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Original Investigation

Plateau zokors on the Qinghai-Tibetan Plateau follow Bergmann's rule latitudinally, but not altitudinally

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ABSTRACT

Since the first description of the Bergmann's rule, body size clines along environmental gradients have been examined in a wide variety of taxa. Broad support for Bergmann's rule has been found for endotherms and even ectotherms; many species, however, do not follow Bergmann's rule or the converse to Bergmann's rule. We tested the relationship between body size (body weight (BW), body length (BL), and 12 skull size measurements) of a typical subterranean rodent plateau zokor (*Eospalax baileyi*) 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. A total of 523 (212 males and 311 females) adult individuals from 21 sampling sites were analyzed. The results indicated that body size of both males and females was positively correlated with latitude, annual temperature (AT), and annual net primary production (ANPP) and negatively correlated with altitude and annual precipitation (AP). These results indicated that the plateau zokor latitudinally followed Bergmann's rule but altitudinally followed the converse to Bergmann's rule. The environmental factors which may influence the zokors' water balance and food availability were the major driving forces latitudinally and altitudinally shaping the body size of this species, respectively.

Introduction

Bergmann's rule predicts a larger body size for warm-blooded vertebrate species (either interspecifically or intraspecifically, see Meiri 2011) in colder areas and is assumed to be an adaptive response to environmental temperature (Mayr 1956). Since first described (Bergmann 1847), body-size clines along environmental gradients have been examined in a wide variety of taxa (Watt et al. 2010). Broad support (>50%) for Bergmann's rule has been found for endotherms; many species, however, do not follow Bergmann's rule or follow its converse (Ashton et al. 2000; Meiri and Dayan 2003; Ochocinska and Taylor 2003; Meiri et al. 2004; and also see Watt et al. 2010).

Subterranean rodents are a widely distributed group of species those live primarily underground and are highly adapted to that environment (Nevo 1999; Lacey et al. 2000). On the one hand, subterranean mammals are likely candidates of those who may not follow Bergmann's rule because they spend most of the time in favorable and relatively constant thermal conditions throughout their distribution range. Instead, other factors such as food availability (rather than heat conservation) may become a major limiting factor for animals' body size (Mayr 1956; Meiri and Dayan 2003; Medina et al. 2007). On the other hand, digging for food and shelter is an energetically demanding process that can result in heavy energy expenditure, more than that required by aboveground animals (Vleck 1979). The high energy cost makes subterranean rodents have a larger resource (e.g., food, water, etc.) demand and subsequently makes the body size of these animals sensitive to various resource constraints in local environments. Two studies investigated the relationships between environmental factors and body size of subterranean rodents both inter- and intraspecifically (Nevo et al. 1986; Medina et al. 2007), which found that subterranean rodents did vary their body size along environmental gradients, although their conclusions were partially non-coincident. Due to the scarcity of related studies, additional evidence is still needed to test the relationships between body size of subterranean rodents and environmental factors.

Plateau zokors (Rodentia, Muroidea, Myospalacinae, *Eospalax baileyi*) are a typical subterranean rodent species that spend most of their daily life underground and only very occasionally move aboveground for foraging and dispersal (Zhou and Dou 1990). The plateau zokors occur in alpine meadows and prairies in the east of the Qinghai-Tibetan Plateau's (QTP, which is the largest and highest plateau on earth) with a relatively large geographical range

