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# Effects of Change in Altitude on the Auditory Bulla of Midday Gerbil, *Meriones meridianus*

**Liming Zhao, Ying Wang, Naifa Liu and Jicheng Liao***
*School of Life Sciences, Lanzhou University, Lanzhou 730000, China*

**Abstract.-** The size of body parts in animals is influenced by environmental factors. Relative to other rodents, those of the subfamily Gerbillinae (gerbils) are characterized by greatly enlarged auditory (tympanic) bullae. To understand the effects of altitude on the size of auditory bullae in the midday gerbil (*Meriones meridianus* Pallas, 1773), 339 adults were collected from areas in Inner Mongolia and northwest China, from –103 m to 3205 m above sea level, and relevant body and skull measurements were taken. Through partial correlation analysis, we found that the relative size of auditory bullae (RSAB) was significantly and positively correlated with increasing altitude. We also looked for correlations between the RSAB and each of 6 environmental factors that change with increasing altitude (mean annual temperature, frost-free period, relative humidity, precipitation, annual sunshine hours, and annual average wind speed). Of these, the results of multiple linear regression analysis indicated that the RSAB was associated with only the frost-free period and annual average wind speed. We believe that the harsh conditions at higher elevations that include lower oxygen concentration, shorter growing season, and constant strong wind work against auditory acuity, and the increase in the size of auditory bullae of *M. meridianus* with altitude is a compensatory adaptation.

**Keywords:** Midday gerbil, *Meriones meridianus*, auditory bulla, altitude, environmental factors.

## INTRODUCTION

The physical size of animals, including the length and width of body parts, are genetic and epigenetic adaptations to various and continuous environmental pressures (Rees, 1969). The rules of Bergmann (1847) and Allen (1877) are the most famous achievements in the study of the effect of the environment on body size. According to Bergmann's rule, endotherm (warm blooded) vertebrates living in cooler climates tend to be larger than members of the same genus in warmer climates. Allen's rule states that endotherms inhabiting colder climates tend to have shorter appendages than those of the same species in warmer areas. However, these traditional tenets are not generally applicable to the size and weight of animals at higher altitudes (Hawkins and Diniz-Filho, 2004), where lower temperatures are often accompanied by decreased atmospheric pressure, enhanced ultraviolet radiation, and constant strong wind (Liao *et al.*, 2006, 2010; Jin *et al*., 2007; Lin *et al*., 2008). In our work, we are interested in the effect of altitude on the auditory organs of animals, a subject that is seldom investigated.

* Corresponding author: liaojch@lzu.edu.cn

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Liao and Liu (2008) reviewed the relevant published studies and reported that the presence and size of the vocal sac and tympanum of anuran (frog) species in China were negatively correlated to increases in altitude. The authors believed that the reduction of these acoustic and auditory organs was probably due to lower population density, low temperature, hypoxia, and food shortage. This reduction in an auditory organ with elevation is paralleled in some mammals. For example, Liao *et al*. (2007) showed that the size of the auditory bullae in the Daurian pika (*Ochotona daurica*) in the Tibetan Plateau and northern China became smaller with increasing altitude. However, Musser and Dagosto (1987) reported the opposite, that is, that the bullae of a mammal increased at higher altitudes. These researchers found that *Tarsius pumilus*, a smaller-sized and high-altitude-inhabited pygmy tarsier in Central Sulawesi, possessed larger auditory bullae than lowland populations (*T. spectrum*, *T. syrichta*, and *T. bancanus*), apparently as an adaptation to sound attenuation in the higher altitude forest.

Members of the subfamily Gerbillinae, or gerbils, are differentiated relative to other rodents by enlarged auditory bullae whose greatest dimension is more than a quarter of the greatest length of the skull (Martin *et al*., 2011). The midday gerbil (*Meriones meridianus* Pallas, 1773) is medium-sized in the genus, with a head and body length of approximately 120 mm. These animals are widespread and common in sandy areas of Inner Mongolia and northwest China as far west as the Caspian Sea (Luo *et al*., 2000), where altitudes range from –150 m to 3200 m above sea level (Wang and Yang, 1983). The midday gerbil is active throughout the year, living in groups in networks of underground burrows (Zhao, 1981; Ma *et al*., 1987; Wang and Xu, 1993; Lu *et al*., 1997). The wide geographical distribution of midday gerbils enabled us to investigate in the present study whether an association exists between the size of their auditory bullae and altitude.

