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Elevational variation in body size of *Phrynocephalus vlangalii* in the North Qinghai-Xizang (Tibetan) Plateau

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ABSTRACT. We examined elevational and environmental aspects of body size variation in the Qinghai toad-headed lizard, *Phrynocephalus vlangalii*, using principal component analysis (PCA) of 9 morphological traits taken from 565 lizards from 17 populations. The first principal component (PC1) accounted for 67% of the size variation in males and 62% in females. For both males and females, PC1 decreased with increasing elevation. When analyzed in relation with respect to environmental variables, body size showed positive relationship with temperature, air pressure, and activity season length, but showed weaker or inconsistent relationships with rainfall and humidity. The described pattern is the converse of Bergmann's rule for this lizard species and suggests that this body size pattern is driven by temperature, air pressure or length of the activity season.

KEY WORDS : Altitudinal variation, Bergmann's rule, *Phrynocephalus vlangalii*, Body size

INTRODUCTION

Bergmann's rule predicts larger body size in colder areas and is assumed to be an adaptive response to environmental temperature (MAYR, 1956). Substantiated for endotherms (ASHTON et al., 2000; ASHTON, 2002; MEIRI & DAYAN, 2003), Bergmann's rule also holds for some ectothermic groups (ASHTON, 2002; ASHTON & FELDMAN, 2003), but this excludes squamates, which, in general, are smaller in colder areas (ASHTON & FELDMAN, 2003). Detailed studies of individual squamate species are necessary to better understand why they represent an exception to the general vertebrate pattern.

Here we evaluate body size changes in the Qinghai toad-headed lizard, *Phrynocephalus vlangalii,* across an elevational gradient in the Tibetan Plateau. Based on previous surveys (ASHTON & FELDMAN, 2003), we predict that *P. vlangalii* will decrease in body size with increased elevation and decreased temperature. Body sizes of lizards could also respond to other environmental factors, thus we also evaluate the effects of relative humidity, rainfall, oxygen pressure, and activity season length on body size variation. We predict shorter activity period and lower oxygen pressure could lessen net energy acquisition of lizards in high environments and have a negative impact on body size through reduced growth. Humidity and rainfall might also play a role in determining size variation in this arid-environment sand lizard.

Understanding the causal basis of geographic variation in body size has been the focus of much work in life-history evolution (STEARNS, 1992; ROFF, 2001). Elevational variation in body size is often correlated with environmental factors since body size is determined by both genetic and environmental factors (ENDLER, 1977). The relationship between variation in environmental gradients and the consequent variation in growth and body size has been of particular interest to evolutionary ecologists (ATKINSON, 1994; ATKINSON & SIBLY, 1997; ANGILLETTA & DUNHAM, 2003). Though these general patterns of body size variation relative to environmental factors have been well studied in endothermic vertebrates for many years (RENSCH, 1936; MAYER, 1963; NEVO, 1981; DUNHAM et al., 1989; BEAUPRE, 1995; ASHTON et al., 2000), relative to the large number that have focused latitude-based differences (ANGILLETTA et al., 2004; SEARS & ANGILLETTA, 2004). Ancestors of *Phrynocephalus* evolved into viviparous lizards during the uplifting of the Tibetan Plateau (WANG & MACEY, 1993; ZENG et al., 1997). With increasing elevation, air temperature becomes cooler, relative humidity increases, annual rainfall increases, and partial pressure of oxygen (pO_2) decreases (YOSHINO, 1975). Cooler environments could certainly promote evolutionary shifts (HEULIN et al., 1991; SHINE, 1995; ANDREWS, 2000; BLACKBURN, 2000; SURGET-GROBA et al., 2001). Because studies (LIAO et al., 2006) have indicated that morphological trait variation may have been influenced by the Tibetan Plateau uplift, *P. vlangalii* is a good model organism for studying body size evolution in response to variation of environmental factors across its broad elevational range from 2000 to 4600meters (ZHAO et al., 1999). We surveyed the size variation and explained the environmental factors that drive the pattern of body size.

