



# Thermal dependence of feeding performance and resting metabolic expenditure in different altitudinal populations of toad-headed lizards

Ying-Chao Hu<sup>a</sup>, Hong-Liang Lu<sup>a,\*</sup>, Kun-Ming Cheng<sup>a</sup>, Lai-Gao Luo<sup>b</sup>, Zhi-Gao Zeng<sup>c</sup>

<sup>a</sup> Hangzhou Key Laboratory for Animal Adaptation and Evolution, School of Life and Environmental Sciences, Hangzhou Normal University, Hangzhou 310036, Zhejiang, China

<sup>b</sup> School of Biology and Food Engineering, Chuzhou University, Chuzhou 239000, China

<sup>c</sup> Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China

## ARTICLE INFO

### Keywords:

*Phrynocephalus vlangalii*  
Altitude variation  
Assimilation efficiency  
Growth rate  
Resting metabolic rate

## ABSTRACT

Inter-population variations in growth rate can result from independent or interactive effects of genetic and environmental factors, and be induced by some physiological differences as well. Toad-headed lizards (*Phrynocephalus vlangalii*) from a higher-elevation population were shown to have a higher growth rate than those from a lower-elevation population. The physiological basis of growth rate variation in this species is not well understood. Here, we investigated the feeding performance and resting metabolic rate (RMR) of lower- and higher-elevation individuals at different test ambient temperatures to evaluate the role of differences in energy intake, assimilation efficiency and metabolic expenditure on growth rate variations. Within the range of 25–35 °C, lizard RMR increased with increasing test ambient temperature, but food intake, apparent digestive coefficient (ADC, food energy minus faecal energy divided by food energy), and assimilation efficiency (AE, food energy minus faecal and urinary energy divided by food energy) were less thermally sensitive in both populations. Higher-elevation lizards tended to eat more food and have a lower RMR than lower-elevation ones, despite the lack of differences in ADC and AE. Our result showed that more energy intake and reduced maintenance cost may be associated with the higher growth rate of higher-elevation lizards. Accordingly, inter-population differences in energy acquisition and expenditure could act as potential sources for geographic variation in growth rate.

## 1. Introduction

Growth rate of organisms is one of the most important life history traits and may vary among geographic populations (Niewiarowski, 2001; Morrison and Hero, 2003). However, the pattern of growth rate variation along a geographic (latitudinal or altitudinal) gradient is not identical across different species. For example, high-elevation populations have relatively higher growth rates than low-elevation populations in some lizard species (Niewiarowski and Roosenburg, 1993; Sears, 2005; Iraeta et al., 2013), but low-elevation or intermediate-elevation individuals can grow faster in others (Grant and Dunham, 1990; Sorci et al., 1996). The sources of growth rate variation are rather complex. Research efforts have mainly been concentrated on the proximate and ultimate components of inter-population variation in growth rate (Sinervo and Adolph, 1994; Andrews et al., 2000; Goodman, 2010; Du et al., 2012). However, knowledge of the physiological basis underlying geographic variation in growth rate remains

limited.

Intrinsic differences in food acquisition and conversion efficiency, and energetic costs associated with metabolic processes may potentially contribute to variation in growth rate (Imsland et al., 2000; Niewiarowski, 2001). Studies on some species of fish and amphibians have demonstrated that higher growth rates are often associated with higher food intake, or greater food conversion and assimilation efficiency (Wieser, 1994; Present and Conover, 1992; Billerbeck et al., 2000; Imsland et al., 2000; Jonassen et al., 2000; Lindgren and Laurila, 2005). On the other hand, energy resources acquired by organisms should be differentially allocated to satisfy various demands, such as maintenance, growth, activity and reproduction (Hill et al., 2008). Therefore, the amount of energy required for maintenance, which is often estimated using resting metabolic rate (RMR), may influence other physiological processes including growth (Burggren and Roberts, 1991; Stahlschmidt et al., 2015). With the amount of resources that can be allocated in different individuals or populations being similar, high

\* Corresponding author.