## MATERIALS AND METHODS

*Meriones meridianus* individuals were caught using rattraps at 25 sampling sites in the years 2004 and 2010, from March to October, in the Xinjiang, Gansu, Qinghai, Ningxia, and Inner Mongolia provinces of northwest China, at elevations ranging from –103 m to 3205 m above sea level (Fig. 1). These sites in the wilderness were all at shrub-coppice dunes, which mainly consisted of drought resistant eremophytes such as *Tamarix chinensis*, *Haloxylon ammodendron*, *Nitraria sibirica*, and *Calligonum mongolicum*. At each site, 100 rattraps were placed in a row and 10 meters apart. We set the traps at dusk and checked them the next morning for 3 consecutive days. Latitude, longitude, and altitude at each sampling site were recorded using an Etrex GPS (global positioning system) unit (Garmin, Taiwan). Statistical analyses were performed with latitude and longitude in decimal degrees.

A total of 339 adult midday gerbils were caught and measured. Body measurements were carried out directly using rulers at the sampling site, and recorded to the nearest 1 mm. Cleaned skull measurements were taken with vernier calipers and recorded to the nearest 0.01 mm. Six measurements were taken: head and body length (BHL), pinna length (PL), greatest length of skull (GLS), mastoid breadth (MB), width of auditory bulla (WAB), and length of auditory bulla (LAB). The one-sample (nonparametric) Kolmogorov-Smirnov test was used to determine if the data were normally distributed. The independent samples *t*-test (with a 95% confidence interval) was applied when comparing the sample means of males and females.

In this study, relative size was adopted to prevent the confounding influence of variations in skull size over altitude (Musser and Dagosto, 1987; Liao *et al*., 2006; Lin *et al*., 2008). Because no variation in the shape of the skull was found, the same formula was used for all individuals. In accordance with the method of Liao *et al*. (2007), we treated the midday gerbil's skull as a cone shape so that the skull size (SS) was calculated as $1/3 \cdot \pi \cdot (MB/2)^2 \cdot GLS$. The size of the auditory bulla (SAB) was simply calculated as $LAB \cdot WAB^2$; the relative size of auditory bulla (RSAB) as SAB/SS; and the relative pinna length (RPL) as PL/BHL. To exclude the influence of latitude and longitude, analysis of covariance (ANCOVA) was used. To perform the ANCOVA, we selected SAB, RSAB, PL, and RPL as the dependent variables in the general linear model, altitude as the independent variable, and latitude and longitude as the covariates. Partial correlation analysis was then conducted to investigate the effect of altitude on SAB, RSAB, PL, and RPL.

Meteorological data was collected from 65 weather stations near the sampling sites for the years 1971 to 2000. Six environmental factors were used in the analysis: mean annual temperature (MAT), frost-free period (FFP), relative humidity (RH), precipitation (PRC), annual sunshine hours (SUN), and annual average wind speed (WIN).

We constructed the multiple linear regression model by analyzing correlations between meteorological data and altitude, longitude, and latitude. Then the regression model was used to obtain estimated values of meteorological data at sampling sites (Table I). Because of a non-normal distribution in the above estimated values, Spearman's coefficient of rank correlation was adopted to test correlations among the 6 environmental factors and the altitude and RSAB. We then applied multiple linear regression analysis with the 6 environmental factors as independent variables and the RSAB as the dependent variable to determine which of these caused variations in the

RSAB. Z-scores of the environmental factors and stepwise regression (criteria: probability of F-to-enter $\leq$ 0.05, probability of F-to-remove $\geq$ 0.1)

