

Uplift of the Tibetan Plateau Influenced the Morphological Evolution of Animals

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Abstract

This is a review of the results reported by studies on the impact of the Tibetan Plateau uplift on the body size, external organs, auditory organ and sexual dimorphism of animals. In high-altitude areas, strong selection pressures, such as low temperature, oxygen deficit, high frequency of strong winds, long periods of animal inactivity, and food shortages, have led to reduction in animal size, variations in the sizes of external organs, atrophy or degradation of auditory organs and increased sexual dimorphism. These evolutionary morphological changes along a gradient in the altitude are determined by differential energy distribution in the organisms.

Keywords: Tibetan Plateau, animal morphological evolution, altitudinal gradient, low temperature, oxygen deficit, differential energy distribution

1. Introduction

Morphology and genetic characteristics of organisms are constantly influenced by the ecological environment (Ray, 1960). Bergmann's rule and Allen's rule describe the interplay between ecology–morphology–geography on the characteristics of an organism. Bergmann (1874) famously proposed that warm-blooded vertebrates living in cold weather conditions tend to be larger when compared to the same species living in warm weather conditions. This rule could be universally applied to all warm-blooded animals (Ashton & Tracy, 2000; Meiri & Dayan, 2003) along various environmental gradients (Watt et al., 2010) and some cold-blooded vertebrates and invertebrates (Lindsey, 1966; Atkinson, 1994; Atkinson & Sibly, 1997; Arnett & Goteli, 1999; Porter & Hawkins, 2001; Ashton, 2002; Olalla-Tárraga et al., 2006; Timofeev, 2001). According to Allen's rule animals in colder regions tend to have shorter protruding parts of the body, such as limbs, tail and ears when compared to those living in warmer climates (Ray, 1960). Since this theory has not been tested vigorously on cold or warm-blooded animals, it is considered a "biological illusion" (Gaston et al., 1998). In addition, there are two other popular rules termed as Rensch's rule and Jordan's rule. Rensch's rule proposes that in species where males are larger than females, the difference in sexual dimorphism is increase with increasing body length. However, in species with larger females than males, the difference in sexual dimorphism is decrease with increasing body length (Rensch, 1950, 1960). According to Jordan's rule, the number of vertebrate fish in cold waters is larger than in warm waters (McDowall, 2007). Majority of the studies that tested these rules by observations were limited by defined geographic latitude and temperature gradients set at the laboratory (Atkinson, 1994; Van Voorhies, 1996), but only a few studies have examined changes over an altitude gradient such as the Tibetan Plateau, which is the highest plateau in the world. The average height of the Tibetan Plateau is 4500 m.a.s.l and, the altitude gradient formed by the uplift of the Tibetan Plateau is a naturally created site for conducting altitude based studies (Li et al., 1979). Many animals living there evolve gradually with the uplift of the plateau and often encounter environmental stress, such as low temperature, hypoxia, strong solar radiation, short growing season and low food availability. Comprehensive scientific investigation on the Tibetan Plateau has been conducted since the last century by Chinese biologists focusing on the impact of the formation of the Tibetan Plateau on the evolution of animal morphology (Cao et al., 1981; Yin, 1984). Here, I review literature relevant to this topic and examine how morphological characteristics adapt to extreme environments, to determine how these animals respond to extreme environmental conditions and whether the three rules mentioned above still fit along the elevation

gradient. This review provides useful information to understand the mechanisms regulating the morphological evolution of animals along altitudinal gradient.