E-mail address: [honglianglu@live.cn](mailto:honglianglu@live.cn) (H.-L. Lu).

<https://doi.org/10.1016/j.jtherbio.2019.01.001>

Received 16 September 2018; Received in revised form 6 December 2018; Accepted 1 January 2019

Available online 02 January 2019

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growth rate is expected to be correlated with low energetic cost of maintenance; but such a situation can be altered if inter-individual or inter-population variations in resource allocation are large (van Noordwijk and de Jong, 1986). Consequently, discrepant results are exhibited in different cases. For example, a negative relationship between RMR and growth rate was demonstrated in some fish and lizard species (Angilletta, 2001; Álvarez and Nicleza, 2005; Sears, 2005; Seppänen et al., 2010), whereas no significant or even positive relationship was found in other fish or amphibian species (Galarowicz and Wahl, 2003; Lindgren and Laurila, 2009; Reid et al., 2011). Additionally, alternative hypotheses that the energetic cost of maintenance is disproportional to growth or increased by accelerated growth due to tissue production are also proposed to explain the inconsistent relationships (Wieser, 1994; Pörtner et al., 2005; Lindgren and Laurila, 2009).

The Qinghai toad-headed lizard (*Phrynocephalus vlangalii*) is a small, viviparous agamid species, that is widely distributed in the northern area of the Tibetan Plateau and exhibits significant geographic variations in life history traits (Jin and Liu, 2007; Li et al., 2014). There is an increase in adult (but not neonate) body size with increasing elevation (Jin and Liu, 2007). Despite having smaller size at birth, higher-elevation individuals can grow faster and reach a larger body size at adulthood than lower-elevation ones, possibly due to higher food availability (Lu et al., 2018a). However, whether this adaptive growth variation partially contributes from intrinsic metabolic and physiological differences is unclear. In this study, we compared the food intake, assimilation efficiency, and RMR at different constant temperatures between two populations of *P. vlangalii* that we studied previously to investigate the physiological mechanisms underlying growth rate variation. The specific aims of the present study were to test whether: (1) individuals from different populations differed in food intake, assimilation efficiency and RMR; (2) temperature effects on food intake, assimilation efficiency and RMR differed between populations; and (3) these observed variations could explain the difference in growth rate. Based on the results of our previous comparative studies and those reported for other species, we predicted that lizards from the higher-elevation site would have greater food intake and assimilation efficiency than those from the lower-elevation site; and higher-elevation lizards would have a higher RMR than lower-elevation lizards if there was a significant between-population difference in food acquisition.

## 2. Materials and methods

In mid-August of 2011, we collected adult males (snout-vent length > 48 mm, Zhang et al., 2005) of *P. vlangalii* at two different altitudinal sites (lower-elevation site: 2930 m, Maqu, Gansu Province, 34°00'N, 102°04'E; higher-elevation site: 4250 m, Maduo, Qinghai Province, 34°55'N, 98°12'E) in the northeast part of Qinghai-Tibetan Plateau. These two populations of *P. vlangalii* have been demonstrated to belong to a single lineage (Jin et al., 2008). A field investigation conducted during the active season (from June to September) showed that, even when the daily air temperature (at 10 cm above the substrate) at the lower-elevation site (mean  $\pm$  SE = 16.0  $\pm$  0.4 °C, range of 9.7–24.8 °C) is higher than that at the higher-elevation site (13.1  $\pm$  0.3 °C, range of 8.4–20.0 °C) (Lu et al., 2018b), the mean body (cloacal) temperatures of lizards do not differ between our two study populations [lower-elevation vs higher-elevation: 32.0  $\pm$  0.2 °C (range of 17.2–38.3 °C) vs 31.3  $\pm$  0.3 °C (range of 13.5–42.2 °C), Wu et al. (2018)]. A total of 80 males (40 individuals from each site) with a body mass ranging from 3.81 to 8.26 g, were transported to our laboratory in Hangzhou, and randomly maintained 5–6 in each 60  $\times$  40  $\times$  30 cm<sup>3</sup> (length  $\times$  width  $\times$  height) terrarium with 10-cm depth of sand. These terraria were placed in an artificial atmospheric phenomena room that set at 18 °C. A 60 W light bulb was suspended 15 cm above the floor in each terrarium, to provide thermoregulation opportunities for lizards from 08:00–18:00 h. The surface temperature of the substrate in