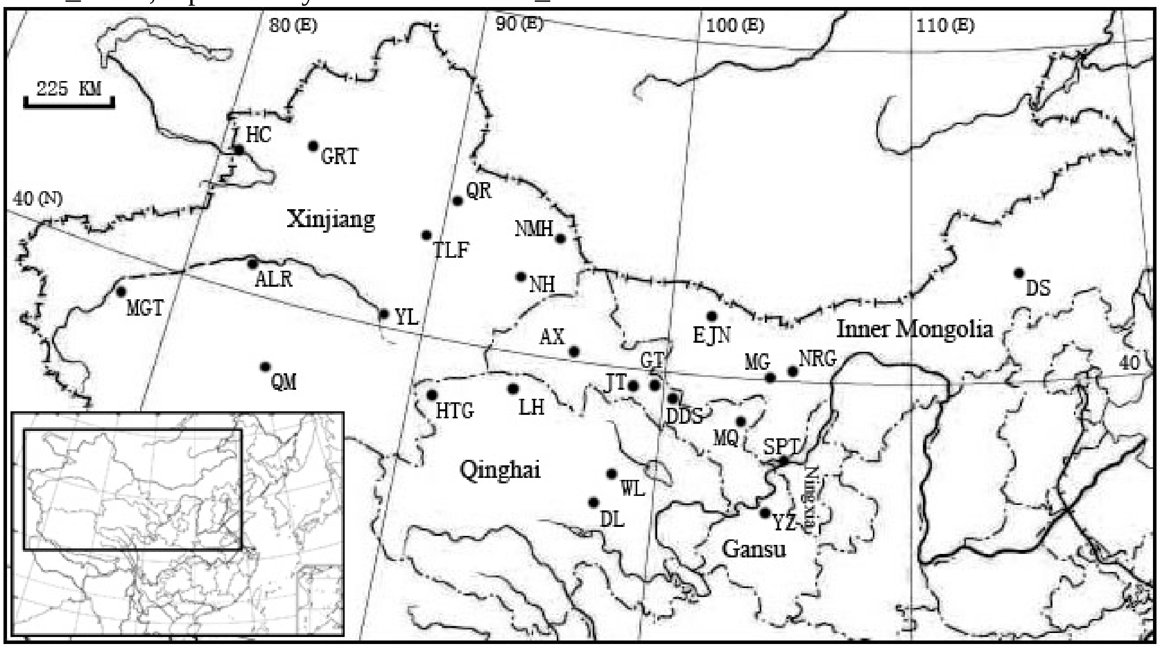



Fig. 1. The map of locales where specimens of midday gerbil (*Meriones meridianus*) were collected.

