Sexual dimorphism in morphology and bite force in the mountain dragon, Diploderma batangense (Squamata: Anguidae), from the Hengduan Mountains in western China

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Abstract

Lizards exhibit sexual dimorphism in various phenotypic traits and capability performance (e.g. bite force), while the patterns of sexual dimorphism vary among genera and species. The relationship between morphology and function is dynamic, and selective pressures can differentially affect bite performance in different sexes. Here, we analyzed sexual dimorphism in morphological traits and bite force and explored the determinants of bite force in the mountain dragon (Diploderma batangense) from western China. A total of 135 individuals were collected, and nine morphological characteristics and bite force were measured. We found a significant male bias in morphology and bite force performance, with males found to be larger than females in regard to head size, body size, limb length, tail length and bite force, which could be explained by sexual selection. Results also showed that bite force was positively correlated with head size, with the determinant affecting bite force differing between males(mouth length) and females(head width), which may be related to their different roles in reproduction. This study provides a reference for understanding the ecological adaptability of mountain dragons in the field and lays a foundation for revealing the mechanism of bite force variation between the sexes.

Sexual dimorphism in morphology and bite forceinthe mountain dragon,Diploderma*batangense* **(Squamata: Anguidae), from the Hengduan Mountains in western China**

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Abstract: Lizards exhibit sexual dimorphism in various phenotypic traits and capability performance (e.g. bite force), while the patterns of sexual dimorphism vary among genera and species. The relationship between morphology and function is dynamic, and selective pressures can differentially affect bite performance in different sexes. Here, we analyzed sexual dimorphism in morphological traits and bite force and explored the determinants of bite force in the mountain dragon (*Diploderma batangense*) from western China. A total of 135 individuals were collected, and nine morphological characteristics and bite force were measured. We found a significant male bias in morphology and bite force performance, with males found to be larger than females in regard to head size, body size, limb length, tail length and bite force, which could be explained by sexual selection. Results also showed that bite force was positively correlated with head size, with the determinant affecting bite force differing between males (mouth length) and females (head width), which may be related to their different roles in reproduction. This study provides a reference for understanding the ecological adaptability of mountain dragons in the field and lays a foundation for revealing the mechanism of bite force variation between the sexes.

Keywords: Bite force; Lizards; Sexual dimorphism; Morphology; Sexual selection

Introduction

Sexual dimorphism, including differences in size, color, and capability performance between the two sexes of a species, is widespread in amphibians (Schäuble, 2004), reptiles (Zhong et al., 2017), mammals (Mitani et al., 1996), birds (Fairbairn & Shine, 1993), and invertebrates (Jozet-Alves et al., 2008). Three main hypotheses have been proposed to explain the evolution of sexual dimorphism in animals (Cruz-Elizalde et al., 2021). The first proposes that male-biased sexual dimorphism can be explained by sexual selection, in which larger males gain greater advantages in resource allocation, territorial defense, and mate choice (Endler & Houde, 1995; Cruz-Elizalde et al., 2021). In contrast, the female-biased fecundity advantage hypothesis suggests that larger females are selectively favored by natural selection and tend to produce larger litter clutches/size or egg production/offspring size (Cox et al., 2003; Pincheira-Donoso & Hunt, 2017; Cruz-Elizalde et al., 2021). The third hypothesis of intraspecific niche divergence proposed by Rand (1967) and Schoener (1967) suggests that differential use of one or several resources (e.g., food, microhabitats, and territory) can reduce male-female competition when resources were limited (Bolnick & Doebeli, 2003; Pincheira-Donoso et al., 2018). Sexual dimorphism in morphological traits and performance is prominent in many lizard species, which can be explained by the above hypotheses (Cruz-Elizalde et al., 2020, 2021). Indeed, sexual selection, fecundity advantage, and niche divergence are not mutually exclusive and may have combined effects on body size and other sexually dimorphic characteristics (Ji et al., 2006; Dashevsky et al., 2013; Zhu et al., 2022). In general, males are larger in body size (e.g., body length and mass) but smaller in reproductive-related characteristics (e.g., body cavity) than females (Olsson et al., 2002). Consequently, it can be difficult to determine the causes of sexual dimorphism associated with each hypothesis (Cox et al., 2003; Kuo, 2009).

