

# Sex Ratio and Sexual Size Dimorphism in a Toad-headed Lizard, *Phrynocephalus guinanensis*

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**Abstract** *Phrynocephalus guinanensis* has sexual dimorphism in abdominal coloration, but its ontogenetic development of sexual size dimorphism (SSD) is unknown. Using mark-recapture data during four days each year from August from 2014 to 2016, we investigated the development of sex ratios, SSD, sex-specific survivorship and growth rates in a population of *P. guinanensis*. Our results indicated that the sex ratio of males to females was 1:2.8. Males had a lower survival rate (6%) than females (14%) across the age range from hatchling to adult, which supported the discovered female-biased sex ratio potentially associated with the low survival rate of males between hatchlings and juveniles. Male-biased SSD in tail length and head width existed in adults rather than in hatchling or juvenile lizards. The growth rates in body dimensions were undistinguishable between the sexes during the age from hatchling to juvenile, but the growth rate in head length from juvenile to adult was significantly larger in males than females. Average growth rate of all morphological measurements from hatchling to juvenile were larger compared with corresponding measurements from juvenile to adult, but only being significant in tail length, head width, abdomen length in females and snout-vent length in males. We provided a case study to strengthen our understanding of the important life history traits on how a viviparous lizard population can survive and develop their morphology in cold climates.

**Keywords** toad-headed lizard, mark-recapture, sexual size dimorphism, growth rate, survivorship, sex ratio

## 1. Introduction

Life history characteristics are associated with growth, reproduction, and survivorship that can affect the life table of an organism, which were thought to be strongly influenced by natural selection (Fox *et al.*, 2001; Roff, 1992). Only populations with adaptive life history can survive, reproduce and evolve in an unstable environment (Stearns, 1992). Recently, there have been multiple ecological research about life history characteristics, which includes body size and growth pattern, sex ratio, age-specific survivorship (i.e., Galliard *et al.*, 2005; Molinazuluaga *et al.*, 2015; Wu *et al.*, 2005; Zhao and Liu, 2014).

Sex ratio is an important topic in population demographic studies (Caswell, 2001; Jirotkul, 1999;

Kvarnemo and Ahnesjö, 1996). Fluctuations in sex ratio are regulated (Pettersson *et al.*, 2004), and mainly influenced by intrasexual competition and sex-specific mortality or emigration in a population (Cluttonbrock *et al.*, 2002; Wolff *et al.*, 2002). Sex-specific mortality is also likely to result from different predator preference on males or females (Johnston, 2011; Stuart-Fox *et al.*, 2003). Males generally expend more energy in displaying and fighting during the breeding season, which leads to increased mortality due to injury and greater exposure to predation (Christe *et al.*, 2006; Owensmith, 1993). In addition, females likely invest more energy in reproduction than males which could lead to higher female mortality (Schwarzkopf and Shine, 1992).

Sexual dimorphism is frequently illustrated as sexual difference in body size, body shape and coloration (Bonnet *et al.*, 1998; Parker, 1992; Pinto *et al.*, 2005), and generally driven by sexual selection and natural selection (Cooper and Vitt, 1989; Ji *et al.*, 1997). Sexual selection is generally determined by intensity of male-

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male competition and female mate choice (Anderson, 1994), while natural selection is mainly associated with sex-specific growth rate, survivorship, life span, feeding divergence and different partitioning of energy for growth (Berry and Shine, 1980; Cooper and Vitt, 1989; Cox *et al.*, 2006; Haenel and John-Alder, 2002; Johnston, 2011; Powell and Russell, 1985; Stamps, 1993). Recently, SSD is viewed as a developmental process, and the proximate mechanisms of SSD have been determined in some lizards from an ontogenetic perspective (Cox *et al.*, 2006; Cox *et al.*, 2009; John-Alder *et al.*, 2007; Johnston, 2011). The SSD is likely caused by different ecological conditions for males and females during the developmental process (Cox *et al.*, 2009). Hence comparison of development pattern in both sexes is a critical necessary step to clarify the different pressures responsible for SSD.

The toad-headed lizard, *Phrynocephalus guinanensis* was named recently based on its morphological differences (Ji *et al.*, 2009). This species is restricted to small areas of sand dunes in Guinan County, Qinghai Province (Jin *et al.*, 2014), which is largely different to other *Phrynocephalus* species in China and middle Asian countries. It is sexually dimorphic in abdominal coloration and showed SSD in tail, head and limbs (Ji *et al.*, 2009). Nonetheless, our knowledge on population ecology of the species is very lack (Jin *et al.*, 2016; Zhang *et al.*, 2017). This study conducted three years' mark-recapture investigation and studied the survivorship, sex ratio, growth rate and the ontogenetic development of SSD in *P. guinanensis*.