MATERIALS AND METHODS

Specimens were collected from 17 populations in the North Tibet Plateau (Table 1) during the breeding period (from July to August of 2004). The following traits were measured: snout-vent length (SVL), total tail length (TL), head length (HL), head width (HW), head depth (HD), arm length (AL; distance between axilla and wrist), leg length (LL, distance between groin and ankle), distance between axillae (DBA) and distance between iliac crests (DBI). Specimens were preserved in the Lab of Zoology, School of Life Sciences, Lanzhou University. All traits were measured to 0.1mm using vernier calipers. At sampled sites, elevation was measured by GPS.

Sex was determined based on the morphological descriptions of *P. vlangalii* (Zhao et al., 1999). Female adult body size was based on the shortest SVL of a pregnant female. For males, the right testis, as well as part of the ductus epididymis, was dehydrated in ethanol, cleared in xylene, embedded in paraffin wax, sectioned at 8-10µm, and stained with Erlich's haematoxylin and eosin (Humason, 1967). Maturity in males was based on a testicular stage of 4-5 (Vieira et al., 2001) or presence of sperm.

Climatic data for the sampling areas of annual mean temperature, mean air pressure, mean rainfall and mean relative humidity was collected for all sampling areas from the Chinese National Climatic Data Center (CDC).

We used multivariate analysis of variance (MANOVA) to determine whether there were significant differences between the sexes. We performed principal component analyses (PCA) using the correlation matrix of the 9 morphological variables for each sex. Only PC1 was used into subsequent analyses, because it had an eigenvalue greater than 1.0. PC1 was essentially used as a surrogate for "size". We regressed the first principal component score (PC1) against elevation, air pressure, temperature, rainfall and humidity using least-square regression to determine whether clinal variation exists. All analyses were performed using population means and individual datapoints. All morphological data were expressed as mean ± S.E.M. Probability values below 0.05 were considered to be statistically significant.

TABLE 1

Morphological data: Mean ± S.E.M. of male (N=233) and female (N=332) adults in 17 populations of *Phrynocephalus vlangalii.* (SVL, snout-vent length; TL, tail length; AL, arm length; LL, leg length; HL, head length; HW, head width; HD, head depth; DBA, distance between axillae; DBI, distance between iliac crests; f, female; m, male).