In reptiles, bite force is a comprehensive measure of performance across multiple ecological and behavioral activities, including resource allocation, territorial defense, aggressive interactions, and mate acquisition (Huyghe et al., 2005; Kaliontzopoulou et al., 2012; Naretto et al., 2022). In general, adults with a greater bite force are more likely to win intrasexual contests (Wegener et al., 2019; Taverne et al., 2020). Furthermore, during copulation, male lizards often bite the abdomen or neck of the female to restrict movement or escape, thereby increasing their mating success rate (Noble & Bradley, 1933; Herrel et al., 1996; Herrel et al., 2010). In most reptile species, males tend to exhibit larger biting capacity than females (Herrel et al., 2007; Sagonas et al., 2014; Naretto et al., 2022). For example, male Achala copper lizards (*Pristidactylus achalensis*) demonstrate stronger bite force than females, including lateral and frontal bites (Naretto et al., 2022). Furthermore, in species showing no differences in body size between males and females, head size may still exhibit dimorphism due to the intrinsic differences in energy requirements between males and females, leading to dimorphism in bite force (McBrayer & Anderson, 2007). In this context, females may evolve specific physical structures (e.g., feeding structure) to enhance energy acquisition under selective pressure (Bulte et al., 2008). For example, female northern map turtles (*Graptemys geographica*) can consume larger snails and access more food resources than males due to their stronger biting capacity (Bulte et al., 2008).

Investigating the association between sexual dimorphism in morphology and bite force has been a topic of research in reptiles for many years. Notably, several studies have reported that head morphology directly affects bite force (Herrel et al., 2007; Sagonas et al., 2014; Naretto et al., 2022) and differences in head size generate different functional consequences (McBrayer & Anderson, 2007). In general, taller and wider heads are associated with larger bite force, resulting in species, age, and sex differences (Taverne et al., 2020). As such, differences in bite performance between males and females are expected due to sexual dimorphism in head size, which is common in lizards (Herrel et al., 2007). However, the best predictors of bite force tend to differ between the sexes due to differences in bite use (e.g., intrasexual competition, intersexual interactions, and diet) (Herrel et al., 2007; Naretto et al., 2022). For example, the traits that best predict bite force differ between male and female tuatara (*Sphenodon punctatus*), which is likely due to sexual selection (Herrel et al., 2010). Variation in bite force between the sexes is often caused by differences in overall size, especially variation in bite force driven by specific head traits (e.g., head width and depth) (Lappin et al., 2006; McBrayer & Anderson, 2007). Despite the assumption that observed differences in head size lead to parallel differences in bite force, which are dependent on the bones and muscles of the head, the relationship between head size and bite force remains unclear (Herrel et al., 2007; Huyghe et al., 2009). Differences in jaw muscle architecture and physiology, including skeletal lever system, pennation angle, muscle arrangement, and relative size, may result in differences in bite force (Herrel et al., 2007; Fabre et al., 2014). Consequently, exploring the link between bite force and morphology in sexual dimorphism may help to disentangle the potential mechanisms related to the evolution of sexual dimorphism (Kaliontzopoulou et al., 2012). A significant association between morphology and bite force in sexually dimorphic species may provide empirical evidence for the co-evolution of both traits and may point to the joint effect of selection on form and function.

In the current study, we explored sexual dimorphism in morphological traits and bite force in*Diplodermabatangense* , an oviparous lizard species endemic to small areas of brush habitat along the upper Jinsha River near Batang County, Sichuan Province, China (Wang et al., 2021). The species has been listed as a "National Protected Key Wild Animal" in China since 2021, primarily due to anthropogenic disturbance and habitat loss caused by hydropower and road construction, resulting in fewer thermoregulatory sites. At present, little is known about the biology and ecology of *D. batangense* , thereby limiting species-specific management strategies. Here, we investigated a *D. batangense* population in the type locality and addressed two main questions: (1) Do males and females differ in morphological traits and bite force? (2) Is there a relationship between head morphology and bite force in this species?