## 2. Materials and Methods

**2.1. Data Collection** The study site is located on sand dunes (35.79° N, 101.04° E; datum = National Geodetic Coordinate System 1980; 3190 m above sea level) in Guinan County, Qinghai Province, China. The quadrat is about 200 m in length and 100 m in width, and covered all areas that active *P. guinanensis* were observed. The potential dispersion of the lizard is limited as the quadrat is a semi isolated area surrounded with mountainous slopes or river bank. In August 2014, we randomly collected active hatchling and juvenile lizards by hand during four days, and measured and numbered each captured individual with a unique toe-clip before release. We recaptured the active lizards by hand and released them after measurements were taken during four days in August 2015. We recaptured surviving lizards throughout the quadrat and all potential dispersing areas by hand and

digging holes during four working days of August 2016. The hatchling, juveniles and adults could be distinguished easily based on their distinct non-overlapping range of body size, and the sex of hatchlings could be determined through the sex of corresponding recaptured juveniles or adults. The following measurements were made for each lizard: snout-vent length (SVL); tail length (TL, from the vent to the tail tip); head length (HL, from the snout to the posterior end of the skull); head width (HW, taken at the posterior end of mandible); forelimp length (FLL, humerus plus ulna); hindlimp length (HLL, femur plus tibia); abdomen length (AL, from the posterior base of the fore-limb to the anterior base of the hind-limb); abdomen width (AW, maximum width of abdomen); distance between axillae (DBA); distance between iliac crests (DBI). Newly-born lizards in the first year of growth, annotinous lizards in the second year, and mature lizards with two or more years of age are clearly different each other in body size, which were considered as hatchling, juvenile and adult lizards, respectively. Individuals with two or more years of age were considered to be mature as some female individuals could be pregnant after two years of growth. SSD was determined for each age, and all measurements on body sizes were compared between two sexes.

**2.2. Data analysis** Kolmogorov-Smirnov test and the Levene's test were employed to test the variable normality and homogeneity. Analysis of variance (ANOVA) was used to test for differences in mean SVL between males and females of the same age, while body-length adjusted size differences were tested using analysis of covariance (ANCOVA, with SVL as a covariate). We used two-way ANOVA to compare the SVL between sexes and among ages, while two-way ANCOVA was used to compare other morphologies when SVL was controlled for.

For each age category, growth rate was calculated by the following function:  $(SVL_{t_2} - SVL_{t_1}) / (\Delta t)$ , where  $SVL_{t_2}$  is the SVL at recapture,  $SVL_{t_1}$  is the SVL at birth or last recapture, and  $\Delta t$  is the time difference between birth and recaptures (mm/month as unit, May to September, not including hibernation). We tested for correlations between the growth rate and average SVL of the initial capture. If there was no significant correlation, ANOVA was used to examine the difference in growth rate between two sexes, otherwise ANCOVA was used (using mean SVL as the covariate). The same approach was used to test for intrasexual differences in growth rate between age categories.

The survivorship of a lizard was determined by the final capture time. If a lizard disappeared and was

not subsequently observed in all potential dispersed areas described above, it was treated as having died. The primary sex ratio was assumed to be 1:1, and the life tables for each sex were made up by survivorship, survival rate and life expectancy.

### 3. Results

A total of 100 hatchlings and 24 juveniles were marked in 2014; 16 juveniles (14 females, 2 males) and 10 adults (6 females, 4 males) with toe-clipping marking were recaptured in 2015; 10 adults (7 females, 3 males) were recaptured in 2016. In 2016, 105 individuals (79 females, 26 males) were captured in total, comprising 69 adults (51 females, 18 males) and 36 juveniles (28 females, 8 males). The growth rate of 29 lizards were successfully determined, including 14 females and 2 males from hatchling to juveniles, and 8 females and 5 males from juvenile to adult.

**3.1. Survivorship and Sex Ratio** There was a considerable difference in survival rate between males and females. Males had a lower survival rate (6%) than females (14%) between hatchling and adult. The average sex ratio of males to females was 1:3 in this population, with 1:3.5 in juveniles and 1:2.8 in adults.

**3.2. Sexual Size Dimorphism** There was no significant difference of SVL between males and females for hatchlings ( $F_{1,21} = 0.173$ ,  $P = 0.681$ ), juveniles ( $F_{1,38} = 1.807$ ,  $P = 0.187$ ) or adults ( $F_{1,18} = 0.016$ ,  $P = 0.900$ ) (Figure 1A). And, there was no age/sex interaction for SVL ( $F_{2,80} = 0.686$ ,  $P = 0.507$ ).