Population	Elevation (m)	Sex	n	SVL (mm)	TL (mm)	AL (mm)	LL (mm)	HL (mm)	HW (mm)	HD (mm)	DBA (mm)	DBI (mm)
Guide	2289	f	10	60.8±1.5	63.3±0.8	9.4±0.2	26.0±0.4	15.5±0.3	13.8±0.2	10.2±0.2	12.5±0.3	8.8±0.2
		m	10	57.3±1.4	66.0±1.7	19.1±0.5	24.7±0.7	15.2±0.2	13.8±0.2	10.2±0.2	11.9±0.2	8.2±0.3
Tianzhu	2751	f	9	64.0±1.5	58.8±1.1	19.1±0.5	23.9±0.5	15.5±0.3	13.4±0.1	10.4±0.1	12.7±0.4	8.8±0.2
		m	7	63.3±1.1	65.0±1.2	20.5±0.6	25.3±0.5	15.9±0.2	14.2±0.2	11.0±0.3	12.3±0.3	8.8±0.2
Lenghu	2756	f	9	57.3±1.1	55.3±2.1	20.9±0.4	26.9±0.4	12.9±0.3	12.6±0.3	9.3±0.3	10.7±0.3	7.8±0.2
		m	6	55.6±2.0	53.0±2.7	20.6±0.7	26.3±0.9	12.9±0.3	12.6±0.4	9.1±0.3	11.1±0.5	7.7±0.5
Lumuhong	2857	f	6	59.0±3.3	65.8±3.7	21.5±0.8	28.2±0.6	14.0±0.8	14.5±0.7	9.8±0.4	11.2±0.7	6.5±0.4
		m	6	62.6±2.1	70.3±3.3	23.3±0.5	31.5±0.4	14.0±0.2	14.7±0.4	10.6±0.6	11.5±0.7	7.8±0.6
Delingha	2873	f	23	67.7±1.4	67.2±1.4	22.7±0.5	29.5±0.5	15.0±0.2	14.8±0.2	10.4±0.2	14.2±0.4	7.9±0.3
		m	17	67.3±1.0	73.0±1.2	23.2±0.6	31.3±0.5	15.2±0.2	15.2±0.2	11.2±0.3	14.6±0.2	8.1±0.3
Wutumeiren	2894	f	11	53.6±0.7	55.3±0.8	18.6±0.2	23.3±0.2	12.8±0.2	11.7±0.2	8.5±0.1	10.1±0.2	7.6±0.2
		m	9	56.2±1.5	62.1±1.6	19.1±0.5	26.2±0.3	13.9±0.2	12.5±0.2	9.4±0.2	10.2±0.1	7.5±0.1
Maqu	2926	f	32	57.8±0.6	56.6±0.5	15.9±0.2	21.9±0.2	14.2±0.2	13.2±0.1	10.1±0.1	11.6±0.2	8.1±0.1
		m	25	57.5±0.6	60.3±0.7	16.7±0.1	23.4±0.2	13.7±0.1	12.9±0.1	10.3±0.1	11.7±0.2	8.1±0.1
Wulan	2929	f	45	56.5±0.8	53.8±0.7	21.1±0.4	24.6±0.3	13.2±0.1	12.3±0.1	9.0±0.1	11.6±0.2	8.2±0.1
		m	18	56.6±1.4	61.1±1.6	22.0±0.6	26.6±0.7	13.4±0.4	12.7±0.4	9.8±0.3	11.8±0.3	7.7±0.2
Xiangride	3074	f	27	61.2±1.0	61.4±1.0	20.1±0.4	24.9±0.5	12.4±0.2	12.7±0.2	9.4±0.2	11.5±0.2	6.8±0.1
		m	9	59.0±1.7	63.9±1.7	19.1±1.1	24.0±0.8	12.1±0.4	12.6±0.4	9.5±0.4	10.5±0.4	5.7±0.3
Mangya	3174	f	8	56.4±1.5	55.6±1.1	21.3±0.5	25.5±0.5	13.5±0.3	12.7±0.3	9.9±0.4	11.5±0.2	8.3±0.2
		m	7	60.5±1.2	62.2±1.9	22.5±0.5	29.8±0.9	13.6±0.4	13.8±0.2	9.8±0.3	11.3±0.4	7.1±0.4
Doulan	3190	f	20	59.0±1.1	56.0±0.9	19.8±0.4	25.9±0.4	13.3±0.2	13.4±0.1	9.8±0.1	11.1±0.2	7.2±0.2
		m	17	54.1±1.0	56.8±1.4	19.3±0.3	26.0±0.5	13.3±0.2	12.6±0.2	10.0±0.1	11.2±0.2	7.3±0.2
Dachaidan	3200	f	8	55.3±1.9	52.5±3.4	19.1±1.0	24.9±1.2	12.8±0.4	12.3±0.2	8.8±0.2	10.6±0.4	7.3±0.1
		m	8	59.3±1.7	64.0±2.6	22.9±1.4	30.0±1.3	13.8±0.1	14.0±0.1	9.9±0.2	11.1±0.4	7.5±0.1
Ganzihe	3242	f	10	57.3±1.8	48.3±1.3	18.7±0.4	22.9±0.3	12.7±0.2	11.9±0.3	8.9±0.2	10.7±0.3	7.9±0.3
		m	14	57.3±1.3	54.5±2.0	19.2±0.4	24.9±0.5	13.4±0.2	12.7±0.2	9.8±0.2	11.2±0.2	7.8±0.1
Guinan	3370	f	19	54.6±1.1	54.2±1.4	18.7±0.4	25.3±0.6	13.4±0.2	12.2±0.2	9.0±0.2	11.5±0.3	7.6±0.2
		m	18	60.3±1.7	62.8±2.4	20.6±0.5	28.5±0.8	14.6±0.3	13.0±0.3	10.0±0.3	12.1±0.4	8.4±0.2
Xiaman	3470	f	14	61.2±0.8	59.8±0.6	20.6±1.2	27.3±1.5	14.4±0.2	13.9±0.3	10.5±0.1	12.2±0.3	8.2±0.1
		m	10	58.5±0.8	63.2±0.8	17.4±0.2	24.5±.0.3	14.4±0.1	13.3±0.2	10.3±0.2	11.8±0.2	7.9±.0.1
Maduo	4250	f	23	54.5±1.3	52.1±1.2	18.4±0.3	24.4±0.5	12.3±0.2	12.4±0.2	9.3±0.1	11.0±0.3	7.0±0.2
		m	19	54.1±0.8	56.6±0.8	19.0±0.3	25.0±0.5	12.9±0.2	12.6±0.2	9.8±0.1	10.5±0.2	6.0±0.2
Beiluhe	4565	f	58	52.7±0.5	49.4±0.6	17.8±0.2	23.6±0.2	12.0±0.1	11.7±0.1	8.5±0.1	10.7±0.1	7.1±0.1
		m	33	52.0±0.5	52.4±0.6	17.9±0.2	24.1±0.2	11.8±0.1	11.5±0.1	8.4±0.1	10.4±0.1	6.3±0.1