Materials and Methods

Study site

The study was carried out in the upper Jinsha Valley in Batang County (29.46degN, 99.06degE, 2 497 m a.s.l.) on the Sichuan-Tibet border in western China (Fig. 1). The area is characterized by a typical dry-hot valley-plateau climate, with a dry spring, cool summer, rainy autumn, and warm winter. Annual average temperature is 13.8 degC, with minimum and maximum monthly means of 3.9 degC and 19.9 degC in December and June, respectively. Annual mean precipitation is 500 mm, with more than 80% falling between June and September. The region shows sparse vegetation habitat, low vegetation cover (less than 50%), and sandy and rocky soil substrate. The vegetation is dominated by shrubs (e.g.,*Indigofera lenticellata* , *Sophora moorcroftiana* , and*Rumex hastatus*) and herbs (e.g., *Incarvillea arguta* and*Artemisia stechmanniana*).

Fig. 1 Distribution (a), habitat (b), and a male specimen (c) of *Diploderma batangense* . Red dot represents specific study site.

Animal sampling

A total of 135 *D. batangense* lizards (77 males and 58 females) were captured by lasso during daylight hours (10:00am–17:00pm) in August 2020. The capture location was marked using a uniquely coded plastic card. Each lizard was sexed by hemipenis eversion and dorsal color pattern. Bite force and body temperature (BT) were measured immediately after capture. All lizards were numbered and taken to a makeshift laboratory in cloth bags. All lizards were released to their original capture site after collection of data. All animal procedures were carried out in accordance with and approved by the Animal Care and Use Committee at

Yibin University (YBU2020005).

Morphometrics

For all lizards, the following data were collected using a digital caliper (DL91200, Deli, Ningbo, China) to the nearest 0.01 mm: snout-vent length (SVL); tail length (TL, distance from vent to tail tip); abdomen length (AL, distance from posterior base of forelimb to anterior base of hindlimb); head length (HL, distance from anterior tip of rostral scale to posterior aspect of parietal); head width (HW, maximum width of head taken at posterior end of mandible); head height (HH, distance from gular region to highest part of head); mouth length (ML, distance from tip of snout to end of opening); forelimb length (FLL, distance from forelimb to wrist joint); and hindlimb length (HLL, distance from hindlimb to ankle joint). Body mass (BM) was determined using a digital scale (I-2000, Mengfu, Dongguan, China) to the nearest 0.01 g.

Bite force

To explore the relationship between bite force and BT, anal temperature was collected before each bite using an ultra-thin catheter electronic thermocouple (UT323, +0.01deg C; Victor, Shenzhen, China) in the cloaca. *In vivo* bite force was measured using a piezoelectric force transducer instrument (VXT500, 0–50 N; Viste, Shenzhen, China), consisting of a pair of bite plates (2 mm thick, accurate to 0.1 N), hand-charged amplifier, and digital display. To reduce damage to teeth, the end of each steel plate was covered with non-toxic rubber. The instrument was calibrated before each bite. The bite plate was placed at the unilateral molar, a posterior bite position where maximum bite force can be recorded. During measurement, bite force data were collected by gently pinching the head and tail. Bite force was measured three times per individual, and the maximum value was the maximal bite force for each lizard (McBrayer & Anderson, 2007). Bite force trials were separately conducted three times in the field and indoors to minimize variation. Based on the six tests, only the maximum bite force value and the corresponding anal temperature were retained for further analysis.

Statistical analysis

To investigate differences in morphological traits and bite force between males and females, we first performed analysis of variance (ANOVA) for morphological measurements (SVL, BM, HL, HW, FLL, and HLL) and bite force values. As some samples (TL, AB, HH, ML, and bite force) showed non-normality, we also used the nonparametric Mann-Whitney (U) test. To determine the effect of individual SVL on morphology and bite performance, we further examined the relative differences in morphological traits and bite force between the sexes using similar methods while controlling for the effect of SVL (covariate).