**Table I.- Environmental data of locales where specimens of midday gerbil (*Meriones meridianus*) were collected.**

| Locale | Alt (m) | Latitude (N) | Longitude (E) | MAT (°C) | FFP (day) | RH (%) | PRC (mm) | SUN (hour) | WIN (m/s) |
|---|---|---|---|---|---|---|---|---|---|
| TLF | –103 | 42°51′ | 89°11′ | 13.9 | 266 | 41 | 16 | 2999 | 1.7 |
| GRT | 311 | 44°41′ | 83°59′ | 7.3 | 174 | 61 | 91 | 2634 | 2.0 |
| NMH | 422 | 43°48′ | 94°53′ | 3.6 | 154 | 40 | 89 | 3003 | 2.7 |
| NH | 555 | 42°36′ | 93°26′ | 9.8 | 229 | 41 | 35 | 3352 | 2.8 |
| HC | 576 | 43°58′ | 80°35′ | 8.4 | 154 | 66 | 258 | 2786 | 2.2 |
| QR | 756 | 44°12′ | 90°08′ | 4.7 | 160 | 60 | 176 | 3053 | 3.4 |
| YL | 833 | 40°40′ | 87°36′ | 10.7 | 214 | 45 | 34 | 3087 | 2.2 |
| EJN | 920 | 41°59′ | 101°05′ | 8.3 | 130 | 32 | 40 | 3446 | 3.2 |
| ALR | 985 | 40°37′ | 81°48′ | 10.7 | 211 | 50 | 43 | 2733 | 1.9 |
| DS | 1087 | 43°07′ | 114°29′ | 5.1 | 160 | 46 | 211 | 3179 | 3.2 |
| MGT | 1174 | 38°42′ | 77°52′ | 11.4 | 212 | 53 | 43 | 2909 | 1.8 |
| NRG | 1297 | 40°10′ | 104°50′ | 7.3 | 153 | 37 | 99 | 3238 | 3.7 |
| QM | 1298 | 37°45′ | 84°08′ | 10.4 | 217 | 40 | 18 | 2851 | 2.3 |
| JT | 1300 | 39°22′ | 98°55′ | 7.5 | 141 | 47 | 88 | 3031 | 2.4 |
| GT | 1350 | 39°31′ | 99°31′ | 7.4 | 150 | 52 | 103 | 3088 | 2.3 |
| AX | 1365 | 40°15′ | 96°17′ | 8.8 | 198 | 39 | 46 | 3214 | 3.7 |
| MQ | 1375 | 38°34′ | 102°59′ | 8.3 | 162 | 45 | 113 | 3074 | 2.8 |
| MG | 1389 | 40°01′ | 103°52′ | 7.5 | 152 | 36 | 86 | 3318 | 3.3 |
| SPT | 1400 | 37°32′ | 104°50′ | 9.0 | 167 | 57 | 186 | 2800 | 2.4 |
| YZ | 1700 | 36°00′ | 104°45′ | 6.7 | 114 | 56 | 312 | 2424 | 3.8 |
| DDS | 2100 | 39°02′ | 100°48′ | 7.0 | 120 | 52 | 200 | 3033 | 3.6 |
| LH | 2752 | 38°45′ | 93°22′ | 2.8 | 93 | 29 | 160 | 3443 | 4.0 |
| HTG | 2898 | 38°14′ | 90°50′ | 1.4 | 90 | 30 | 44 | 3173 | 5.1 |
| WL | 3050 | 36°57′ | 98°29′ | 3.8 | 96 | 45 | 189 | 2991 | 4.2 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| DL | 3205 | 36°18′ | 98°04′ | 3.2 | 125 | 39 | 194 | 3092 | 4.5 |

Alt, altitude above sea level; MAT, mean annual temperature; FFP, frost-free period; RH, relative humidity; PRC, precipitation; SUN, annual sunshine hours; WIN, annual average wind speed.