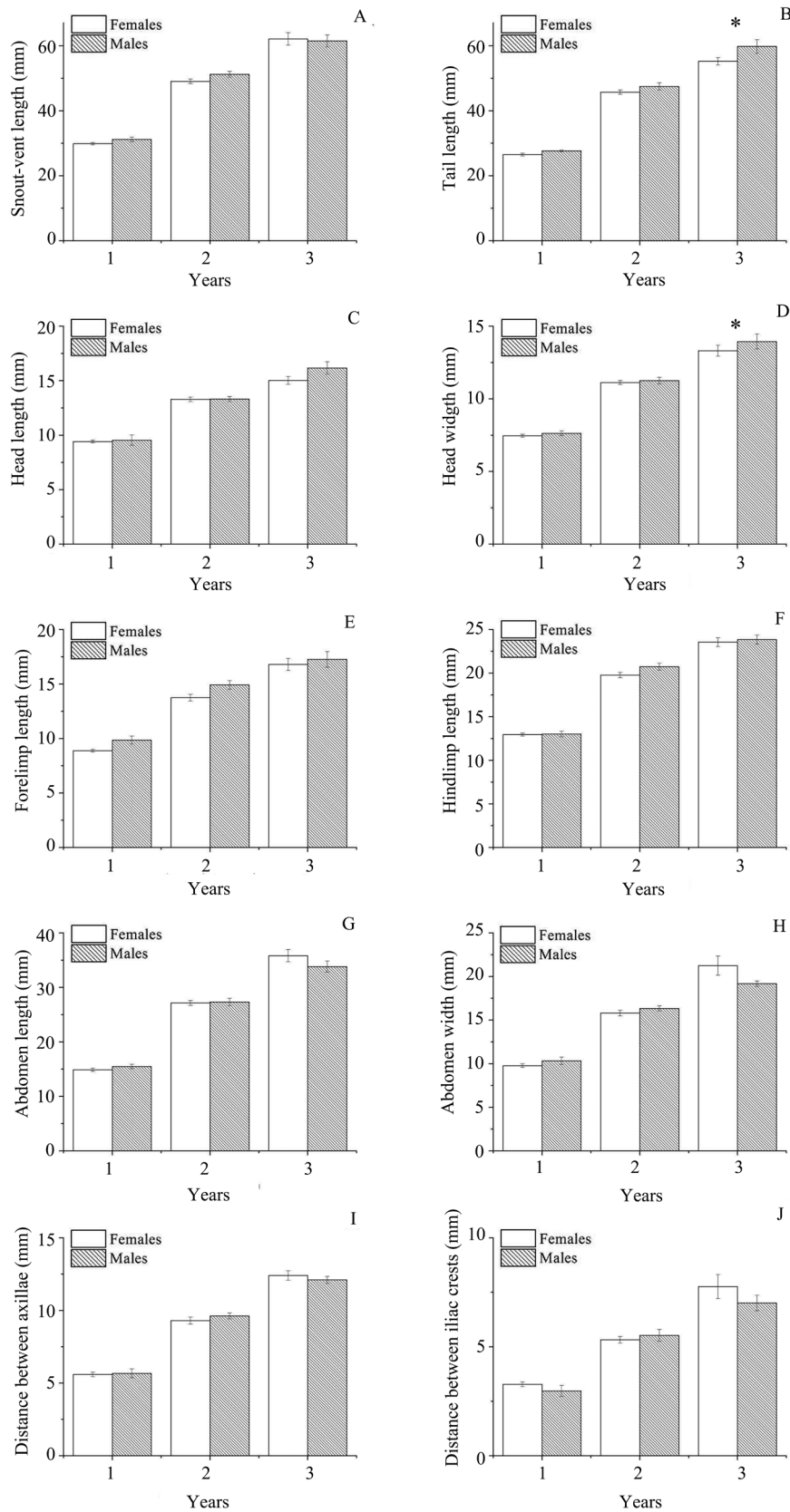
In hatchling lizards, the following measurements (see in Figure 1B–1J) were not different between sexes while SVL was controlled for (TL:  $F_{1,21} = 0.008$ ,  $P = 0.928$ ; HL:  $F_{1,21} = 0.839$ ,  $P = 0.371$ ; HW:  $F_{1,21} = 0.020$ ,  $P = 0.888$ ; FLL:  $F_{1,21} = 0.015$ ,  $P = 0.903$ ; HLL:  $F_{1,21} = 0.010$ ,  $P = 0.992$ ; AL:  $F_{1,21} = 0.700$ ,  $P = 0.413$ ; AW:  $F_{1,21} = 0.078$ ,  $P = 0.783$ ; DBA:  $F_{1,21} = 0.133$ ,  $P = 0.719$ ; DBI:  $F_{1,21} = 0.015$ ,  $P = 0.905$ ). The same result was obtained for juvenile lizards (TL:  $F_{1,38} = 0.004$ ,  $P = 0.952$ ; HL:  $F_{1,38} = 0.632$ ,  $P = 0.432$ ; HW:  $F_{1,38} = 0.858$ ,  $P = 0.360$ ; FLL:  $F_{1,38} = 0.242$ ,  $P = 0.625$ ; HLL:  $F_{1,38} = 0.386$ ,  $P = 0.538$ ; AL:  $F_{1,38} = 0.344$ ,  $P = 0.561$ ; AW:  $F_{1,38} = 0.006$ ,  $P = 0.939$ ; DBA:  $F_{1,38} = 2.053$ ,  $P = 0.160$ ; DBI:  $F_{1,38} = 0.103$ ,  $P = 0.750$ ). In adult lizards, significant sexual difference was found in TL ( $F_{1,18} = 4.964$ ,  $P = 0.040$ ) and HW ( $F_{1,18} = 4.963$ ,  $P = 0.045$ ), but not in HL ( $F_{1,18} = 3.430$ ,  $P = 0.081$ ), FLL ( $F_{1,18} = 3.316$ ,  $P = 0.086$ ), HLL ( $F_{1,18} = 2.926$ ,  $P = 0.105$ ), AL ( $F_{1,18} = 0.043$ ,  $P = 0.838$ ), AW ( $F_{1,18} = 1.416$ ,  $P =$