To test whether morphological traits could explain the observed sexual dimorphism in bite performance, we first examined the relationship between bite force and head morphology for both sexes using univariate linear regression. Next, we performed stepwise multiple regression analysis to confirm which morphological traits were the best predictors of variation in bite force for males and females.

Significance level was set to $P < 0.05$. All data analyses were performed using SPSS v26.0 (SPSS Inc., Chicago, IL, USA) and graphs were generated using OriginLab Professional v2021b.

Results

Sexual dimorphism inmorphology

Marked morphological dimorphism was observed between the male and female lizards. Males were significantly larger than females in all morphological traits measured (SVL: $F_{1,\ 133}$=13.047, $p = 0.001$; BM: $F_{1,\ 133} = 18.797$,$p < 0.001$; HL: $F_{1,\ 133} = 64.170$,$p < 0.001$; HW: $F_{1,\ 133} = 53.253$,$p < 0.001$; TL: $Z_{1,\ 133} = -7.656$,$p < 0.001$; HH: $Z_{1,\ 133} = -5.810$,$p < 0.001$; ML: $Z_{1,\ 133} = -6.585$,$p < 0.001$; FLL: $F_{1,\ 133} = 63.407$, $p < 0.001$; HLL, $F_{1,\ 133}= 73.092$, $p < 0.001$, Table 1, Figure 2), except for AL ($Z_{1,\ 133} = -0.691$, $p = 0.498$, Table 1, Figure 2d). In addition, for a given SVL, males had greater head size (HW: $F_{1,\ 133} = 44.112$, $p = 0.005$; HL:$F_{1,\ 133} = 71.294$, $p < 0.001$; logHH: $F_{1,\ 133}= 30.462$, $p <0.001$; logML: $F_{1,\ 133} = 43.027$, p

< 0.001), weight ($F_{1,\,133} = 5.513$,$p = 0.020$), TL ($F_{1,\,133} = 79.160$, $p < 0.001$), and limb length (FLL: $F_{1,\,133} = 49.567$, $p < 0.001$; HLL:$F_{1,\,133} = 54.447$, $p < 0.001$, Table 1) compared to females.

Figure 2 Comparison of morphological characteristics and bite force between male and female *Diploderma batangense* . a) SVL, snout-vent length; b) BM, body mass; c) TL, tail length; d) AL, abdomen length; e) HL, head length; f) HW, head width; g) HH, head height; h) ML, mouth length; i) FLL, forelimb length; j) HLL, hindlimb length; k) Bite force; l) Ventral surface of male and female. Gray filled is male and no fill is female; * Significant differences ($p < 0.001$).

Sexual dimorphism in bite force and itsdeterminants

No significant relationship was detected between bite force and BT in*D. batangense* ($F_{1,\,133} = 0.22$, $p = 0.133$). However, significant differences in bite force were found between males and females. In comparison to females, males had significantly larger absolute bite force ($F_{1,\,133} = -4.494$, $p < 0.001$, Table 1, Figure 2k) and relative bite force ($F_{1,\,133} = 10.610$, $p = 0.001$).

Univariate linear regression analysis showed that bite force was positively correlated with HL, HW, HH, and ML (Table 2, Figure 3). Multiple stepwise regression analysis showed that the determinants of bite force were ML in males ($R^2 = 0.467$, $p = 0.002$; Table 2) and HW in females ($R^2 = 0.378$, $p < 0.001$; Table 2).

Figure 3 Relationship between bite force and head morphology in*Diploderma batangense* . Relationships between bite force and head length (HL) (a), head width (HW) (b), head height (HH) (c), and bite force and mouth length (MF) (d). Red points represent females and black points represent males.