TABLE 2

Loading and the percentage of total variance explained for the first three principal components among 9 morphological traits of males (N=233) and females (N=332) of *Phrynocephalus vlangalii.*

Character	**Male**			**Female**		
	PC1	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**
SVL	0.915	0.016	-0.019	0.877	-0.002	-0.161
TL	0.890	0.015	-0.174	0.836	0.057	-0.312
AL	0.721	0.583	0.149	0.697	0.528	0.323
LL	0.758	0.543	0.124	0.717	0.568	0.119
HL	0.868	-0.281	-0.084	0.833	-0.339	0.020
HW	0.880	-0.013	-0.301	0.860	-0.047	-0.262
HH	0.805	-0.269	-0.316	0.779	-0.235	-0.242
DBA	0.814	-0.010	0.263	0.836	-0.040	0.154
BDI	0.666	-0.109	0.525	0.606	-0.465	0.596
Total variance	66.747	11.109	6.783	61.916	11.059	8.318

RESULTS

The minimum adult male and female sizes were 49mm and 46mm. MANOVA with sex as the independent variable and the 9 morphological traits as the dependent variables indicated substantial sexual dimorphism in the *P. vlangalii* ($F_{9,555}$=21.21, $P<0.001$), so genders were separated for further analyses.

PC1 accounted for 66.7% of the variation in males, and all variables had positive loading values of 0.666 or above (Table 2). There was a significant linear regression (N=233, F=77.5, $P<0.001$ or N=17, F=6.9, P=0.019) with a decrease in PC1 score with increased elevation, with elevation accounting for 25.1% (N=233) or 31.7% (N=17) of the variation (Fig. 1A). PC1 accounted for 61.9% of the variation in females and all variables had positive loading values of 0.606 or above (Table 2). There was a significant (N=332, F=91.5, $P<0.001$; N=17, F=7.5, $P<0.015$) decrease in PC1 score with increased elevation, with elevation accounting for 21.7% (N=233) or 33.3% (N=17) of the variation (Fig. 1B). These results confirmed the hypothesis that both male and female lizards at higher elevations are smaller than at lower elevations.

TABLE 3

General linear regression was used depending on the relationship between the first principal component and each annual mean climatic factor. R^2, unstandardized coefficient, and constant of model, and significance of ANOVA analyses for testing the model were shown.