$0.250$ ), DBA ( $F_{1,18} = 0.236$ ,  $P = 0.633$ ) or DBI ( $F_{1,18} = 3.153$ ,  $P = 0.094$ ). The influence of interaction between age and sex was significant to variation of TL ( $F_{2,80} = 6.685$ ,  $P = 0.002$ ), HL ( $F_{2,80} = 5.240$ ,  $P = 0.007$ ) and HW ( $F_{2,80} = 4.339$ ,  $P = 0.016$ ) between each age, but not to the variation of FLL ( $F_{2,80} = 0.007$ ,  $P = 0.993$ ), HLL ( $F_{2,80} = 0.615$ ,  $P = 0.543$ ), AL ( $F_{2,80} = 0.931$ ,  $P = 0.399$ ), AW ( $F_{2,80} = 2.684$ ,  $P = 0.075$ ), DBA ( $F_{2,80} = 0.270$ ,  $P = 0.764$ ) and DBI ( $F_{2,80} = 0.593$ ,  $P = 0.555$ ).

**3.3. Growth Rate** The growth rate of SVL in the age group from hatchling to juvenile was significantly larger than that in the age group from juvenile to adult in males ( $t_{1,5} = 4.821$ ,  $P = 0.005$ ), but no significant difference was found in females between different age groups ( $F_{1,20} = 2.272$ ,  $P = 0.151$ ). In each age group, the growth rate was not different between males and females (age group from hatchling to juvenile:  $t_{1,14} = -1.252$ ,  $P = 0.231$ ; age group from juvenile to adult:  $F_{1,11} = 0.721$ ,  $P = 0.414$ ) (Figure 2A).