2. Body Size

There are 102 endemic locust species in the Tibetan Plateau including 74 small sized insects (male < 20 mm, female < 25 mm). The body sizes of the same locust species living at different altitudes are different, with individuals becoming smaller as elevation increases (Yin, 1984). It is reported that the average body size of both male and female Tibetan mountain frog, *Nanorana parkeri*, endemic to the Tibetan Plateau and distributed in the altitudes of 2850 – 4700 m.a.s.l. (Hu, 1987) decrease significantly with increasing altitude (Ma et al., 2009). Similarly, the body sizes of both male and female Qinghai toad-headed lizard (*Phrynocephalus vlangalii*), which is the most widely distributed oviparous sand lizard in the Tibetan Plateau found at higher altitudes of 2289 – 4565 m.a.s.l. are significantly smaller than the same species at lower altitudes (Jin et al., 2007). These results were also confirmed by another recent investigation on the body sizes of eight lineages of the Tibetan Plateau sand lizards along altitudinal gradient, which shows that the body size gradually becomes smaller as altitude increases (Jin et al., 2013). Further, it was found that the Tibetan snowcock, an endemic poultry species in the Tibetan Plateau, with smaller body size and, lighter weight, grow slowly at high altitudes than at low altitudes (Zhang et al., 2007a, 2007b). Such negative correlation between high altitude and animal body size also holds true for Daurian pikas (*Ochotona daurica*), which are smaller relatives of rabbits and hares and are distributed in the third terrace in China at an altitude of 400–4000 m.a.s.l (Liao et al., 2006) and Plateau zokor (*Eospalax baileyi*), a mammal endemic to the Tibetan Plateau that exists at an altitude of 3020–4550 m.a.s.l (Zhang et al., 2012). It was proposed that food shortage and energy distribution caused by hypoxia (low oxygen pressure) and short frost-free period at high altitudes limit growth and development resulting in smaller head size of *O. daurica* at higher altitudes (Liao et al., 2006). These studies clearly demonstrate that the body sizes of most animals including invertebrates, and warm-blooded and cold-blooded vertebrates decreased as altitude increased in the Tibetan Plateau and do not support Bergmann's rule. Based on the explanation of animal morphology at different altitudes offered by various authors mentioned above, I presume that the combined effects of several factors could limit the growth and development of animals thus resulting in smaller body size. Many animals may be confined by natural features such as rivers or mountains – the new group selection might occur under natural selection processes - which results in adaptations (Grafen, 1984). Their social behaviors include altruism, cooperation, mutualism, strong reciprocity and group selection (West et al., 2007). Hence, social behaviors could involve in the morphological evolution of animals in the Tibetan Plateau. Also these factors include low temperature, hypoxic conditions, strong solar radiation, short growing season and low food availability.

I suggest that energy distribution could play a major role in limiting the growth of organisms at high altitudes because hypoxia at high altitudes could provide less energy compared to the low altitudes. Yet the amount of energy needed to maintain body activities at high altitudes is larger than at low altitudes, thereby reducing the energy distributed for animal growth and development resulting in smaller body size.

However, a contradicting result was observed in plateau pika (*Ochotona curzoniae*), endemic to the Tibetan Plateau at altitudes of 3164 – 4807 m.a.s.l. Both skull and body sizes of *O. curzoniae* positively correlated with geographic latitude and altitudes, consistent with Bergmann's rule. The authors proposed that the body size of *O. curzoniae* tend to increase with inclement weather and food shortage, and that *O. curzoniae* adopted an ecological strategy different from *O. daurica* (Lin et al., 2008)

3. External Organs

The external organs of animals that are directly exposed to the environment respond strongly to any changes in the environment, and thereby are subjected to environmental selection. These external organs include the integumentary skeleton of tetrapods (Vickaryous & Sire, 2009), the wings and legs of insects, wings, legs and feet of birds, limbs of amphibians, scales, fins and tentacles of fish, scales and limbs of reptiles, and limbs and tails of mammals. The results showed that osteoderm formation is associated with structural properties of the dermis, and an extracellular matrix, for an environment which is conducive to skeletal formation (Main et al., 2005; Vickaryous & Hall, 2008).

3.1 Locust Wings

Among the 102 locust species endemic to the Tibetan Plateau, 35 are wingless, accounting for 34.3% of all locusts; 30 species (29.4%) have side wings, 22 species (21.6%) are short-winged and only 15 species (14.7%) are long-winged. At high altitudes, the wings of locusts in the Tibetan Plateau gradually degrade (Yin, 1984), which may be an adaptation to survival in the high altitudes because flying is an energy consuming process. Flying at high altitudes under the hypoxic and windy environment may pose a fatal risk for locusts. Therefore,

the degradation or atrophy of locust wings serves to reduce wind resistance and energy consumption at higher altitude. In other words, high altitude selects wingless locusts. Smaller body size of populations in higher altitude also was found in carabid beetle *Carabus tosanus* on Shikoku Island, Japan. These may be for adaptations to different altitudes and may be important for the process of incipient speciation (Tsuchiya et al., 2012).

