rather than ZB). Although the R^2 values were small (perhaps because of the complex relationships between environment and biosystem), the multiple regression analysis also showed significant relations between these three environmental variables and each of the three skull size measurements (Table 3).

DISCUSSION

In our study, the skull size of plateau pika increased with increasing latitude and altitude. In contrast to LIAO *et al.* (2006) and JIN *et al.* (2007), our results show that the skull size variations of plateau pika on the Qinghai-Tibetan Plateau followed Bergmann's rule.

Table 1. Sample size of plateau pika and the information about the sampling sites.

Site	Sample size	Latitude (N, °)	Longitude (E, °)	Altitude (m)	AT (°C)	AP (mm)	ANPP (g cm^{-2})
Anduo1	8	32.31	91.73	4675	–2.6	468.96	97.76
Anduo2	3	32.18	91.59	4586	–2.0	433.69	119.7
Basu1	4	30.19	97.30	4338	2.2	468.13	278.19
Basu2	7	30.53	97.13	4348	2.0	715.87	165.82
Chengduo	3	33.36	97.24	4348	–2.4	595.34	171.20
Dangxiong	8	30.72	91.04	4807	–1.0	527.83	132.83
Gangcha	4	37.50	100.48	3164	–1.6	457.52	198.04
Huashixia	14	35.08	98.85	4237	–3.5	400.40	115.23
Jiangzi	7	28.90	90.10	4660	1.6	452.45	137.77
Kunlunshan	13	35.71	94.06	4532	–4.0	192.38	51.34
Langkazi	7	29.11	90.42	4425	2.9	559.60	114.57
Naqu	6	31.44	92.28	4420	–0.7	487.94	143.81
Nimu	5	29.50	90.27	3908	5.2	479.85	126.43
Qilian	18	37.96	100.25	3645	–2.5	486.20	238.26
Qinghaihu	9	36.63	100.11	3175	0.9	344.63	200.50
Qumalai	12	34.14	95.88	4389	–3.1	484.24	96.33
Shiqu	13	33.03	98.02	4254	–0.6	563.03	154.64
Tianjun	5	37.17	99.28	3275	0.0	366.26	166.14
Tuotuohe	6	34.33	92.59	4533	–4.1	296.06	34.89
Xidatan	7	35.73	94.31	4110	–2.1	97.36	125.11
Xingxinghai	8	34.83	98.13	4194	–3.3	319.64	91.30
Zhalinghu	5	35.07	97.72	4234	–3.1	362.72	121.79
Zhiduo	11	33.54	96.06	4308	–1.7	479.83	112.91

There are many suggested mechanisms or hypotheses to explain Bergmann's rule, the most common one being the 'Heat Conservation Hypothesis' (BLACKBURN *et al.* 1999). BROWN and LEE (1969) indicated that, rather than modifications of body temperature or metabolic rate, modifications of the factors influencing rates of heat loss could be the potential mechanisms for thermal adaptation. Larger body size reduces the surface area to mass ratio and thereby decreases heat loss per unit mass (MAYR 1963). Thus, races of a species that live in cooler environments should be larger in order to adapt to the ambient temperature. Our results, that the three skull size variables were negatively correlated with the annual temperature, support this view.

Table 2. Correlation values (R) between environmental variables and the skull size of plateau pika (* = *P* <0.05; ** = *P* <0.01; N.S. = not significant).

Skull measurement	Latitude (a)	Altitude (b)	AT (c)	AP (c)	ANPP (c)
GLS	0.248** df =180	0.164* df =180	–0.279** df =183	–0.289** df =183	–0.194** df =183
ZB	0.348** df =180	N.S. df =180	–0.191** df =183	–0.281** df =183	N.S. df =183
NL	0.236** df =180	N.S. df =180	–0.233** df =183	–0.199** df =183	–0.166* df =183

a = Partial correlation between latitude and the skull size with altitude as the control variable

b = Partial correlation between altitude and the skull size with latitude as the control variable

c = Spearman correlation between the three environmental variables and the skull size

Moisture (precipitation) is considered another important factor that underlies Bergmann's rule (JAMES 1970, BURNETT 1983, WIGGINTON & DOBSON 1999, YOM-TOV & GEFFEN 2006). Our study showed that annual precipitation was negatively correlated with body size variables. One possible explanation is related to the need to conserve water in dry environments (BURNETT 1983). CHEW (1955) indicated that the loss of surface water (from skin and respiratory surface) greatly affects the water balance of small animals. At the same time, water loss is positively correlated with surface area as well as metabolic rate (CHEW 1955, CHEW & DAMMANN 1961). Moreover, surface area and metabolic rate decrease with increasing body size, according to the so called Allometric Scaling Law (Kleiber's rule) (WEST *et a*l. 1997, HOPPELER & WEIBEL 2005). As a result, a larger body size can help an organism conserve water in dry environments. Because annual rel-

Table 3. The three best models in the multiple regression of skull size (GLS, ZB, and NL; the dependent variables) on environment (AP, AT, and ANPP; the independent variables) (** = *P* < 0.01). K is the number of parameters in the model; R^2, the squared multiple correlation.