**Table II.- Physical parameters of midday gerbils at different sampling sites (Mean ± SE).**

| Locale | n | SAB ($mm^3$) | RSAB | PL (mm) | RPL |
|---|---|---|---|---|---|
| TLF | 31 | 883.02 ± 16.85 | 0.4584 ± 0.0042 | 13.84 ± 0.12 | 0.1314 ± 0.0011 |
| GRT | 18 | 1191.51 ± 22.11 | 0.5193 ± 0.0063 | 14.00 ± 0.20 | 0.1215 ± 0.0019 |
| NMH | 14 | 1309.18 ± 37.66 | 0.4880 ± 0.0095 | 14.36 ± 0.23 | 0.1133 ± 0.0018 |
| NH | 5 | 1421.41 ± 32.37 | 0.4840 ± 0.0050 | 14.20 ± 0.20 | 0.1104 ± 0.0014 |
| HC | 19 | 1035.75 ± 15.15 | 0.4882 ± 0.0080 | 14.21 ± 0.15 | 0.1265 ± 0.0018 |
| QR | 18 | 1144.53 ± 28.14 | 0.5127 ± 0.0077 | 13.83 ± 0.17 | 0.1227 ± 0.0015 |
| YL | 13 | 1421.76 ± 33.51 | 0.4855 ± 0.0071 | 14.85 ± 0.15 | 0.1219 ± 0.0021 |
| EJN | 11 | 1384.18 ± 46.85 | 0.5103 ± 0.0106 | 13.82 ± 0.23 | 0.1086 ± 0.0022 |
| ALR | 17 | 1333.75 ± 42.70 | 0.4692 ± 0.0060 | 15.53 ± 0.19 | 0.1283 ± 0.0018 |
| DS | 15 | 1182.83 ± 35.48 | 0.4925 ± 0.0063 | 13.20 ± 0.24 | 0.1135 ± 0.0012 |
| MGT | 5 | 1306.88 ± 57.21 | 0.4615 ± 0.0109 | 15.40 ± 0.51 | 0.1112 ± 0.0025 |
| NRG | 10 | 1273.82 ± 41.80 | 0.5044 ± 0.0075 | 13.70 ± 0.26 | 0.1102 ± 0.0026 |
| QM | 12 | 1352.43 ± 44.44 | 0.4990 ± 0.0092 | 14.83 ± 0.17 | 0.1154 ± 0.0027 |
| JT | 25 | 1324.29 ± 21.54 | 0.6204 ± 0.0093 | 15.40 ± 0.26 | 0.1279 ± 0.0022 |
| GT | 20 | 1384.97 ± 35.71 | 0.6203 ± 0.0086 | 13.85 ± 0.20 | 0.1201 ± 0.0021 |
| AX | 10 | 1305.27 ± 36.36 | 0.4919 ± 0.0074 | 15.00 ± 0.21 | 0.1245 ± 0.0018 |
| MQ | 19 | 1351.72 ± 25.06 | 0.5854 ± 0.0166 | 14.16 ± 0.25 | 0.1180 ± 0.0024 |
| MG | 11 | 1286.43 ± 30.17 | 0.5003 ± 0.0064 | 14.00 ± 0.19 | 0.1154 ± 0.0028 |
| SPT | 12 | 1357.26 ± 35.66 | 0.6237 ± 0.0112 | 15.17 ± 0.24 | 0.1266 ± 0.0021 |
| YZ | 13 | 1350.86 ± 22.63 | 0.6077 ± 0.0095 | 16.15 ± 0.39 | 0.1398 ± 0.0033 |
| DDS | 4 | 1317.99 ± 122.40 | 0.6076 ± 0.0178 | 15.50 ± 0.29 | 0.1316 ± 0.0032 |
| LH | 9 | 1478.80 ± 34.29 | 0.5816 ± 0.0150 | 15.89 ± 0.20 | 0.1287 ± 0.0041 |
| HTG | 10 | 1433.64 ± 44.39 | 0.6059 ± 0.0099 | 15.00 ± 0.21 | 0.1221 ± 0.0040 |
| WL | 11 | 1439.80 ± 39.38 | 0.6044 ± 0.0101 | 15.73 ± 0.24 | 0.1219 ± 0.0018 |
| DL | 7 | 1450.22 ± 64.56 | 0.6229 ± 0.0176 | 15.71 ± 0.42 | 0.1206 ± 0.0056 |
| Total | 339 | 1269.41 ± 11.00 | 0.5350 ± 0.0038 | 14.56 ± 0.06 | 0.1225 ± 0.0006 |

SAB, size of auditory bulla; RSAB, relative size of auditory bulla; PL, pinna length; RPL, relative pinna length.

of model selection were used to avoid the influence of multicollinearity. All statistical analyses were performed using PASW Statistics 18.0.0 for Windows software.

## RESULTS

Regarding the midday gerbil measurements, the results of the one-sample (nonparametric) Kolmogorov-Smirnov test showed that all data had a normal distribution for BHL ($Z$ = 1.008, $P$ = 0.262), PL ($Z$ = 1.220, $P$ = 0.102), GLS ($Z$ = 0.673, $P$ = 0.756), MB ($Z$ = 1.092, $P$ = 0.184), LAB ($Z$ = 0.908, $P$ = 0.382), and WAB ($Z$ = 1.187, $P$ = 0.120). The results of the independent-sample $t$-test indicated that there was no significant difference between males and females in BHL ($t$ = 1.864, $P$ = 0.063), PL ($t$ = 1.117, $P$ = 0.265), GLS ($t$ = 1.654, $P$ = 0.099), MB ($t$ = 0.714, $P$ = 0.476), LAB ($t$ = 1.472, $P$ = 0.142), or WAB ($t$ = 0.732, $P$ = 0.466). Therefore we did not consider any further effects that could be due to gender.