Discussion

Lizards exhibit sexual dimorphism in various phenotypic traits and behaviors, such as size, shape, weight, coloration, bite force, and locomotor performance (Cox et al., 2003). Three patterns of sexual dimorphism have been identified in lizards (Cruz-Elizalde et al., 2021), including male-biased (Herrel et al., 2010), female-biased (Cox et al., 2009), and unbiased (Schwarzkopf, 2005), which vary among different genera and families (Cox et al., 2007; Cruz-Elizalde et al., 2021). The*D. batangense* population from the Hengduan Mountains demonstrated obvious male-biased morphology and bite force performance. Notably, the*D. batangense* males were markedly larger (i.e., equivalent body size) than females in terms of head size (HL, HW, HH, and ML), body size (SVL and BM), limb length (FLL and HLL), and tail length (TL), with stronger bite force, although no differences in AL were observed. This male-biased pattern has been widely reported in the lizard family, including in *Tropidurus*(Tropiduridae), *Anolis*(Dactyloidae), *Varanus* (Varanidae), *Sceloporus*(Phrynosomatidae), and *Diploderma* (Anguidae) (Cox et al., 2007; Kuo et al., 2009; Jimenez-Arcos et al., 2017). Interestingly, Kuo et al., (2009) reported that closely related species *D. swinhonis*(previously *Japalura swinhonis*) shows marked male-biased sexual dimorphism in all morphological variables, but when controlling for body size, males had proportionately longer and wider heads, but shorter body length and limbs. Xiong et al., (2022) also found that *D. micangshanensis*shows significant male-biased sexual dimorphism in all morphological variables, except for trunk length, but when controlling for SVL, only head shape (HL, HW, HH, and ML) and trunk length differ significantly between the sexes. Differences in sexual dimorphism between closely related species may be related to differences in habitats (Da et al., 2014), as reported in*Podarcis hispanica* and*P. bocagei* (Kaliontzopoulou et al., 2012).

Male-biased sexual dimorphism is usually explained by sexual selection, which predicts that males will evolve morphological features and capacities that enhance mating success, whether through improved fighting ability against other males or a better chance of attracting females (Endler & Houde, 1995; Cruz-Elizalde et al., 2021). Previous studies have shown that larger males (e.g., larger body size and head shape) are more likely to outcompete and gain access to better resources such as food, territory, and mates during antagonistic encounters (Herrel et al., 2010; Hierlihy et al., 2013). Food availability is a determining factor of intraspecific competition in many lizard species (Pafilis et al., 2009; Donihue et al., 2016).*Diploderma batangense*inhabits dry-hot valleys characterized by relatively scarce food sources. In the studied *D. batangense* population, aggressive male-male interactions were relatively common during and outside the mating season, with larger individuals more likely to win in aggressive interactions for food (unpublished data). Forced copulation is an important reproductive strategy in various territorial lizards (Rodda, 1992; Herrel et al., 2010), in which females struggle physically and violently in an apparent attempt to escape mounting males (Burghardt & Rand 1982). *Diploderma batangense* also showed aggressive and forceful behavior during copulation, in which a male approached a female and grasped her neck with his jaws. Therefore, the larger body size and bite force in *D. batangense* may be related to actual mating success and fitness (Lappin & Husak, 2005; Herrel et al., 2010).

Bite force is a comprehensive measure of trait performance in multiple activities, including courtship, conflict, and hunting, especially in males (Herrel et al., 2007; Kaliontzopoulou et al., 2012; Sagonas et al., 2014; Herrel et al., 2018). Individual bite force capacity is directly related to head size (McBrayer & Anderson, 2007; Herrel et al., 2010; Kaliontzopoulou et al., 2012), generally increasing with head size (Deeming et al., 2022; Naretto et al., 2022). This phenomenon was found in present study, where bite force was positively correlated with head size (HL, HW, HH and ML). Understandably, a larger head results in a larger cross-sectional area of jaw muscles and more developed jaw-cranial musculature, thus generating greater bite force (Herrel et al., 2001). Therefore, increasing head height and cross-sectional area of the jaw muscles may be a mechanism for increasing occlusal force (McBrayer & Anderson, 2007). Head length, head width, and mouth length can also affect bite force (Herrel et al., 2001; Sagonas et al., 2014), not unexpectedly as bite performance can be influenced by the size of the jaw musculature, ratio of the upper and lower jaws, insertion point and direction of jaw musculature, and microstructure of the muscle fibers (Herrel et al., 1998; Kaliontzopoulou et al., 2012). Thus, external head morphology is a readily accessible proxy for the joint action of structural components. Interestingly, Lappin and Husak (2005) found only a weak correlation between external head size and bite force in male collared lizards (*Crotaphytus collaris*) and suggested that internal skull structure may be a key determinant of bite force. Consequently, there is growing recognition that the underlying musculature may drive changes in bite force, as demonstrated in various *Anolis* lizard species, in which the adductor externus and pseudotemporalis muscles are considered good determinants of bite force (Wittorski et al., 2016). Herrel et al., (2007) also proposed that testosterone levels can affect the size of the adductor muscles of the outer jaw and may play an important role in regulating bite force. However, further study is necessary to fully elucidate the determinants of bite force.