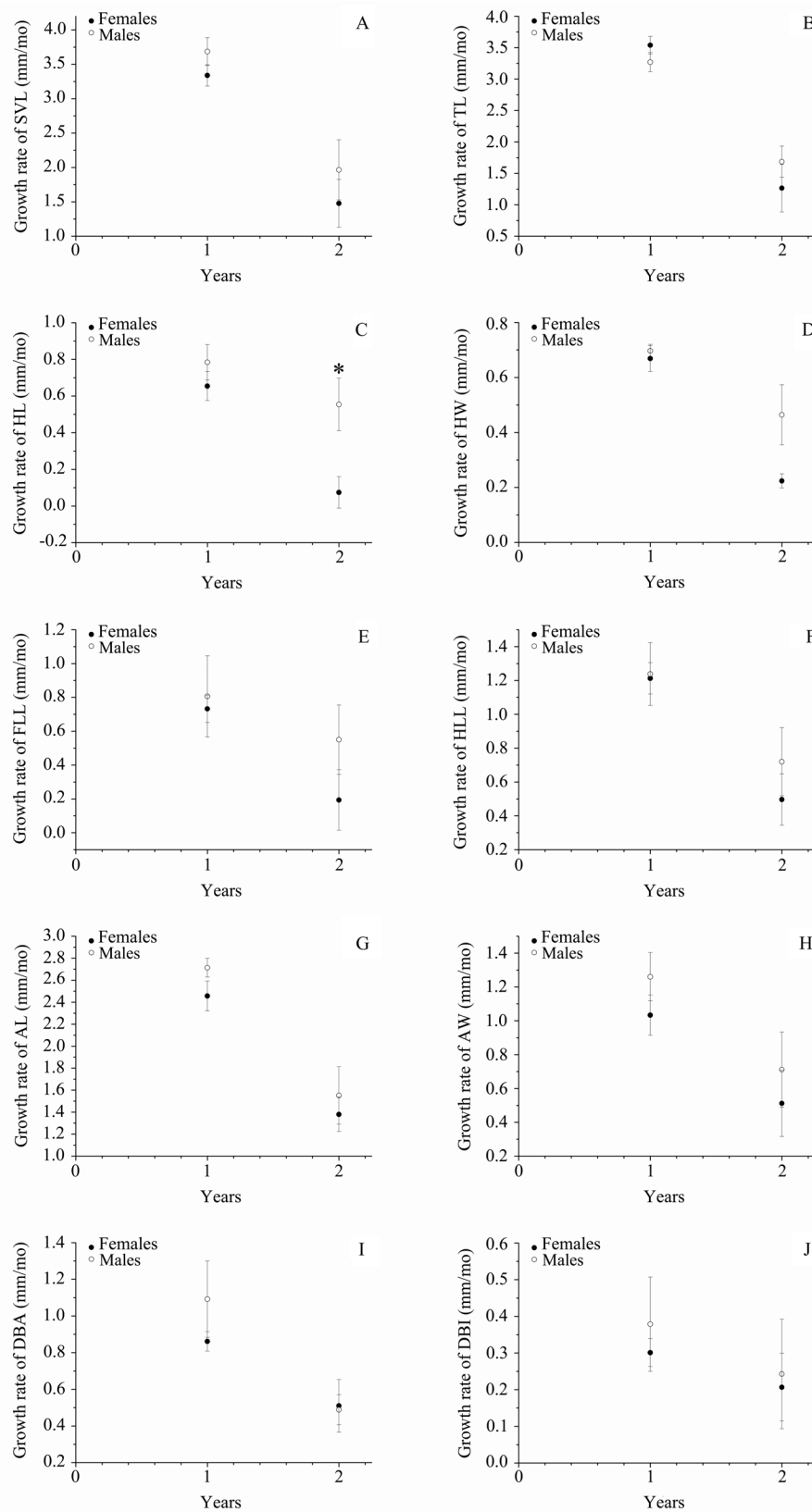
The growth rates of TL ( $F_{1,20} = 4.522$ ,  $P = 0.0491$ ), HW ( $F_{1,20} = 8.610$ ,  $P = 0.010$ ), AL ( $F_{1,20} = 9.282$ ,  $P = 0.008$ ) and AW ( $F_{1,20} = 5.609$ ,  $P = 0.030$ ) in the age group from hatchling to juvenile were significant larger than the age group from juvenile to adult in females, although no difference was found in other measurements between age group (HL:  $F_{1,20} = 0.581$ ,  $P = 0.457$ ; FLL:  $F_{1,20} = 0.202$ ,  $P = 0.659$ ; HLL:  $F_{1,20} = 0.980$ ,  $P = 0.337$ ; DBA:  $F_{1,20} = 0.368$ ,  $P = 0.553$ ; DBI:  $F_{1,20} = 1.296$ ,  $P = 0.271$ ). In males, there was no difference between two age groups (TL:  $F_{1,5} = 0.962$ ,  $P = 0.359$ ; HL:  $F_{1,5} = 960$ ,  $P = 0.356$ ; HW:  $F_{1,5} = 1.802$ ,  $P = 0.216$ ; FLL:  $F_{1,5} = 0.523$ ,  $P = 0.490$ ; HLL:  $F_{1,5} = 2.362$ ,  $P = 0.163$ ; AL:  $F_{1,5} = 0.291$ ,  $P = 0.606$ ; AW:  $F_{1,5} = 2.312$ ,  $P = 0.167$ ; DBA:  $F_{1,5} = 0.159$ ,  $P = 0.702$ ; DBI:  $F_{1,5} = 0.299$ ,  $P = 0.600$ ) (Figure 2B–2J).

During growth from hatchling to juvenile, the growth rates of all other measurements (except SVL) showed no differences between males and females (TL:  $F_{1,14} = 3.276$ ,  $P = 0.093$ ; HL:  $F_{1,14} = 0.558$ ,  $P = 0.467$ ; HW:  $F_{1,14} = 0.075$ ,  $P = 0.788$ ; FLL:  $F_{1,14} = 0.136$ ,  $P = 0.718$ ; HLL:  $F_{1,14} = 0.014$ ,  $P = 0.906$ ; AL:  $F_{1,14} = 0.089$ ,  $P = 0.771$ ; AW: ( $F_{1,14} = 0.747$ ,  $P = 0.402$ ; DBA:  $F_{1,14} = 2.610$ ,  $P = 0.128$ ; DBI:  $F_{1,14} = 0.636$ ,  $P = 0.439$ ). During the juvenile to adult growth period, the growth rate of HL in males was significant large than females ( $F_{1,11} = 7.490$ ,  $P = 0.019$ ), but other measurements showed no significant differences between both sexes (TL:  $F_{1,11} = 0.915$ ,  $P = 0.359$ ; HW:  $F_{1,11} = 3.939$ ,  $P = 0.073$ ; FLL:  $F_{1,11} = 1.665$ ,  $P = 0.223$ ; HLL:  $F_{1,11} = 0.744$ ,  $P = 0.407$ ; AL:  $F_{1,11} = 0.295$ ,  $P = 0.598$ ; AW:  $F_{1,11} = 0.441$ ,  $P = 0.520$ ; DBA:  $F_{1,11} = 0.019$ ,  $P = 0.894$ ; DBI:  $F_{1,11} = 0.039$ ,  $P = 0.847$ ).