terraria ranged from 18.5° to 24.6 °C over a day (24 h period). Lizards were fed a combination of mealworms (larvae of *Tenebrio molitor*) and house crickets (*Acheta domestica*), and water enriched with vitamins and minerals was provided ad libitum.

One week later, 60 lizards (30 individuals for each population) were used to measure food intake and assimilation in three constant-temperature rooms set at 25, 30, and 35 °C. These temperatures were selected in order to represent low, medium and high field body temperatures of *P. vlangalii* during activity, respectively (Wu et al., 2018). Lizards were randomly divided into three groups (10 lower-elevation and 10 higher-elevation individuals in each group), and individually housed in a 20  $\times$  15  $\times$  20 cm glass terrarium, which were placed in one of three constant temperature rooms. Animals were starved at the test ambient temperatures for three days prior to feeding to ensure uniform post-absorptive states. Body (cloacal) temperatures of lizards were confirmed multiple times using a UT-325 electronic thermometer (Unitrend Group Ltd., Shanghai, China) during the experimental period. Five weighed mealworms that placed in a Petri dish were provided daily to each lizard at morning (07:30–08:30). Mealworms are the larval form of Coleoptera species, which are the main diet items of *P. vlangalii* (accounted for approximately 55% and 52% of the total number for lower-elevation and higher-elevation lizards, Lu et al., 2018b). Faeces and urates of each lizard were collected at least three times daily. Uneaten mealworms in each terrarium were removed every afternoon (16:00–17:00 h), and weighed again. Water was provided throughout the experimental period. Trials lasted for a minimum of 20 days to allow the accumulation of sufficient faeces and urates for calorimetry. Faeces, urates and mealworms were dried to constant mass at 65 °C and weighed. The energy densities of these samples were determined by burning them in a Parr 6300 automatic adiabatic calorimeter (Parr instrument company, Moline, Illinois, USA). The apparent digestive coefficient (ADC) and assimilation efficiency (AE) was calculated as  $ADC = (I - F)/I \times 100\%$  and  $AE = (I - F - U)/I \times 100\%$ , respectively, where I = total energy consumed, F = energy in faeces, and U = energy in urates (e.g., Van Damme et al., 1991; Sun et al., 2009).

The remaining lizards (10 individuals for each population) were measured for RMR in a repeated-measures design with three test ambient temperatures (25, 30 and 35 °C) after one week of maintenance under laboratory conditions. Each lizard was measured once at each test ambient temperature. Lizards were given a 48 h rest between test ambient temperatures, and maintained in their terraria during the test intervals. An open-flow respirometry system (Qubit Systems, Kingston, ON, Canada) was used to measure the carbon dioxide production ( $V_{CO_2}$ ) of each lizard in a 220 mL acrylic metabolic chamber with an air flow rate of 200 mL/min. Lizards were deprived of food for approximately 2 days and allowed to acclimate to the chamber for approximately 30 min prior to the beginning of the metabolic recording. While the lizards were resting, CO<sub>2</sub> concentration in the outflowing air was measured by a flow-through CO<sub>2</sub> analyser and displayed by the Logger Pro 3.7 analysis software (Vernier, Inc., Beaverton, OR, USA). Normally, CO<sub>2</sub> concentration fluctuated during the initial 15–30 min period. Therefore, we still kept recording the CO<sub>2</sub> concentration continuously for no less than 20 min after it was shown to be in a relatively stable state. Baseline measurements were made using the same experimental chamber at the end of each measurement period. RMR was estimated as the mean of the 3–5 min stable state of CO<sub>2</sub> production during periods of inactivity, and normalized as per gram body mass. All metabolic rates were measured between 18:00 and 21:00 h in order to minimize potential temporal effects.