Variables selected		K	R^2
GLS	1. AP	1	0.074**
	2. AP, AT	2	0.083**
	3. AP, AT, ANPP	3	0.086**
ZB	1. AP	1	0.129**
	2. AP, ANPP	2	0.179**
	3. AP, ANPP, AT	3	0.192**
NL	1. AP	1	0.048**
	2. AP, AT	2	0.059**
	3. AP, AT, ANPP	3	0.061**

ative humidity and annual precipitation are closely correlated (based on the data from China Meteorological Administration, http://www.cma.gov.cn), we suggest the Allometric Scaling Law as a possible mechanism for the significant negative correlations between precipitation and body size in our study.

Recent studies are paying more attention to the effects of food availability on body size variations. As a herbivorous species, the plateau pika directly relies on primary productivity, and ANPP could be an adequate index of the average food conditions of a year. A question that cannot be ignored is whether larger or smaller individuals are better adapted to surviving food scarcity. Most studies tend to consider that food scarcity selects for a smaller body size (OCHOCINSKA & TAYLOR 2003, YOM-TOV & YOM-TOV 2005, LIAO *et al.* 2006, MEIRI *et al.* 2007). We argue, however, that food scarcity could be a positive driver of body size. According to the Allometric Scaling Law mentioned above, larger individuals will have lower relative metabolic rates and this will help them save energy in arid environments. Larger body size and lower metabolic rates should also help organisms survive when food is scarce.

Both bivariate correlation and multiple regressions indicated a similar effect of the three environmental variables, i.e., bad environmental conditions (cold, drought, and food scarcity) apparently generate larger plateau pika. In other words, a larger body size, causing a smaller ratio of surface area to mass and a relatively slow metabolic rate, will reduce the loss of heat, water, and energy, and thereby help the plateau pika survive bad environmental conditions.

Daurian pika and plateau pika are very similar in many ways. For example, the GLS was 40.40 ± 1.12 g for the Daurian pika (LI 1989) and 40.48±1.83 g for the plateau pika. The two species also have similar food resource niches (FAN *et al.* 1995), and both form burrows and store food to survive the winter (ZHANG *et al.* 2005). Interestingly however, the two species differ with respect to Bergmann's rule. Although we were unable to compare all aspects of the two studies, the difference between the species in the relationship between altitude and skull size is incontestable. LIAO *et al.* (2006) attribute their results to hypoxia and food shortage in the sites with high altitude. However, the stresses from hypoxia (altitude) and food shortage (ANPP) in our study were negatively rather than positively correlated with body size of plateau pika. As a result, this difference between Daurian pika and plateau pika must reflect different adaptive strategies of the two species. The Daurian pika is mainly distributed on relatively lower altitudes (less than 2500 m) and inhabites only a small area on the higher East Qinghai-Tibetan Plateau, while the plateau pika mostly occurs higher than 3200 m (FAN *et al.* 1995). Recent studies showed that the plateau pika has developed many peculiar adaptations to the environmental stresses on the plateau. For example, the plateau pika has a sensitive nonshivering thermogenesis system, which is a rapid and effective way to generate heat (WANG *et al.* 1999). ZHAO *et al.* (2004) suggested that HIF–1α may play an important role in the adaptation of plateau pika to hypoxia, especially in the brain and kidney. Also, WANG *et al.* (2006) indicated that plateau pikas mainly depend on increasing thermogenic capacities (for example, on enhancing non-shivering thermogenesis, cytochrome c oxidase activity, and mitochondrial uncoupling protein 1 (UCP1) contents in brown adipose tissues in winter) rather than decreasing body size to cope with cold. We suggest that, based on the special adaptive strategies of the plateau Pika, increasing rather than decreasing body size (as its counterpart, the Daurian pika, does) helps plateau pikas survive serious environmental stresses on the Qinghai-Tibetan Plateau.

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