The measurements of SAB, RSAB, PL, and RPL for midday gerbils from different localities are shown in Table II. Controlling for the effects of latitude and longitude, the results of ANCOVA showed that there was a significant effect due to altitude on the SAB ($F_{[22, 335]}$ = 14.275, $P$ < 0.001), RSAB ($F_{[22, 331]}$ = 20.839, $P$ < 0.001), PL ($F_{[22, 339]}$ = 5.098, $P$ < 0.001), and RPL ($F_{[22, 338]}$ = 9.813, $P$ < 0.001). In addition, the partial correlation analysis (controlling for latitude and longitude) showed that SAB ($r$ = 0.331, $P$ < 0.001, $n$ = 331), RSAB ($r$ = 0.262, $P$ < 0.001, $n$ = 327), and PL ($r$ = 0.130, $P$ =

0.017, *n* = 335) were significantly and positively correlated with altitude, while RPL ($r$ = –0.133, $P$ = 0.014, $n$ = 334) was negatively correlated with altitude.

Spearman's rank correlation coefficients suggested that all 6 environmental factors were significantly correlated with altitude, and 4 environmental factors (*i.e.*, excluding RH and SUN) were significantly correlated with RSAB (Table III). However, the results of multiple linear regression analysis indicated that only the effects caused by FFP and WIN ($y_{RSAB}$ = 0.536 – 0.055$x_{Z\text{-}FFP}$ – 0.023$x_{Z\text{-}WIN}$, $R^2$ = 0.444, $F$ = 131.093, $P$ < 0.001) were environmental predictors for RSAB. The association of RSAB with altitude, FFP, and WIN can be visualized more directly in the scatter diagrams in Figure. 2.

**Table III.- Spearman's coefficients of rank correlation analysis of altitude, RSAB, and environmental factors.**

| | | MAT (°C) | FFP (day) | RH (%) | PRC (mm) | SUN (hour) | WIN (m/s) |
|---|---|---|---|---|---|---|---|
| Altitude | Spearman Correlation | –0.415 * | –0.647 * | –0.215 * | –0.408 * | 0.279 * | 0.705 * |
| | Sig. (2-tailed) | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |
| | N | 339 | 339 | 339 | 339 | 339 | 339 |
| RSAB | Spearman Correlation | –0.460 * | –0.625 * | 0.105 | 0.434 * | 0.105 | 0.446 * |
| | Sig. (2-tailed) | <0.001 | <0.001 | 0.057 | <0.001 | 0.056 | <0.001 |
| | N | 331 | 331 | 331 | 331 | 331 | 331 |

* Correlation is significant at the 0.01 level (2-tailed).

## DISCUSSION

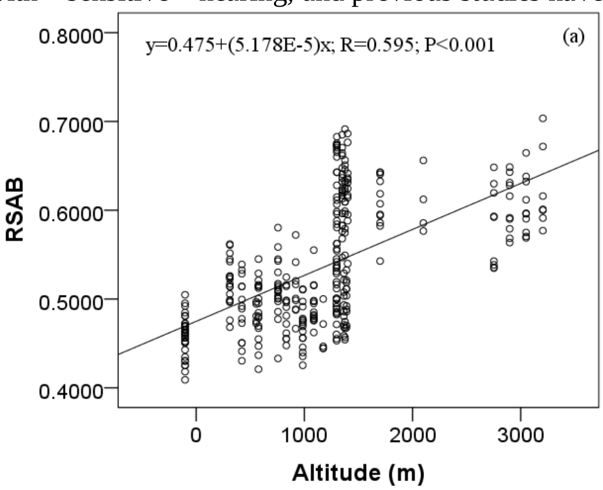
In the present study, we collected 339 skulls of adult *M. meridianus* from 25 sampling sites in Inner Mongolia and northwest China at elevations that ranged from –103 m to 3205 m above sea level to determine if the size of auditory bullae correlated with change in altitude. We found no variation in the shape of the auditory bullae, but SAB, RSAB, and PL significantly and positively correlated with increasing altitude, while RPL was negatively related.