Individuals that refused to eat or died (lower-elevation: 2 at 35 °C; higher-elevation: 2 at 25 °C, 1 at 30 °C and 1 at 35 °C) were excluded from analyses. All experimental procedures complied with the current laws on animal welfare and research in China, and were approved by the Animal Care and Ethics Committee of Hangzhou Normal University. Prior to conducting statistical analyses, we first determined whether

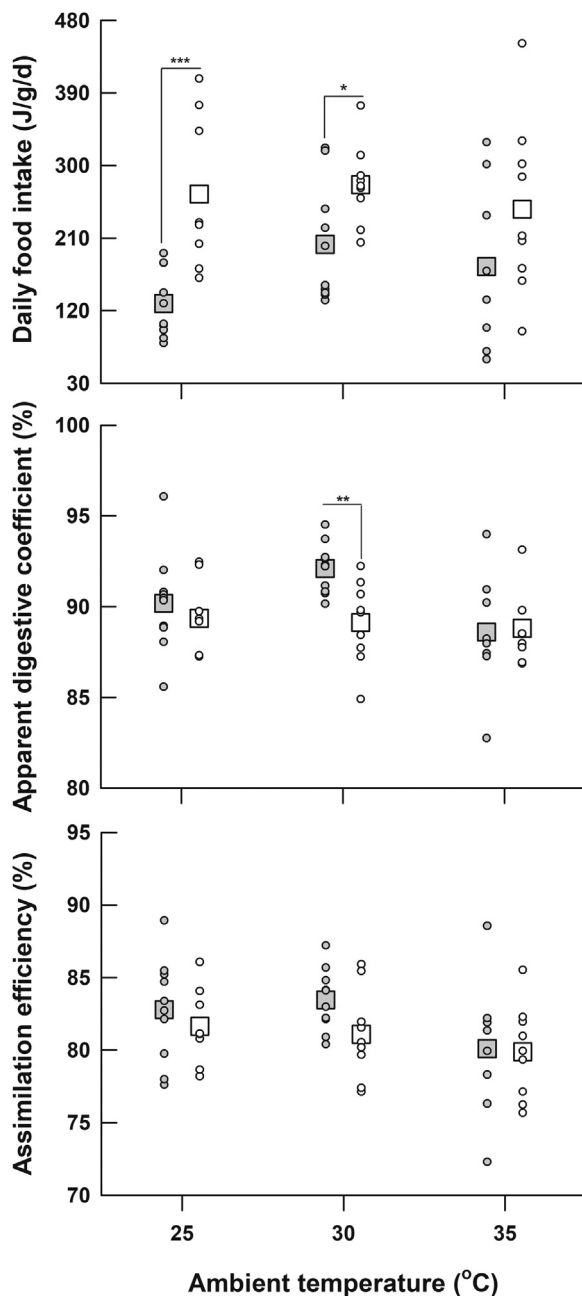


Fig. 1. Daily food intake, apparent digestive coefficient, and assimilation efficiency at different test ambient temperatures of adult male *Phrynocephalus vlantalii* from the two study sites (gray symbols: lower-elevation; white symbols: higher-elevation). Enlarged gray- and white-filled squares show the mean values for the lower- and higher-elevation populations, respectively. The asterisks indicate significant differences (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ).

our data met the assumptions of parametric statistical tests. After running the Kolmogorov-Smirnov and Bartlett's tests, all data were shown to be normally distributed and homoscedastic. A two-factor analysis of variance (ANOVA) was performed to determine the differences in daily food intake, ADC and AE between populations and between temperature treatments; repeated-measures ANOVA with population as the between-subject factor and test ambient temperature as the within-subject factor was performed to determine the effects of population and test ambient temperature on RMR. Throughout this paper, values were presented as mean  $\pm$  SE, and the significance level was set at  $\alpha = 0.05$ .