Bite performance is expected to vary between males and females due to differences in head shape and size (Herrel et al., 2007). Therefore, the best predictors of maximal bite force capacity tend to differ by sex. For example, lower jaw length is the best predictor of bite force in *Anolis carolinensis* males, whereas head width and jaw-closing in-lever are the best predictors in females (Herrel et al., 2007). In our study, the best predictors of bite force also differed between the males (ML) and females (HW). This difference may be explained from a structure-function relationship: i.e., with the relative increase in head width, the adductor cavity in males is significantly larger than that in females, which may accommodate larger mandibular adductor muscles and enhance interactions between muscles and skull, thus improving bite force strength (Lappin et al., 2006; Sagonas et al., 2014). The jaw musculature and skeletal system are closely related to bite force, and it is clear from the principle of leverage that the larger the male force arm (lower jaw length), the greater the bite force generated (Herrel et al., 2007; Herrel et al., 2010; Wittorski et al., 2016). Sexual dimorphism in lizard bite force is generally thought to be related to fighting or territorial defense in males, with an added advantage in intrasexual competition (Naretto et al., 2022) and forced mating success (Sagonas et al., 2014). Even among males of similar body length, success in combat and forced mating appears to favor those with greater body robustness, head size, and bite force (Lappin et al., 2006). Differences in head size and performance may also be related to differences in reproductive allocation between the sexes, with females investing more in reproduction than males and requiring higher energy intake (Bulte et al., 2008). Thus, head width, the best predictor of bite force in females, may be related to energy requirements for follicular development and offspring rearing (Naretto et al., 2022). Although there was no advantage in head width between the *D. batangense* females and males, females with wider heads had a larger bite force compared to other females, and thus may be able to feed on larger food items and provide more energy for their offspring.

Summary

Relatively few studies have been conducted on sexual dimorphism in *Diploderma* species, although previous studies suggested that male-biased sexual dimorphism was the dominant pattern in the genus (Kuo et al., 2009; Xiong et al., 2022). In the present study, *D. batangense* showed male-biased sexual dimorphism in morphology and bite force, consistent with the sexual selection hypothesis. Furthermore, the best predictors of bite force differed between the sexes (ML in males and HW in females). However, it remains unclear how the intrinsic skull and muscle structures affect bite force in this species. As such, further anatomical analysis of the head structure is required, together with intraspecific (sex) comparisons of body color, behavior, and resource use (diet and microhabitat). In addition, given the high diversity of species and habitats in the genus, further study on interspecific differences in bite force among species in different habitats is necessary.

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Competing Interests

The authors declare no competing interests.

Author Contributions

Ling Li : Data curation (Lead), Formal analysis (Lead), Investigation (Lead), Resources (Lead), Visualization (Lead), Writing – original draft (Lead), Writing – review & editing (Equal);**Gang Wang** : Formal analysis (Supporting), Writing – review & editing (Equal); **Yuhao Wen** : Data curation (Supporting), Investigation (Equal); **Yihua Xiang** : Data curation (Supporting), Investigation (Equal); **Peng Guo** : Conceptualization (Equal), Writing – review & editing (Equal); **Bingjun Dong** : Conceptualization (Equal), Writing – review & editing (Equal);**Yayong Wu** : Funding acquisition (Lead), Investigation (Equal), Supervision (Lead), Writing – review & editing (Lead).