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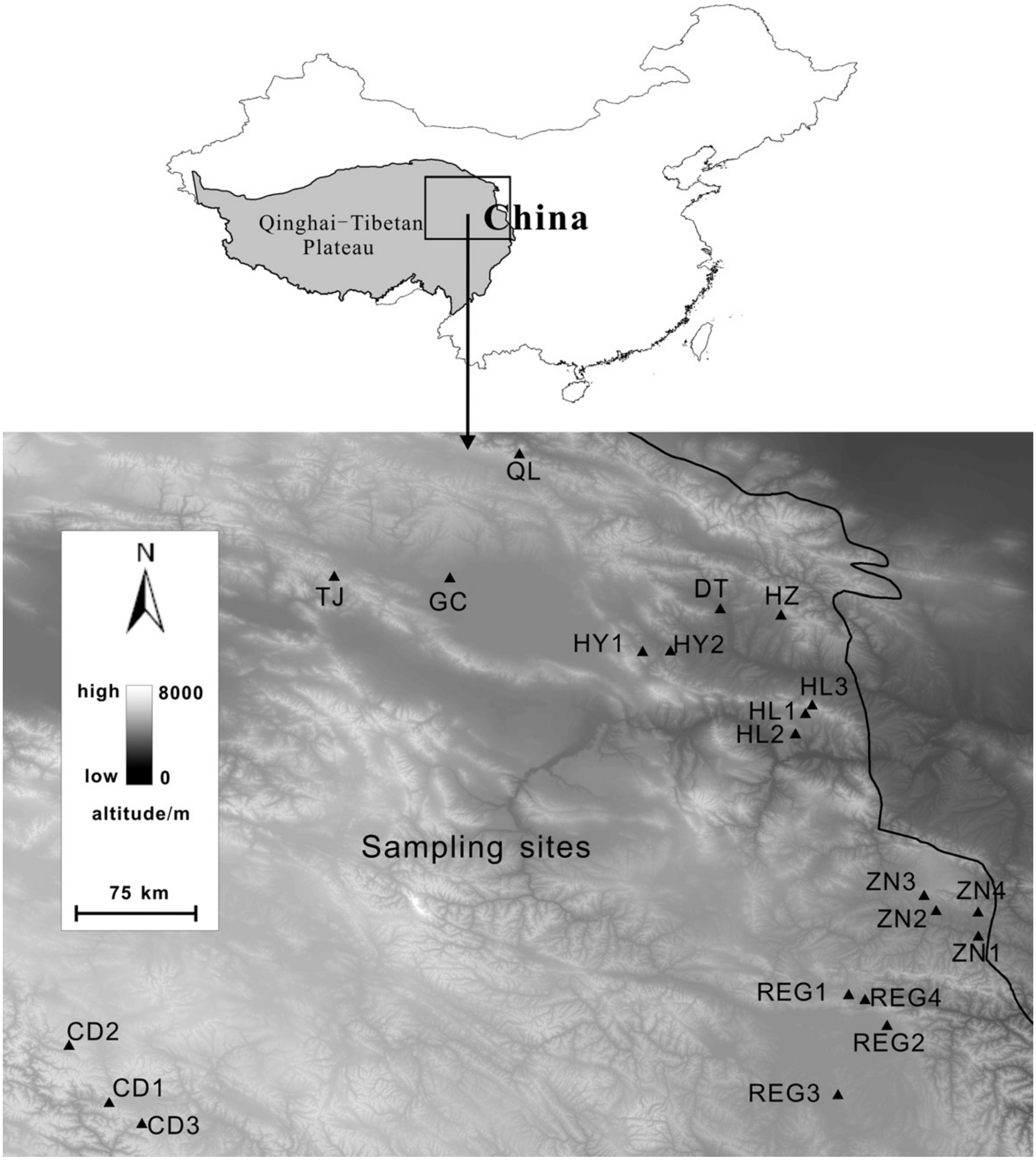

Fig. 1. Sampling sites of plateau zokor in the east of Qinghai-Tibetan Plateau located in the west of China (see Table 1 for geographical details); the lighter tint in the magnified region defines higher altitude.

(96–104°N, 33–38°E; elevations ranging from 2600 to 4600 m; see Tang et al. 2010), which facilitates their body size variation and relationships with geographical as well as climatic factors.

Latitude is usually viewed as a general geographical factor, but in QTP, altitude is also tested as an important geographical factor. At the meantime, temperature, precipitate, hypoxia (represented as altitude) and food availability are viewed as potential environmental factors that directly or indirectly influencing the body size of animals in the plateau (Liao et al. 2006; Jin et al. 2007; Lin et al. 2008). We addressed the following questions in this study: (i) whether the body-size traits (body weight, body length, and skull size) of the subterranean plateau zokors follows latitudinally and/or altitudinally the Bergmann's rule, and (ii) if size trends do occur, what environmental factors annual temperature (AT), annual precipitation (AP), annual net primary production (ANPP) and hypoxia can account for them.