### 3. Results

There was no significant inter-population difference in body mass of toad-headed lizards that were transported to the laboratory (lower-elevation vs higher-elevation:  $6.07 \pm 0.16$  g vs  $5.82 \pm 0.14$  g,  $t = 1.15$ ,  $df = 78$ ,  $P = 0.253$ ). Within the temperature range of 25–35 °C, the test ambient temperature had no significant influence on lizard daily food intake ( $F_{2, 48} = 1.32$ ,  $P = 0.278$ ), ADC ( $F_{2, 48} = 2.96$ ,  $P = 0.061$ ) or AE ( $F_{2, 48} = 2.69$ ,  $P = 0.078$ ) (Fig. 1). The mean daily food intake of higher-elevation lizards was greater than that of lower-elevation ones ( $F_{1, 48} = 17.76$ ,  $P < 0.001$ ). Overall, inter-population differences in ADC ( $F_{1, 48} = 3.53$ ,  $P = 0.066$ ) and AE ( $F_{1, 48} = 1.90$ ,  $P = 0.175$ ) were not statistically significant (Fig. 1). The interaction between test ambient temperature and population had no significant effects on daily food intake ( $F_{2, 48} = 0.90$ ,  $P = 0.415$ ), ADC ( $F_{2, 48} = 2.18$ ,  $P = 0.124$ ) or AE ( $F_{2, 48} = 0.48$ ,  $P = 0.620$ ). Lower-elevation lizards had higher ADC than higher-elevation lizards at intermediate temperature ( $t = 3.49$ ,  $df = 17$ ,  $P < 0.01$ ), but not at cool ( $t = 0.70$ ,  $df = 16$ ,  $P = 0.496$ ) or warm temperatures ( $t = 0.11$ ,  $df = 15$ ,  $P = 0.915$ ) (Fig. 1).

Overall, the RMR of toad-headed lizards increased with increasing test ambient temperature ( $F_{2, 36} = 6.52$ ,  $P < 0.01$ ). Lower-elevation lizards had a significant higher RMR than higher-elevation ones ( $F_{1, 18} = 5.33$ ,  $P = 0.033$ ) (Fig. 2). However, the interaction of test ambient temperature and population also had no significant effect on RMR ( $F_{2, 36} = 0.53$ ,  $P = 0.594$ ). In fact, between-population difference in RMR was statistically significant at intermediate test ambient temperature ( $t = 2.37$ ,  $df = 18$ ,  $P = 0.029$ ), but not at cool ( $t = 1.39$ ,  $df = 18$ ,  $P = 0.181$ ) or warm temperatures ( $t = 0.76$ ,  $df = 18$ ,  $P = 0.455$ ) (Fig. 2).

### 4. Discussion

In this study, physiological measurements of lizards were performed under identical laboratory conditions, probably differing from those experienced by them in natural habitats. The observed differences in several physiological performances (e.g., food intake and RMR) between the two study populations should be substantive because the current procedure had erased some of the differences that occur in nature. In addition, the current comparison of two different altitudinal lizard populations may be not sufficient to draw a general altitudinal pattern of physiological variation. However, it did not prevent us to

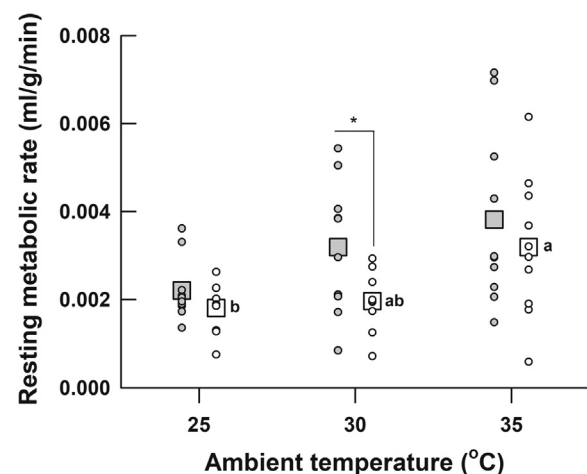


Fig. 2. Resting metabolic rate at different test ambient temperatures of adult male *Phrynocephalus vlantalii* from the two study sites. See Fig. 1 caption for explanation of symbols. Different letters on the right side of white-filled squares represent significant differences between temperature treatments for the higher-elevation population (Tukey's test;  $a > b$ ).