**Figure 1** Comparison of morphologies between sexes and among ages in toad-headed lizard *P. guinanensis* in Guinan County, Qinghai Province, China. The data are presented as means  $\pm$  SE.  $P < 0.05$  was considered as statistically significant ( $*P < 0.05$ ).





**Figure 2** Growth rates of SVL and other proportional measurements of male and female *P. guinanensis* in Guinan County, Qinghai Province, China. The abbreviation in each graph represents that: SVL (snout-vent length); TL (tail length); HL (head length); HW (head width); FLL (forelimp length); HLL (hindlimp length); AL (abdomen length); AW (abdomen width); DBA (distance between axillae); DBI (distance between iliac crests). The data are presented as means ± SE.  $P < 0.05$  was considered as statistically significant (\* $P < 0.05$ ).

#### 4. Discussion

Our study concluded that the female-biased sexual ratio is correlated with a sex-specific survival rate. There was no SSD of SVL in any age group of *P. guinanensis*, except for adult male-biased SSD in head width and tail length which might be resulted from sexual selection. Male lizards had a very high mortality during the first year of life and relative low mortality in the second year, and female lizards had a relative low and stable mortality. The differential mortality between both sexes might be responsible for the female-biased sex ratio of this population. Males usually have larger home ranges than females and male-male conflict could force smaller male lizards to disperse (Qi *et al.*, 2013; Stamps, 1993; Wang *et al.*, 2004), which will lead to increased mortality of males due to injury and greater exposure to predation (Christe *et al.*, 2006; Owensmith, 1993), while the locomotor costs of pregnancy in *Phrynocephalus* could potentially increase the injury of adult females (Lu *et al.*, 2015).

While there is no significant SSD in SVL in *P. guinanensis* among age groups, the ontogenetic SSD of male-biased head size and tail length might result from male-male competition. Male-male competition and female mate choice likely favor males with large head and high bite force, to increase the advantages during male-male conflict and strength female preference (Herrel *et al.*, 2010; Kaliontzopoulou *et al.*, 2012). The tail in lizards was generally related to the speed and balance (Damme *et al.*, 1998; Herrel *et al.*, 2001; Losos, 1990; Vanhooydonck *et al.*, 2006), and maybe used for visual signalling during territory defending of *Phrynocephalus* (Qi *et al.*, 2011). Lizards with long tails likely have advantages in territory defence and social status maintenance (Brecko *et al.*, 2008; Kaliontzopoulou *et al.*, 2007). In addition, SSD in head width and tail length were revealed in adult lizards at the age ranged from juvenile to adult. Therefore, sexual selection should be preferred to be correlated with male biased SSD in head width and tail length.

Alternatively, SSD in head size and tail length might be associated with other selection pressures, such as sexual specific growth rate. For example, sexual difference in growth pattern could give rise to male-biased SSD (Cox, 2006; Johnston, 2011). Individual growth rates are often related to food consumption, energetic cost of reproduction or reproductive behaviour (Cox, 2006; Cox *et al.*, 2006; Cox and Calsbeek, 2010; Haenel and John-Alder, 2002; Pearson *et al.*, 2002). Different sexual trade-offs between growth and reproduction could also give rise

to SSD (Madsen and Shine, 1993; Zhao and Liu, 2014). Nevertheless, we did not find any sexual difference in growth rates of SVL among three different age groups of *P. guinanensis*, implying the less influences of sexual specific growth rate on SSD.

The discovered quite low sexual survival rates from hatchlings to adults should remind researchers of expanding marked sample sizes (at least far more than 100 marked hatchlings) in future recapture experiments on *Phrynocephalus* viviparity. The low sample size used into this study could not rule out the potential weakness of our statistics due to using a small number of recaptured individuals, such as the estimation of growth rate, survival rate etc. However, the intrinsic value of our general conclusion should far outweigh the above weakness.

In conclusion, our study detected individuals of a rare animal when its knowledge on life history characteristics associated with population survival and development is really unknown. The species has a female-biased sexual ratio associated with sexual specific mortality, but the underlying causes of higher male mortality remains unknown while males do have larger head sizes associated with male-male competition, future studies on sex-specific dispersal ability and predation pressure might help to explain this pattern.

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#### References

- Anderson M. 1994. Sexual selection. New Jersey: Princeton University Press
- Berry J. F., Shine R. 1980. Sexual size dimorphism and sexual selection in turtles (Order Testudines). *Oecologia*, 44(2): 185–191
- Bonnet X., Shine R., Naulleau G., Vacher-Vallas M. 1998. Sexual dimorphism in snakes: different reproductive roles favour different body plans. *P Roy Soc Lond B Biol*, 265: 179–183
- Brecko J., Huyghe K., Vanhooydonck B., Herrel A., Grbac I., Van-Damme R. 2008. Functional and ecological relevance of intraspecific variation in body size and shape in the lizard *Podarcis melisellensis* (Lacertidae). *Biol J Linn Soc*, 94: 251–264