Material and methods

During 2006–2007, individual zokors were caught with ground arrows which could be excited to kill zokors when they were plugging the excavated burrows (Han et al. 2003). The site distribution is shown in Fig. 1. Latitude, longitude, and altitude information (Table 1) at each sampling site were recorded using an Etrex GPS (Global Position System) unit (Garmin, Taiwan). The body weight (BW) of each animal was weighed to 1 g with a platform balance; the body length (the head and body length, excluding the tail) (BL) was measured to 1 mm by a measuring tape; the sex and age were identified by body dissection. The age was judged based on the width between the parietal crests (Zheng and Zhou 1984) and only adults were used in this study. The skulls were collected and cleaned in the laboratory and 12 morphological traits (Table 2) were measured to 0.01 mm using vernier calipers. We performed

Table 1
Sample size (Nm, number of males; Nf, number of females) of plateau zokor and the environmental information (AT, annual temperature; AP, annual precipitation; ANPP, annual net primary production of the vegetation) about the sampling sites.

Site[a]	Nm	Nf	Longitude	Latitude	Altitude	AT	AP	NPP
CD1	5	6	97.23539	33.35356	4390	−2.5	479.47	1411.14
CD2	4	7	97.47272	33.20153	4450	−2.2	500.68	1324.71
CD3	8	5	96.94372	33.76964	4550	−3.8	435.36	1101.57
DT	44	61	101.67795	36.94568	3020	3.9	324.84	1545.57
GC	4	8	99.71150	37.16928	3230	−0.2	285.39	1624.71
HL1	8	37	102.30470	36.19031	3230	1.1	423.10	2644.71
HL2	9	29	102.23317	36.07333	3208	1.4	431.51	2276.57
HL3	21	25	102.31389	36.19981	3340	0.9	425.95	2717.57
HY1	32	50	101.11414	36.63522	3110	1.1	360.79	2327.14
HY2	9	9	101.31538	36.63950	3140	1.4	364.49	3047.71
HZ	28	19	102.11956	36.90117	3040	1.1	354.64	3369.14
QL	6	6	100.21706	38.06986	3450	−1.8	272.31	2360.29
REG1	6	6	102.65731	34.12078	3270	1.4	634.48	2534.86
REG2	5	9	102.89000	33.91486	3450	1.2	666.00	2457.57
REG3	8	6	102.53331	33.41025	3490	1.5	694.34	3312.86
REG4	4	6	102.72128	34.10308	3230	2.1	634.07	2438.14
TJ	4	10	98.87097	37.17964	3840	−2.5	263.66	2185.86
ZN1	1	1	103.55315	34.56407	3080	4.5	604.53	3329.00
ZN2	3	3	103.24715	34.74962	3160	2.0	591.92	2695.43
ZN3	2	4	103.16000	34.86000	3270	0.6	585.25	2535.43
ZN4	1	4	103.55194	34.73929	3020	2.4	600.97	4048.29

[a] The acronym of the sites: CD, Chengduo; DT, Datong; GC, Gangcha; HL, Hualong; HY, Huangyuan; HZ, Huzhu; QL, Qilian; REG, Ruoergai; TJ, Tianjun; ZN, Zhuoni.

principal components analyses using the correlation matrix of the 12 morphological variables for each sex. Only the first component of the skull (SPC1) that had an eigenvalue greater than 1.0 was used in subsequent analyses.

The data for mean annual temperature (AT), annual precipitation (AP), and annual net primary production of the vegetation (ANPP) were extracted from three data sources using Spatial Analysis Tools in ArcGIS 9.0 (Environmental Systems Research Institute). The AT and AP data 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 ANPP data sets from the years 2000 to 2006.

Because some of the data did not conform to normal distribution, means were compared using the nonparametric Mann–Whitney *U* test. Also, the nonparametric Spearman test was used for bivariate correlation among independent environmental variables. We used both Spearman correlation and multiple regression analyses (with backward method) to test the effects of AT, AP, and ANPP on body size. There was significant sex dimorphism (see below), so each analysis was based on a separate gender. All statistical analyses were calculated using SPSS 15.0.

Results

A total of 523 (212 males and 311 females) adult individuals from 21 sampling sites were measured. Sample size, geographic information, AT, AP, and ANPP are listed in Table 1. The BW, BL, and SPC1 of male and female zokors are listed in Table 2. The data of the 12 skull measurements are shown in Table 3. The SPC1 accounted for 79.67% and 69.85% of the variation of skulls in males and females, respectively, and all variables had positive loading

Table 2
Body weight (BW), body length (BL), and the first component of the skull (SPC1) of plateau zokor in each sample site (mean ± SD).