3.2 Fish Scales, Pharyngeal Teeth and Tentacles

External organs of fish surviving at high altitudes also vary from their counterparts at lower altitudes. The genus, *Schizothorax*, under the Cyprinidae family is distributed at altitudes of 1250–500 m.a.s.l in the Tibetan Plateau. This genus has fine scales covering the entire body with 3 rows of pharyngeal teeth and 1-2 pairs of tentacles. However, the genus *Diptychus*, which is distributed at higher altitudes of 2750–3750 m.a.s.l, has partial or no body scales, 2 rows of pharyngeal teeth, and 1 pair of tentacles. At an even higher altitude of 3750–4750 m exists genera, *Schizopygopsis* and *Gymnocypris*, which have no body scales, 1-2 rows of pharyngeal teeth, and no tentacles (Cao et al., 1981). Another dominant fish group in the Tibetan Plateau belongs to the genus *Triplophysa*. Those in the Yongding River have their entire body covered with scales, in the Loess Plateau majority of their body and the tail are covered with scales, in the Tibetan Plateau the entire body is scale less and/or tail scales are hidden beneath the skin, and above 5000 m.a.s.l their entire body is scale less (Zhu, 1989). In the Tibetan Plateau, water temperature drops as altitude increases; fish living in these environments adapt to cold water temperatures and evolve hibernation, which eventually results in degradation of the body scales. Temperature decrease with increasing altitude causes changes in the biological components of aquatic ecosystems, and fishes acquired omnivorous and overeating habits, resulting in degradation of pharyngeal teeth. Since fish became omnivorous their need to forage decreased resulting in the degradation of the tentacles.

3.3 Head, Tail and Limbs of Lizards and Mammalian Pinna Length

Similarly, significant negative correlation is observed between the head, tail and limb lengths of the Qinghai toad-headed lizard and the altitudes it resides. Compared to Qinghai toad-headed lizard, oviparous sand lizards at low altitudes of the Tibetan Plateau have significantly reduced number of tailbones (Jin et al., 2006), which follows Allen's law. Such shorter external organs could be explained by the relationships between volume–temperature–physiology. However, the pinna length of *Ochotona daurica* and the midday jird (*Meriones meridianus*) increase significantly with increasing altitude (Liao et al., 2007; Zhao et al., 2013), which is inconsistent with Allen's rule. Liao et al. (2007) proposed that the increase in pinna length was a compensation for the decrease in the size of the auditory bulla. Such morphological compensations were found in plateau animals. For example, degradation of locust wings is compensated by the protruding pronotum side lobes, which are shaped like wings, in addition to the pads between the claws at the tarsus that are enlarged, an adaptation to jumping (Yin, 1984).

3.4 Auditory Organs

Animals use auditory organs to receive external information that helps them determine their behavior. Auditory organs are sensitive to external information and are strongly influenced by the ambient sound environment. Among the 102 locust species in the Tibetan Plateau, 39 have tympanal organs, accounting for 38.2% of all locusts, and 54 species (52.9%) lack a sound producing organ (Yin, 1984). Degradation or atrophy of wings leads to degradation or atrophy of sound producing organs, which in turn leads to the loss of sound receiver. *Oreolalax* and *Scutiger* are two related genera distributed at altitudes 700–3300 m.a.s.l and 2000–5100 m.a.s.l, respectively. Significant differences are observed between these two species; while the columella of *Oreolalax* is rod-shaped, *Scutiger* has no or short columella; *Oreolalax* has spoon-shaped cartilage but *Scutiger* has no cartilage; the Eustachian tube aperture in *Oreolalax* is large, whereas in *Scutiger* it is small (Fei & Ye, 1990). Similarly, among the three species of the genus *Nanorana*, *Nanorana parkeri* which is distributed at the highest altitude does not have columella, tympanic membrane or tympanic ring while the other two species distributed at slightly lower altitudes have columella, tympanic membrane and tympanic ring (Wen, 2004). Liao and Liu (2008) examined the relationship between vocal sac/tympanic membrane and altitudes among 162 species of anurans, and found that the auditory organs of anurans differed significantly at different altitudes; the size of the vocal sac and tympanic membrane were inversely proportional to the altitudes, while the size of the vocal sac was directly proportional to the size of the tympanic membrane. These studies demonstrate that with an increase in the altitude a corresponding decline in the auditory organs of anurans is observed. The likely cause for this is the geographic isolation; while *Oreolalax* lives in cold streams in deep valleys isolated by mountains, *Scutiger* lives in freshwater marshes in the plateau. Frogs that are physically isolated do not benefit from croaking, which is mainly performed to communicate. Also the low air density with thin air at alpine, which resulted in the slow speed of sound. Moreover, croaking in a hypoxic environment at high altitudes consumes a large amount of