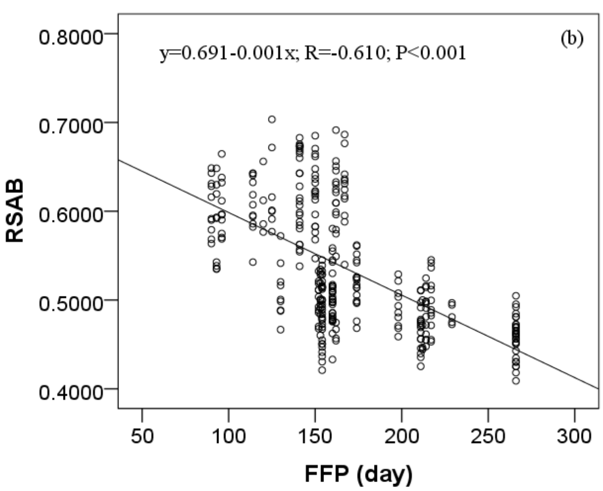
The positive association between the SAB and PL and increasing elevation is in accordance with Bergmann's rule (1847), that species and populations are larger in colder geographic areas. The temperature was lower at high altitudes, and to maintain constant body temperature, the midday gerbil had to increase volume to reduce relative surface area that would reduce heat loss. Conversely, the inverse association between the RPL and altitude appears to bear out Allen's rule (1877) that endotherms tend to have shorter appendages in colder climates. The reduction in RPL reduces the surface area available to heat loss, and therefore could be an adaptation to the lower temperatures at high altitudes. Yet, it must be noted that the increase in RSAB of *M. meridianus* with altitude cannot be explained by thermoregulation theory, and therefore factors other than temperature must come into play in this instance.

To search for an explanation for the inverse association between relative size of the auditory bullae and elevation, we first considered the effect of lower oxygen concentrations at higher altitudes. It is well known that atmospheric pressure decreases with increasing altitude, and the partial pressure of oxygen also decreases with reduced air density and pressure, making animals susceptible to tissue hypoxia, a condition with far-reaching detrimental effects on physiological and biochemical processes (Scherrer *et al*., 2010; Sinha *et al*., 2010; Xiong *et al*., 2010; Maiti *et al*., 2010). As an important part of the nervous system of animals, the auditory system also would be affected by hypoxic conditions.

Previous studies have indicated that hypoxia associated with exposure to high altitudes in humans leads to a significant reduction in auditory sensitivity and deterioration in the accuracy of sound localization (Rosenberg and Pollard, 1992; Rosenberg *et al*., 1994; McAnally *et al*., 2003). Although these results were drawn from acute exposure of mountaineers and not from humans living as long-term inhabitants of higher elevations, yet they are helpful in understanding the audile variation of *M. meridianus* to some extent. We believe that the decrease in partial pressure of oxygen with increasing altitude might result in reduction of auditory sensitivity and sound localization accuracy, thus putting *M. meridianus* at a disadvantage in the competition for resources and ability to escape from predators.

Selective pressure tends to favor individuals with sensitive hearing, and previous studies have



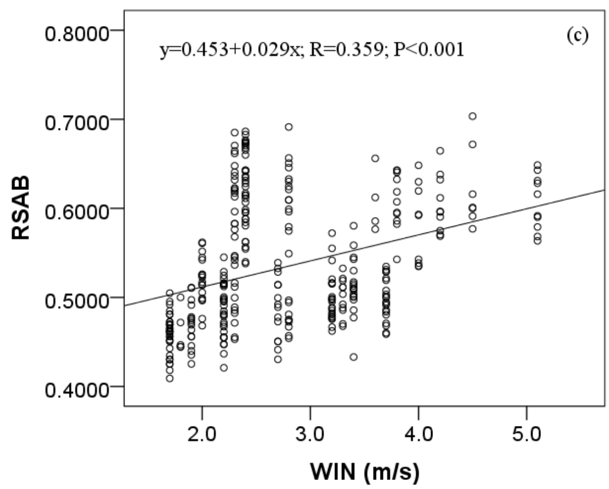




Fig. 2. Scatter diagram of the association between the RSAB with altitude (a), FFP (b) and WIN (c).