Site	BW/g		BL/mm		SPC1	
	Male	Female	Male	Female	Male	Female
CD1	300.8 ± 37.9	223.0 ± 30.0	190.4 ± 15.5	173.0 ± 7.6	−1.282 ± 0.312	−1.164 ± 0.951
CD2	219.3 ± 88.9	207.1 ± 28.4	175.5 ± 20.3	174.4 ± 8.4	−1.937 ± 0.981	−1.620 ± 0.562
CD3	273.3 ± 37.1	257.0 ± 29.7	178.4 ± 9.4	182.0 ± 7.0	−1.551 ± 0.502	−1.275 ± 0.547
DT	360.0 ± 48.4	260.9 ± 39.0	222.8 ± 9.7	203.2 ± 11.7	0.776 ± 0.443	0.468 ± 0.804
GC	301.3 ± 45.4	188.3 ± 33.1	176.3 ± 8.5	162.4 ± 11.3	−0.957 ± 0.618	−1.574 ± 0.747
HL1	310.1 ± 54.6	226.7 ± 28.2	221.3 ± 12.4	203.0 ± 7.3	0.348 ± 0.531	0.155 ± 0.571
HL2	350.4 ± 56.4	246.7 ± 27.7	225.0 ± 16.6	200.4 ± 8.6	0.578 ± 0.404	0.157 ± 0.589
HL3	365.7 ± 53.5	244.9 ± 33.3	222.7 ± 15.1	204.1 ± 9.5	0.156 ± 0.766	0.723 ± 0.895
HY1	343.8 ± 59.4	235.5 ± 34.3	220.0 ± 12.5	199.7 ± 9.7	0.016 ± 0.798	0.223 ± 1.061
HY2	349.9 ± 34.3	226.7 ± 42.5	226.3 ± 10.9	196.3 ± 12.2	−0.143 ± 0.809	0.519 ± 0.296
HZ	362.4 ± 56.0	234.1 ± 34.0	231.0 ± 9.2	204.1 ± 8.0	0.649 ± 0.561	−0.056 ± 0.654
QL	306.7 ± 30.3	204.3 ± 29.4	194.8 ± 7.5	175.3 ± 8.6	−0.881 ± 0.285	−1.443 ± 0.685
REG1	319.2 ± 62.4	253.8 ± 16.9	184.2 ± 13.9	175.8 ± 10.2	−1.262 ± 0.732	0.316 ± 0.727
REG2	371.0 ± 93.8	228.7 ± 24.4	202.0 ± 18.2	177.4 ± 5.4	0.106 ± 0.952	−0.472 ± 0.935
REG3	249.5 ± 108.1	248.3 ± 45.4	170.3 ± 14.4	174.8 ± 18.7	−1.371 ± 0.917	−0.482 ± 0.917
REG4	341.3 ± 62.2	272.8 ± 30.8	192.5 ± 17.1	190.3 ± 6.4	−0.695 ± 0.528	−0.968 ± 0.733
TJ	292.3 ± 69.1	185.5 ± 23.7	192.5 ± 8.7	171.4 ± 10.9	−0.545 ± 0.483	−1.176 ± 0.836
ZN1	204.0 ± –	245.0 ± –	172.0 ± –	208.0 ± –	−0.744 ± –	0.730 ± –
ZN2	197.0 ± 69.4	204.0 ± 18.4	172.3 ± 12	182.7 ± 11.2	−1.527 ± 1.156	−0.579 ± 0.134
ZN3	342.5 ± 123.7	208.3 ± 60.7	183.5 ± 2.1	174.0 ± 12.8	0.313 ± 1.233	−0.683 ± 0.529
ZN4	365.0 ± –	216.0 ± 28.2	230.0 ± –	186.8 ± 12.6	0.521 ± –	0.211 ± 0.914
Total	335.9 ± 67.9	237.2 ± 38.1	212.6 ± 22.4	195.3 ± 15.4	0.000 ± 1.000	0.000 ± 1.000

Table 3
Skull size measurements (Mean ±SD) and component matrix of the PC1 extracted in factor analysis.