Factors	**Sex**	**R^2**	**Slope**	**Constant**	**P**
Air pressure	Male	**0.257**	0.001	-7.544	<0.001
(0.1BPa)	Female	**0.202**	0.001	-6.835	<0.001
Temperature	Male	**0.229**	0.018	-0.181	<0.001
(0.1°C)	Female	**0.238**	0.019	-0.207	<0.001
Rainfall	Male	0.059	-0.0001	0.316	0.004
(0.1mm)	Female	0.012	-0.0006	0.189	0.053
Humidity	Male	0.083	-0.026	1.309	<0.001
(%)	Female	0.027	-0.016	0.075	0.004

Significant positive linear regressions were found between PC1 scores and increased temperature, or air pressure, while significant negative regressions were found between PC1 scores and rainfall or relative humidity (Table 3). The exception to this was the lack of a significant regression between PC1 score and rainfall for females (P=0.053). On investigating the explanatory power of the models, we found that temperature (R^2: male, 0.229; female, 0.238) and air pressure (R^2: male, 0.257; female, 0.202) account for a larger proportion of the body size variation than rainfall (R^2: male, 0.059; female, 0.012) or relatively humidity (R^2: male, 0.083; female, 0.027).

DISCUSSION

Body size of *P. vlangalii* is positively correlated with temperature which is the converse of the pattern predicted by Bergmann's rule. Because some meteorological data are likely inter-correlated, making it difficult to discern between the different factors. However, it is not sufficient to evaluate Bergmann's rule through analysis of only one environmental factor. Consideration of the unique environment on the Tibetan Plateau suggests at least three possible effects on body size: temperature, hypoxia and food shortage caused by shorter activity time at higher elevations.

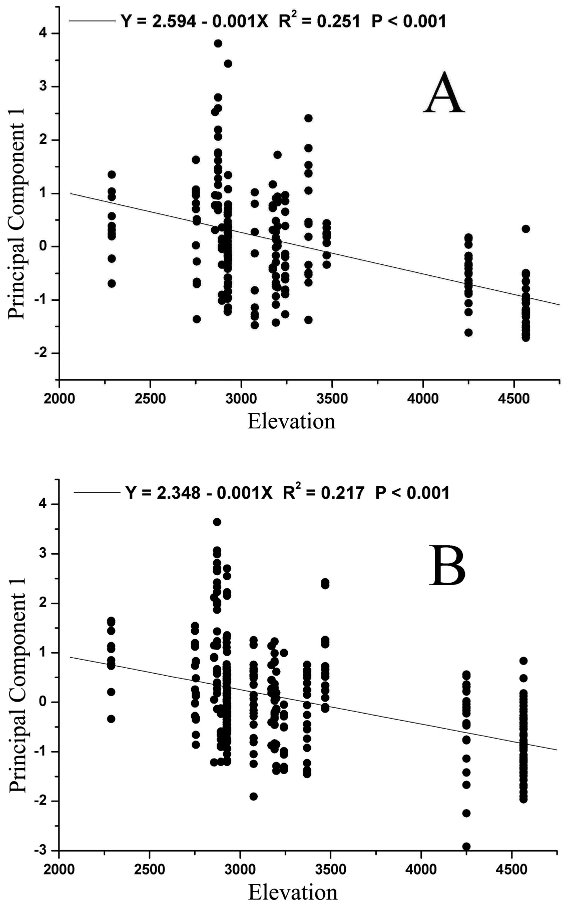

Fig. 1. – Regression analysis plots of the first principal component (PC1) on elevation for (A) males and (B) females.