explore its potential contributions to the between-population difference in growth rate that was confirmed in our previous study.

The mean values of daily food intake, ADC and AE for lower- and higher-elevation populations of *P. vlangalii* were similar to the values reported for another population (daily food intake: 139.2–303.5 J/g/d, ADC: 89.8–92.8%, AE: 80.3–83.0%, Shu et al., 2010), but slightly lower than those for other two species of *Phrynocephalus* lizards (ADC: 90.3–95.0%, AE: 82.5–90.7% for *P. frontalis*, 90.1–94.9% and 81.2–90.8% for *P. versicolor*, Qu et al., 2011). Meanwhile, food intake, ADC and AE showed low thermal sensitivities in both study populations of *P. vlangalii*. In two other species of *Phrynocephalus* lizards and a different population of *P. vlangalii*, there was also no significant thermal dependence in ADC and AE (Shu et al., 2010; Qu et al., 2011). However, these three variables (including food intake of above-mentioned *Phrynocephalus* species) are not thermally insensitive in most lizard species that have been studied previously (Van Damme et al., 1991; Chen et al., 2003; Xu and Ji, 2006; Sun et al., 2009; Qu et al., 2011).

Our results showed that higher-elevation *P. vlangalii* ate and consumed more food than lower-elevation ones at each test ambient temperature. It was consistent with our prediction and previous findings that field lizards at higher-elevation site would acquire more food due to greater local food availability, and field-captured juveniles also tended to eat more under identical laboratory conditions (Lu et al., 2018b). Similarly, in some fish species, high-latitude individuals were reported to have a greater food intake than low-latitude ones (Present and Conover, 1992; Billerbeck et al., 2000). The observed difference in food intake of adult lizards might reflect evolutionary associations with local climatic and food conditions (Lu et al., 2018b), because between-population differences in food intake were greater at low test ambient temperature than at high temperature (Fig. 1). Conversely, the mean values of ADC and AE for higher-elevation lizards were not higher than those for lower-elevation lizards, in disagreement with our prediction. Despite lower ADC and AE observed for higher-elevation lizards at test ambient temperatures of 30 °C, the amount of daily assimilated energy for higher-elevation lizards was still greater than that for lower-elevation ones (about 102%, 33% and 40% more than lower-elevation lizards at 25, 30 and 35 °C, respectively) after taking food assimilation efficiency into account. It is, therefore, inferable that greater field growth rates for higher-elevation lizards might be associated with more food and energy intake rather than the variation in food assimilation or conversion efficiency. Compared with higher-elevation lizards, an increased ADC at the intermediate temperature (near the mean field-active body temperature) might be a compensatory response for lower-elevation lizards living in relatively food-poor areas (Lu et al., 2018b). In contrast, increased food conversion efficiency instead of food consumption or intake primarily contributes to higher growth rates in some species of fish and amphibians (Imsland et al., 2000; Jonassen et al., 2000; Lindgern and Laurila, 2005). Therefore, the physiological mechanisms underlying adaptive variation in growth rate could be diverse among different taxa.