shown that the size of auditory bullae is correlated with auditory sensitivity (Legouix and Wisner, 1955; Lay, 1972). Legouix and Wisner (1955) found that the reduction of bulla volume of *Meriones crassus* resulted in a reduction in cochlear potentials. Lay (1972) has suggested that in gerbilline rodents area of the tympanic membrane increases with volume of the middle ear cavity, and both features enhance low frequency hearing. Therefore, lower oxygen concentration is a probable reason for the increase in the relative size of auditory bullae of *M. meridianus* we observed at high altitudes in the present study.

Although we concentrated on the question of whether the size of auditory bullae correlated with altitude, we also investigated correlations with specific environmental factors that change with increasing elevations. Of the 6 environmental factors we evaluated, only the FFP and WIN had significant influence on the RSAB in the model, with RSAB positively correlated with WIN, and negatively correlated with FFP.

Under natural conditions, strong wind affects the spread of sound because wind carries sound farther, but simultaneously makes it weaker (Du *et al.*, 2001). The auditory acuity of *M. meridianus* could be hampered by constant strong wind, making the sound that transferred to its ear faint. In addition, at increasing elevations the frost-free period becomes shorter and therefore the growing season as well. The vegetative cover is therefore sparser, making it more difficult for midday gerbils living there to obtain sufficient food, and also making them more severely subject to predation (Webster and Webster, 1975; Lima, 1998). An adaptation toward larger bullae would improve the ability of *M. meridianus* inhabiting high altitude areas to hear and hide from predators.

Our results are not consistent with the conclusion of Liao *et al.* (2007), who suggested that the size of auditory bullae of Daurian pikas (*O. daurica*) is inversely correlated with altitude. We attribute this difference to the distinct ecological habits of the two animals. Daurian pikas are characterized by higher activity time budget and faster moving speed during daylight hours (Zheng *et al*., 2008), while sensitive hearing is more necessary to the nocturnal midday gerbils (Luo *et al*., 2000). Pavlinov and Rogovin (2000) found that enlargement of the bullae is responsible for an increase in hearing sensitivity. At high altitudes, midday gerbils possessing larger auditory bullae are better adapted to this harsh environment. This is consistent with the research of Musser and Dagosto (1987) on the pygmy tarsier. Pygmy tarsiers are also nocturnal animals, and enlarged auditory bullae enable them to obtain food in the higher altitude forest.

We believe that the differences in auditory bullae of *M. meridianus* at different altitudes are long-term evolutionary adaptations to a changing environment. The Tibetan Plateau began to rise 50 million years ago (mya), and remarkable increases of altitude occurred about 8-10 mya (Li *et al*., 1979). This greatly influenced the climate of central Asia by preventing the southwest monsoon, creating an arid center, and is directly responsible for the lack of arable land in north China (Zhao *et al*., 1985). Moreover, rise of the Tianshan mountain range in the late Cenozoic further aggravated the aridity of northwest China (Sun and Zhu, 2006). Recent molecular phylogeographic data pertaining to *M. meridianus* (Liang, 2007; Li, 2008) prompted us to speculate that this animal in Qaidam Basin might have migrated to the Tibetan Plateau via the Gansu Corridor, which was initially at a lower altitude. Rapid increases in altitude would result in more rigorous environmental conditions such as lower oxygen concentration, lack of resources, and constant strong wind. These changes may have eventually led to bigger auditory bullae in *M. meridianus* as an adaptation to the environment with higher altitudes. Of course this is a conjecture based on geological events, as few fossils of the midday gerbil are available (Qiu, 2001; Qiu *et al*., 2004). It remains unclear how or if the auditory bullae evolved in association with the rise of the Tibetan Plateau. Further research is necessary to understand the mechanisms, function, and evolution of these phenotypes.

## ACKNOWLEDGEMENTS

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