Data Accessibility Statement

All morphological data for all individuals are deposited in Dryad

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References

Bolnick, D. I., & Doebeli, M. (2003). Sexual dimorphism and adaptive speciation: two sides of the same ecological coin. *Evolution* . 57(11): 2433-2449. doi: 10.1111/j.0014-3820.2003.tb01489.x.

Bulte, G., Irschick, D. J., & Blouin-Demers, G. (2008). The Reproductive Role Hypothesis Explains Trophic Morphology Dimorphism in the Northern Map Turtle. *Functional Ecology* . 22(5): 824–830. doi:10.HH/j.1365-2435.2008.01422.x.

Burghardt, G. M., & Rand, A. S. (Eds.). (1982). Iguanas of the world: their behavior, ecology, and conservation. New Jersey: Noyes Publications.

Cox, R. M., Skelly, S. L., & John-Alder, H. B. (2003). A comparative test of adaptive hypotheses for sexual size dimorphism in lizards.*Evolution* . 57(7): 1653-1669. doi:10.1111/j.0014-3820.2003.tb00371.x.

Cox, R. M., Butler, M. A., & John-Alder, H. B. (2007). The evolution of sexual size dimorphism in reptiles. In D.J. Fairbairn, W.U. Blanckenhorn and T. Szekely (Eds.), Sex, size & gender roles: Evolutionary studies of sexual size dimorphism (pp. 38-49). Oxford, UK: Oxford University Press.

Cox, R. M., Stenquist, D. S., & Calsbeek, R. (2009). Testosterone, growth and the evolution of sexual size dimorphism. *Journal of Evolutionary Biology* . 22(8): 1586-1598. doi:10.1111/j.1420-9101.2009.01772.x.

Cruz-Elizalde, R., Ramirez-Bautista, A., Pacheco, L. F. R., Lozano, A., & Rodriguez-Romero, F. D. J. (2020). Sexual dimorphism in size and shape among populations of the lizard *Sceloporus variabilis*(*Squamata: Phrynosomatidae*). *Zoology* . 140: 125781. doi:10.1016/j.zool.2020.125781.

Cruz-Elizalde, R., Villamar-Duque, T. E., & Ramirez-Bautista, A. (2021). Sexual dimorphism in size and shape in the viviparous lizard*Abronia taeniata* (Squamata: Anguidae) in central Mexico.*Acta Zoologica* . 102(2): 220-226. doi:10.1111/azo.12329.

Dashevsky, D., Meik, J. M., Mocino-Deloya, E., Setser, K., & Schaack, S. (2013). Patterns of sexual dimorphism in Mexican alligator lizards,*Barisia imbricata* . *Ecology and Evolution* .3(2): 255-261. doi:10.1002/ece3.455.

Da Silva, J. M., Herrel, A., Measey, G. J., & Tolley, K. A. (2014). Sexual dimorphism in bite performance drives morphological variation in chameleons. *PLoS One* . 9(1): e86846. doi:10.1371/journal.pone.0086846.

Deeming, D. C. (2022). Inter-relationships among body mass, body dimensions, jaw musculature and bite force in reptiles. *Journal of Zoology* . 318(1): 23-33. doi:10.1111/jzo.12981.

Donihue, C. M., Brock, K. M., Foufopoulos, J., & Herrel, A. (2016). Feed or fight: testing the impact of food availability and intraspecific aggression on the functional ecology of an island lizard.*Functional Ecology* . 30(4): 566-575. doi:10.1111/1365-2435.12550.

Endler, J. A., & Houde, A. E. (1995). Geographic variation in female preferences for male traits in *Poecilia reticulata* .*Evolution* . 49(3): 456-468. doi:10.1111/j.1558-5646.1995.tb02278.x.

Fabre, A. C., Andrade, D. V., Huyghe, K., Cornette, R., & Herrel, A. (2014). Interrelationships between bones, muscles, and performance: biting in the lizard *Tupinambis merianae* . *Evolutionary Biology* . 41(4): 518-527. doi:10.1007/s11692-014-9286-3.