Abbr.	Description of measurement	Male		Female	
		Mean ± SD	PC1	Mean ± SD	PC1
GLS	Greatest length of skull	46.86 ± 3.16	0.967	43.88 ± 2.03	0.944
BAL	Basilar length	41.61 ± 3.09	0.978	38.90 ± 2.06	0.965
BAH	Basion height	17.98 ± 1.35	0.870	17.34 ± 1.12	0.822
ZYB	Zygomatic breadth	32.18 ± 2.99	0.928	29.33 ± 1.89	0.868
GBB	Greatest breadth of braincase	28.89 ± 2.56	0.946	26.34 ± 1.71	0.913
GMB	Greatest mastoid breadth	16.33 ± 1.12	0.722	15.30 ± 0.79	0.762
MPL	Median palatal length	25.97 ± 2.82	0.909	24.45 ± 2.06	0.840
NAL	Nasal length	18.03 ± 1.59	0.891	16.67 ± 1.14	0.771
LTB	Length of tympanic bull	10.33 ± 0.96	0.845	9.86 ± 0.70	0.686
LED	Length of diastema	14.91 ± 1.14	0.923	14.00 ± 0.79	0.887
LMB1	Length of maxillary teeth	9.88 ± 0.54	0.847	9.58 ± 0.42	0.766
LMB2	Length of mandibular teeth	10.35 ± 0.54	0.856	10.07 ± 0.43	0.754

Table 4
Spearman correlation between the geographical as well as environmental variables and the skull size (BW, body weight; BL, body length; SPC1, the first component of the skull) of plateau zokor (NS, not significant; for male, $N = 212$; for female, $N = 311$).

Sex	Index	Latitude	Altitude	AT	AP	ANPP
Male	BW	0.221**	−0.314***	0.174*	−0.184**	0.109 ns
	BL	0.350***	−0.530***	0.206**	−0.335***	0.223**
	SPC1	0.268***	−0.607***	0.372***	−0.403***	0.050 ns
Female	BW	−0.006 ns	−0.266**	0.352***	0.025 ns	−0.124*
	BL	0.181**	−0.455***	0.284***	−0.177**	0.110 ns
	SPC1	0.120*	−0.356***	0.329***	−0.066 ns	0.119*

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

values of 0.686 or above (Table 3). There was a significant difference (male biased) in BW, BL, and each of the 12 skull measurements ($N = 523$, $P < 0.001$) between the two sexes.

Among the significant correlations based on Spearman correlation analysis, all three measurements (BW, BL, and SPC1) of males were positively correlated with latitude but negatively correlated with altitude. As for the females, BL and SPC1 were positively correlated with latitude and all three measurements were negatively correlated with altitude. The Spearman correlation analysis also showed that, all measurements of males and females were positively correlated with AT. All measurements of males and the BL of females were negatively correlated with AP. The BL of males and the SPC1 of females were positively correlated with ANPP; however, the BW of females was negatively correlated with ANPP (Table 4). It should be mentioned that some of the female collections were in a pregnant or lactating state, which is a stage that body weight is extremely changing. Hence, although BW and SPC1 of females showed inconsistent correlations with ANPP, we followed the skull measurements, which were more stable variables to representing animal's body size, showing that the body size of female zokors was also positively correlated with ANPP.

Multiple regression analyses (backward method) showed that the combination of AT, AP, and ANPP was the best model for explaining the variation of BW, BL and SPC1 of both male and female zokors. The squared multiple correlation index (R^2), the probability (P) and the F value (F) of each independent-dependent group are shown in Table 5.

Discussion

Bergmann's rule implies a tendency of organisms to be smaller at high temperatures and low latitudes and larger at low temperatures and high latitudes (Meiri 2011). With this logic, body size will also be expected to increase with altitude, because temperature usually decreases with altitude. Interestingly, based on our analyses, the body size of the plateau zokor showed inconsistent relationships with latitude and altitude, i.e., mainly increased with increasing latitude while decreased with increasing altitude (Table 4).

As a geographical variable, the latitude itself cannot influence the body size of animals: however, environmental factors are very relevant, such as temperature trends. Among the three available environmental factors (i.e., AT, AP, and ANPP), only AP showed significant correlations with latitude ($N = 21$, $R = -0.836$, $P < 0.001$). Also, all three body-size variables of males and the BL of females were negatively correlated with AP, indicating AP might be an important environmental factor influencing the body size of plateau zokor. Based on the so-called Allometric Scaling Law (Kleiber's rule) (West et al. 1997; Hoppeler and Weibel 2005),

Table 5
The best model in the multiple regression (backward method) of body size (BW, BL, and SPC1, the dependent variables) on environment (AT, AP, and ANPP; the independent variables). R^2, the squared multiple correlation; F, F value.