As expected, the RMR increased with increasing test ambient temperatures in both populations of *P. vlangalii*. The amounts of CO<sub>2</sub> production at 35 °C were more than 1.7 times those at 25 °C, which is similar to the values reported for other reptiles (Bennett, 1982; Sears, 2005; Noyola et al., 2013). The rate of metabolic change with temperature can be unisometric. For example, the rate of metabolic change at warm temperatures appeared to be higher than that at cool temperatures for higher-elevation lizards, despite being similar for lower-elevation lizards (Fig. 2). On the other hand, higher-elevation *P. vlangalii* had relatively lower RMRs than lower-elevation ones (especially at the intermediate temperature which was near the active body temperatures in the field), which was similar to that reported in *Sceloporus graciosus* (Sears, 2005), but inconsistent with our prediction. Our results here probably implied that the between-population difference in food acquisition had no, or only a minor impact on the trade-off between resource allocation to maintenance and growth. The RMR reflects the

energy required for maintenance (accounting for the vast majority of the resting energy expenditure) and some other processes, and has been taken as a good indicator of maintenance energetic costs (Ashby, 1998; Zhang et al., 2018). Reduced maintenance energetic costs in higher-elevation lizards (i.e., 13–34% lower than those reported for lower-elevation lizards) would favor allocating energy to growth and other activities. The strategies of energy metabolism of ectothermic species may be affected by their living environments (Chown and Gaston, 1999). In colder environments resulting in shorter growth periods for lizards, diverting more resources to growth might be favoured by selection, and thus lead to a negative relationship between RMR and growth rate (Niewiarowski, 2001). In fact, the relationship between RMR and growth rate is rather complicated, and diverse patterns have been documented in different species (Sears, 2005; Billerbeck et al., 2000; Galarowicz and Wahl, 2003; Lindgern and Laurila, 2009). Despite being a heritable trait, metabolic rate can be changed in response to seasonal acclimatization (Tsuji, 1988; Naya et al., 2008; Toledo et al., 2008). The reduced RMR for high-elevation lizards might be a metabolic response to acclimatization under relatively lower environmental temperatures experienced by them in the field before being captured (Beyer and Spotila, 1994; Hou and Huang, 1999; Xu et al., 2015). Acclimatization to low temperatures and oxygen partial pressures has also been shown to slightly increase metabolic rate (Sandblom et al., 2014; Polymeropoulos et al., 2017). However, such metabolic compensation at low temperatures and oxygen partial pressures below those usually experienced by animals in the natural environment might not occur in our case because of observably higher test ambient temperatures and oxygen partial pressures in the laboratory. Low atmospheric oxygen supply might limit food utilization capacity, and thus reduce individual growth rate (Mcnatt and Rice, 2004; Owerkowicz et al., 2009). Normally, oxygen partial pressure decreases with increasing elevation. Hypoxia exposure might reduce standard metabolic rate and thus maintenance energetic cost in *P. vlangalii* (Li et al., 2016). Additionally, greater food availability might counteract the limited food utilization due to low oxygen supply at the higher-elevation site (Lu et al., 2018b). These findings might suggest that the lower oxygen partial pressure at the higher-elevation site did not necessarily lead to a lower growth rate for our higher-elevation individuals. In fact, no significant association between hypoxia and growth rate has been found in some ectothermic species (Pichavant et al., 2005). Conversely, hypoxia exposure during embryonic stages has been shown to result in smaller, slower growing hatchlings in some reptiles, including turtles, alligators and snakes (Owerkowicz et al., 2009; Stahlschmidt and DeNardo, 2009; Wearing et al., 2016). Whether between-site difference in atmospheric oxygen partial pressure can potentially make a contribution to growth rate variation of *P. vlangalii* should be examined in future studies.

In summary, significant between-population differences in food intake and metabolic rate (but not in assimilation efficiency) were shown in *P. vlangalii*. Despite only being conducted in the laboratory, our observed differences could be used to partly explain growth rate variation in *P. vlangalii*. Compared with lower-elevation *P. vlangalii* individuals, more energy intake but lower energy consumption for maintenance in higher-elevation individuals might potentially lead to a faster growth.

## Acknowledgements

We are grateful to Chuan-Quan Jiang and Yong Wang for their assistance in the field and in the laboratory. This study was supported by the National Natural Science Foundation of China (31670399).

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