- Caswell H. 2001. Matrix population models. Sunderland: Sinauer Associates
- Christe P., Keller L., Roulin A. 2006. The predation cost of being a male: implications for sex-specific rates of ageing. *Oikos*, 114(2): 381–384
- Cluttonbrock T. H., Coulson T. N., Milner-Gulland E. J., Thomson D., Armstrong H. M. 2002. Sex differences in emigration and mortality affect optimal management of deer populations. *Nature*, 415: 633–637
- Cooper W. E., Vitt L. J. 1989. Sexual dimorphism of head and body size in an iguanid lizard: paradoxical results. *Am Nat*, 133(5): 729–735
- Cox R. M. 2006. A test of the reproductive cost hypothesis for sexual size dimorphism in Yarrow's spiny lizard *Sceloporus jarrovii*. *J Anim Ecol*, 75: 1361–1369
- Cox R. M., Calsbeek R. 2010. Severe costs of reproduction persist in *Anolis* lizards despite the evolution of single egg clutch. *Evolution*, 64: 1321–1330
- Cox R. M., Stenquist D., Calsbeek R. 2009. Testosterone, growth and the evolution of sexual size dimorphism. *J Evol Biol*, 22: 1586–1598
- Cox R. M., Zilberman V., John-Alder H. B. 2006. Environmental sensitivity of sexual size dimorphism: laboratory common garden removes effects of sex and castration on lizard growth. *Funct Ecol*, 20: 880–888
- Damme R. V., Aerts P., Vanhooydonck B. 1998. Variation in morphology, gait characteristics and speed of locomotion in two populations of lizards. *Biol J Linn Soc*, 63:409–427
- Fox C. W., Roff D. A., Fairbairn D. J. 2001. *Evolutionary Ecology: Concepts and Case Studies*. New York: Oxford University Press
- Galliard J. F. L., Fitze P. S., Ferrière R., Clobert J. 2005. Sex ratio bias, male aggression, and population collapse in lizards. *P Natl Acad Sci USA*, 102(50): 18231–18236
- Haenel G. J., John-Alder H. B. 2002. Experimental and demographic analyses of growth rate and sexual size dimorphism in a lizard, *Sceloporus undulatus*. *Oikos*, 96: 70–81
- Herrel A., Meyers J. J., Vanhooydonck B. 2001. Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis. *Biol J Linn Soc*, 74: 305–314
- Herrel A., Moore J. A., Bredeweg E. M., Nelson N. J. 2010. Sexual dimorphism, body size, bite force and male mating success in tuatara. *Biol J Linn Soc*, 100: 287–292
- Ji X., Xie Y. Y., Sun P. Y., Zheng X. Z. 1997. Sexual dimorphism and female reproduction in a viviparous snake, *Elaphe rufodorsata*. *J Herpetol*, 31: 420–422
- Ji X., Wang Y. Z., Wang Z. 2009. New species of *Phrynocephalus* (Squamata, Agamidae) from Qinghai, Northwest China. *Zootaxa*, 1988: 61–68
- Jin Y. T., Yang Z. S., Brown R. P., Liao P. H., Liu N. F. 2014. Intraspecific lineages of the lizard *Phrynocephalus putjatia* from the Qinghai-Tibetan Plateau: impact of physical events on divergence and discordance between morphology and molecular markers. *Mol Phylogenet Evol*, 71 (2014): 288–297
- Jin Y. T., Tong H. J., Zhang K. L. 2016. The impact of phenotypic characteristics on thermoregulation in a cold-climate agamid lizard, *Phrynocephalus guinanensis*. *Asian Herpetol Res*, 7(3): 210–219
- Jirotkul M. 1999. Operational sex ratio influences female preference and male-male competition in guppies. *Anim Behav*, 58: 287–294
- John-Alder H. B., Cox R. M., Taylor E. N. 2007. Proximate developmental mediators of sexual dimorphism in size: case studies from squamate reptiles. *Integr Comp Biol*, 47(2): 258–271
- Johnston G. 2011. Growth and survivorship as proximate causes of sexual size dimorphism in peninsula dragon lizards *Ctenophorus fionni*. *Austral Ecol*, 36: 117–125
- Kaliontzopoulou A., Carretero M. A., Llorente G. A. 2007. Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in *Podarcis* lizards. *J Morphol*, 268: 152–165
- Kaliontzopoulou A., Adams D. C., Meijden A. V. D., Perera A., Carretero M. A. 2012. Relationships between head morphology, bite performance and ecology in two species of *Podarcis* wall lizards. *Evol Ecol*, 26: 825–845
- Kvarnemo C., Ahnesjö I. 1996. The dynamics of operational sex ratios and competition for mates. *Trends in Ecol Evol*, 11(10): 404–408
- Li J. Q., Zhou R., Liu N. F. 2014. Life-history variation among three populations of the toad-headed lizard *Phrynocephalus vlangalii* along an elevation gradient on the northeastern Tibetan Plateau. *Herpetological J*, 24(1): 17–23
- Losos J. B. 1990. Ecomorphology, performance capability, and scaling of west Indian *Anolis* lizards: an evolutionary analysis. *Ecol Monogr*, 60(3): 369–388
- Lu H. L., Jiang C. Q., Ji X. 2015. Locomotor costs of pregnancy in a viviparous toad-headed lizard, *Phrynocephalus vlangalii* (Agamidae). *Herpetol J*, 25: 149–154
- Madsen T., Shine R. 1993. Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. *Evolution*, 47(1): 321–325
- Molinazuluaga C., Doherty P. F., Zúñigavega J. J., Zamoraabrego J. G. 2015. Survivorship, growth, and detection of a knob-scaled lizard in Queretaro, Mexico. *J Herpetol*, 47(1): 156–161
- Owensmith N. 1993. Comparative mortality rates of male and female Kudus: The costs of sexual size dimorphism. *J Anim Ecol*, 62: 428–440
- Parker G. A. 1992. The evolution of sexual dimorphism in fish. *J Fish Biol*, 41(Supplement B): 1–20
- Pearson D., Shine R., Williams A. 2002. Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota*, Pythonidae). *Oecologia*, 131: 418–426
- Pettersson L.B., Ramnarine I. W., Becher S. A. 2004. Sex ratio dynamics and fluctuating selection pressures in natural populations of the Trinidadian guppy, *Poecilia reticulata*. *Behav Ecol Sociobiol*, 55: 461–468
- Pinto A., Wiederhecker H. C., Colli G. R. 2005. Sexual dimorphism in the Neotropical lizard, *Tropidurus torquatus* (Squamata, Tropiduridae). *Amphibia-Reptilia*, 26: 127–137
- Powell G. L., Russell A. P. 1985. Growth and sexual size dimorphism in Alberta populations of the eastern short-horned lizard, *Phrynosoma douglassi brevirostre*. *Can J Zool*, 63: 139–154