Independent variables entered	Dependent variable	Male ($df = 211$)		Female ($df = 310$)	
		R^2	F	R^2	F
AT, AP, ANPP	BW	0.149**	12.135	0.155**	18.732
AT, AP, ANPP	BL	0.499**	69.000	0.333**	51.098
AT, AP, ANPP	SPC1	0.455**	57.142	0.254**	34.848

** $P < 0.01$.

a larger body size can help an organism conserve water in dry environments (also see the Discussion in Lin et al. 2008). As a typical subterranean rodent species, plateau zokor can only access water from food resources, thus the moisture in its burrows, which may depend on the amount of local precipitation, becomes rather important to the animal's water balance. The mean of AP in the study area was only 473 mm and some of the sites could be very arid with AP below 300 mm, representing steppic environments. Hence, the larger body size may facilitate water balance and, subsequently, the survival of plateau zokor in higher latitudes with low AP values.

Like latitude, altitude itself cannot influence the body size of animals either. In this study, altitude was significantly and negatively correlated with AT ($N = 21$, $R = -0.731$, $P < 0.001$) and ANPP ($N = 21$, $R = -0.515$, $P < 0.05$). Moreover, besides cooling and food shortage, hypoxia pressure will also increase with increased altitude (Peacock 1998). There are generally two categories of mechanisms in previous literature regarding Bergmann's rule. The first group of mechanisms refers to thermoregulation, and the second group relates to food availability (Watt et al. 2010). Since altitude and AT were negatively correlated, based on the thermoregulation mechanism a positive correlation between altitude and body size could be expected, i.e., increase in body size with increasing altitude (decreasing temperature). However, with increasing altitude, food resources (represented by ANPP) also drastically decrease, and as a result there is a severe constraint on body size of plateau zokor. Also, noteworthy, as a typical subterranean rodent species, plateau zokor depends mainly on digging activities for collecting food resources. Because of the extremely low temperature, soil in the QTP is frozen in the cold season and plateau zokors can dig only in the warm season when the shallow soil layer is thawed. Definitely lower AT in higher altitudes might have reduced the period that zokors can dig, and as a result constrain their body size by constraining their diggings for food. Moreover, with increased altitude, the digging ability is reduced because of decreasing oxygen concentration. These two factors further reduced food availability of zokors in higher altitude. We suggest that the food availability mechanism might have overruled the thermoregulation mechanism and as a result caused a smaller body size of zokors at higher altitudes.

In a word, the body size of plateau zokor in the QTP was positively correlated with temperature and food resource variables, and, negatively correlated with precipitation. Two other studies investigated the relationships between environmental factors and body size of subterranean rodents both inter- and intraspecifically. The first was for *Spalax* (Nevo et al. 1986) and the other was for *Ctenomys* (Medina et al. 2007). The former study concluded that the body size of *Spalax* was negatively correlated with temperature variables, and positively correlated with food resources and precipitation. The latter study concluded that the body size of *Ctenomys* was positively correlated with ambient temperature, food availability, and precipitation. Among the three studies, only food resource variables showed persistently positive relationships with body size, suggesting that food availability was a substantially important factor influencing body size of subterranean rodent species. It should be mentioned that in former studies precipitation was usually viewed as an indirect environmental factor influencing body size of both subterranean and aboveground animals via how it affected food availability (see Discussion in Medina et al. 2007). However, in this study (since no significant correlation between AP and ANPP was found), we suggest that AP might also directly influence body size of subterranean rodents via the water conservation mechanism in higher altitudes. Furthermore, multiple regression analyses showed that the combination of AT, AP, and ANPP could better explain the variations of zokors' body size than each single factor could, indicating that the effects of interactions among environmental factors on zokors' body size should not be ignored. By contrast, body size is a complex adaptive character, and diverse ecologies associated with different combination of abiotic (temperature, rainfall, hypoxia, and productivity) and biotic (parasites and pathogens) factors might become important driving forces of natural selection to generate differential adaptive sizes according to diverse environmental combinations.

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