The validity of Bergmann's rule in ectotherms has been widely questioned (Mousseau, 1997; Blackburn et al., 1999; Belk & Houston, 2002). In particular it has been noticed that lizards in colder environments may grow to a smaller size (Ashton & Feldman, 2003). The traditional heat conservation explanation proposed (Bergmann, 1847; Mayer, 1963) does not apply to these ectotherms (Ashton & Feldman, 2003). Temperature affects the physiological and behavioural performance of ectothermic vertebrates (Navas, 2003). Thermal constraints on ectotherm activity is directly related to the available environmental temperature (De Witt, 1967; Grant & Dunham, 1990). Even when distributed across a wide range of thermal environments, lizards might exhibit only a small and surprisingly consistent range of body temperatures (Bogert, 1949; Andrews, 1998). Consistent patterns of temperature variation are not necessarily associated with elevation within species due to behavioural compensation (Sears & Angilletta, 2004). Behavioural thermoregulation could conceivably be an important buffering mechanism in this small lizard, e.g., shuttling among thermally inhomogeneous patches, though this is thought to be more important in large ectotherms with larger thermal inertia (C. R. Peterson, personal communication, Grant, 1990). Higher body temperatures could help with digestion and development in cooler and unstable environments because most squamates swallow food items whole and retain young for long periods (Ashton & Feldman, 2003). Increased selected body temperature (SBT) by lizards could increase metabolisable energy intake during digestion (Brown & Griffin, 2005), but without optimal warm environments, growth rates of lizards (Dunham et al., 1989) are limited by the rates at which food items passed through the gut. However, energy consumption will be increased by higher body temperatures in an active iguanid lizard relative to an inactive one (Dawson, 1975; Grant, 1990). Therefore there is clearly a trade-off between benefits from thermoregulation activity, such as optimal food assimilation in cooler environments and energy consumption of activity.

At an altitude of 4000m (13,200ft) 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 4000m 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 elevations must deal with (Hammond et al., 2001). Animals at higher elevations must adapt to the stress of limited oxygen availability relative to lower elevation and still sustain aerobic metabolic processes. For example, the oxygen consumption of animals will show a drop under hypoxic conditions (van den Thillart et al., 1992) and this reduces the amount of oxygen available to the tissue (Moran, 1982). Here, the same quantity of food consumed will produce less energy than in normal conditions. However, animals living at high elevations generally have increased energy demands and energy intake and so may experience limitations to aerobic activities such as exercise and heat production due to the lower oxygen availability (Snyder, 1981; Chappell et al., 1988). This is not conducive to increased growth. Organisms may have metabolic rates below normal resting level in response to stressful environmental conditions (Gillooly et al., 2001). This provides a problem in that metabolic rates of reptiles decrease under low oxygen pressure (Thompson et al., 1995; Zari, 1996; Sears, 2005) and low temperature (Kam, 1993; Storey, 1996; Hicks & Wang, 2004), but the rate of energy expenditure per unit mass increases with decreased body size (Peters, 1983). Lizards could therefore benefit from the increased metabolic rate per unit mass to help increase body temperature in cooler environments. *P. vlangalii* has to balance the conflict of hypoxia and lower temperature by maintaining a relatively constant body temperature during activity. Smaller body size appears to be one adaptation that contributes to this.

Daily and seasonal activity periods for a given ectotherm at lower elevations are longer than those for the same ectotherm at higher elevations (Masaki, 1967; Grant & Dunham, 1990). It seems that higher elevational environments could lessen seasonal activity periods, and potentially lessen the available annual forging times and consequently the net energy uptake for an animal at high elevations. This could also lead to a decrease in body size. This pattern has been reported in invertebrates (Mousseau & Roff, 1989) and has been predicted for lizards (Adolph & Porter, 1996; Montgomery et al., 2003).

In conclusion, this study showed that the body size of *P. vlangalii* decreased with increasing elevation. Because temperature decreases with elevation, this represents the converse of Bergmann's rule, and shows that this is not universally valid for interpreting animal body size clines. We attribute this decline to temperature, hypoxia and food shortage caused by shorter activity periods. Different patterns of energy consumption and energy distribution appear to have different effects on body growth, at different elevations.

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