- Qi Y., Wan H. F., Gu H. J., Wang Y. Z.** 2011. Do displays and badges function in establishing the social structure of male toad-headed lizards, *Phrynocephalus vlangalii*?. *J Ethol*, 29: 381–387
- Qi Y., Yang W. Z., Lu B., Fu J. Z.** 2013. Genetic evidence for male-biased dispersal in the Qinghai toad-headed agamid *Phrynocephalus vlangalii* and its potential link to individual social interactions. *Ecol Evol*, 3: 1219–1230
- Roff D. A.** 1992. *The evolution of life histories: theory and analysis*. New York: Chapman and Hall
- Schwarzkopf L., Shine R.** 1992. Costs of reproduction in lizards: escape tactics and susceptibility to predation. *Behav Ecol Sociobiol*, 31: 17–25
- Shine R.** 1994. Sexual size dimorphism in snakes revisited. *Copeia*, 1994: 326–346
- Stamps J. A.** 1993. Sexual size dimorphism in species with asymptotic growth after maturity. *Biol J Linn Soc*, 50: 123–145
- Stearns S. C.** 1992. *The evolution of life histories*. New York: Oxford University Press
- Stuart-Fox D. M., Moussalli A., Marshall N. J., Owens I. P. E.** 2003. Conspicuous males suffer higher predation risk: Visual modelling and experimental evidence from lizards. *Anim Behav*, 66: 541–550
- Vanhooydonck B., Herrel A., Irschick D. J.** 2006. Out on a limb: the differential effect of substrate diameter on acceleration capacity in *Anolis* lizards. *J Exp Biol*, 209: 4515–4523
- Wang S. G., Zeng Z. Y., Wu P. F., Lan Z. J., Wang Y. Z.** 2004. The home range of *Phrynocephalus vlangalii*. *Journal of Sichuan University (Natural Science Edition)*, 41(2): 403–408 (in Chinese with English abstract)
- Wolff J. O., Edge W. D., Wang G.** 2002. Effects of adult sex ratios on recruitment of juvenile gray-tailed voles, *Microtus canicaudus*. *J Mammal*, 83: 947–956
- Wu P. F., Wang Y. Z., Guo H. Y., Wang S. G., Zeng Z. Y., Zeng T., Cai H. X.** 2005. The growth and growth differences between female and male of *Phrynocephalus vlangalii*. *J Sichuan Univ (Nat Sci Edition)*, 42(6): 1252–1257 (in Chinese with English abstract)
- Zhang K. L., Liu Y. H., Tong H. J., Yu X. X., Jin Y. T.** 2017. Correlation between the spatial distribution of active cave and insect resources in *Phrynocephalus guinanensis* (Lacertilia: Agamidae). *Acta Ecol Sin*, 37 (16): 5550–5555 (in Chinese with English abstract)
- Zhao W., Liu N. F.** 2014. The proximate causes of sexual size dimorphism in *Phrynocephalus przewalskii*. *Plos One*, 9(1): 1–9