energy, posing a threat to survival. Therefore, it is conceivable that the auditory organs in amphibians at high altitudes tend to degrade compared to those living at low altitudes.

Additionally, the volume and relative volume of the auditory bulla in *O. daurica* significantly decrease as altitude increases (Liao et al., 2007). Hypoxia, strong wind and food shortage at high altitudes make the auditory bulla small, which leads to decreased hearing at high altitudes. As a compensation for hearing loss and a mechanism for body temperature regulation, the pinna length of *O. daurica* increase as altitude increases (Liao et al., 2007).

4. Sexual Dimorphism

Jin et al. (2013) examined Rensch's rule on sexual dimorphism by studying eight lineages of *Phrynocephalus* in the Tibetan Plateau. Their results showed differences in the body sizes of females and males in eight different lineages. With the increasing altitude, the body length both male and female get decreasing, and female is longer than male. The logarithmic regression of the male body length to female body length slope coefficient was less than 1, which contradicts Rensch's rule (Figure 1A). The authors proposed that the fertility selection in females at different altitudes and the plasticity of gender differences led to variations in body size between the genders of sand lizards along an altitudinal gradient that deviates from Rensch's rule.

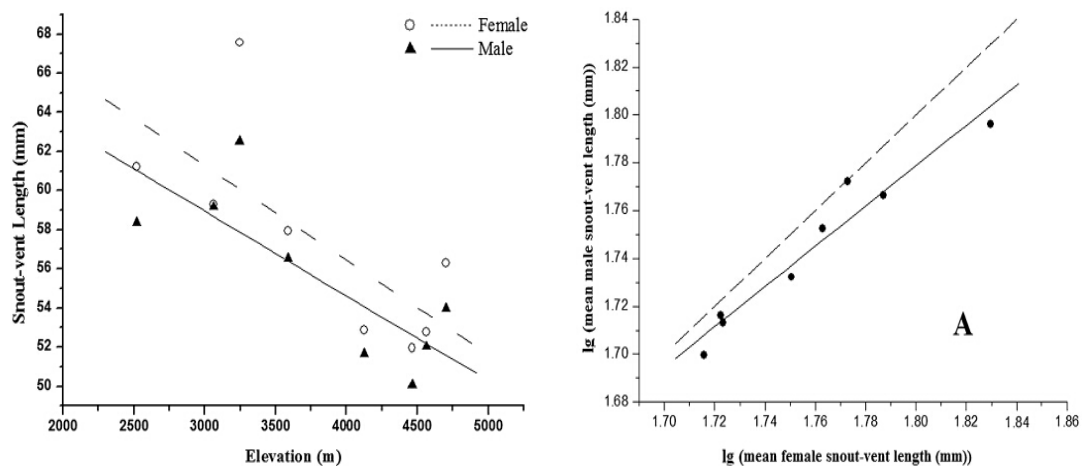


Figure 1. Regression analyses of mean snout-vent length on mean elevation of *Phrynocephalus* from the Tibetan Plateau. (A) is present Lg (mean male) plotted against lg (mean female) for *Phrynocephalus* (solid squares). The solid line is fitted to these data. Slopes are significantly smaller than 1 (dashed line). The dashed line represents a size ratio of 1 (size of males = size of females). From Jin et al. (2013)

In summary, I have reviewed the studies that reported changes in species morphology at different altitudes in the Tibetan Plateau. It is apparent that environmental factors, such as temperature, oxygen, wind power and food resources influence the evolution of animal morphology, and the use and disuse of organs in various species. Some animals however, showed characteristics that deviated from the general rules of morphology and sexual dimorphism. The mechanism causing these effects needs to be investigated.

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