Fairbairn, J., & Shine, R. (1993). Patterns of sexual size dimorphism in seabirds of the Southern Hemisphere. *Oikos* . 68(1): 139-145. doi:10.2307/3545319.

Herrel, A., Van Damme, R., & De Vree, F. (1996). Sexual dimorphism of head size in *Podarcis hispanica atrata* : testing the dietary divergence hypothesis by bite force analysis. *Netherlands Journal of Zoology* . 46 (3.4): 253-262.

Herrel, A., Aerts, P., & De Vree, D. (1998). Static biting in lizards: functional morphology of the temporal ligaments. *Journal of Zoology* . 244(1): 135-143. Doi:10.1111/j.1469-7998.1998.tb00015.x.

Herrel, A., De Grauw, E. D., & Lemos-Espinal, J. A. (2001). Head shape and bite performance in xenosaurid lizards. *Journal of Experimental Zoology* . 290(2): 101-107. doi:10.1002/jez.1039.

Herrel, A., McBrayer, L. D., & Larson, P. M. (2007). Functional basis for sexual differences in bite force in the lizard *Anolis carolinensis* . *Biological Journal of the Linnean Society* . 91(1): 111-119. doi:10.1111/j.1095-8312.2007.00772.x.

Herrel, A., Moore, J. A., Bredeweg, E. M., & Nelson, N. J. (2010). Sexual dimorphism, body size, bite force and male mating success in tuatara. *Biological Journal of the Linnean Society* . 100(2): 287-292. doi:10.1111/j.1095-8312.2010.01433.x.

Herrel, A., Petrochic, S., & Draud, M. (2018). Sexual dimorphism, bite force and diet in the diamondback terrapin. *Journal of Zoology* . 304(3): 217-224. doi:10.1111/jzo.12520.

Hierlihy, C. A., Garcia-Collazo, R., Chavez Tapia, C. B., & Mallory, F. F. (2013). Sexual dimorphism in the lizard *Sceloporus siniferus* : support for the intraspecific niche divergence and sexual selection hypotheses. *Salamandra* . 49: 1-6.

Huyghe, K., Vanhooydonck, B., Scheers, H., Molina-Borja, M., & Van Damme, R. (2005). Morphology, performance and fighting capacity in male lizards, *Gallotia galloti* . *Functional Ecology* . 19(5): 800-807. doi:10.1111/j.1365-2435.2005.01038.x.

Huyghe, K., Herrel, A., Adriaens, D., Tadić, Z., & Van Damme, R. (2009). It is all in the head: morphological basis for differences in bite force among colour morphs of the Dalmatian wall lizard.*Biological Journal of the Linnean Society* . 96(1): 13-22. doi:10.1111/j.1095-8312.2008.01103.x.

Ji, X., Lin, L. H., Lin, C. X., Qiu, Q. B., & Du, Y. (2006). Sexual dimorphism and female reproduction in the many-lined sun skink (*Mabuya multifasciata*) from China. *Journal of Herpetology* . 40(3): 351-357.

Jozet-Alves, C., Modéran, J., & Dickel, L. (2008). Sex differences in spatial cognition in an invertebrate: the cuttlefish. *Proceedings of the Royal Society B: Biological Sciences* . 275(1646): 2049-2054. doi:10.1098/rspb.2008.0501.

Jiménez-Arcos, V. H., Sanabria-Urbán, S., & Cueva del Castillo, R. (2017). The interplay between natural and sexual selection in the evolution of sexual size dimorphism in *Sceloporus* lizards (*Squamata:Phrynosomatidae*). *Ecology and Evolution* . 7(3): 905-917. doi:10.1002/ece3.2572.

Kaliontzopoulou, A., Adams, D. C., van der Meijden, A., Perera, A., & Carretero, M. A. (2012). Relationships between head morphology, bite performance and ecology in two species of Podarcis wall lizards.*Evolutionary Ecology* . 26(4): 825-845. doi:10.1007/s10682-011-9538-y.

Kuo, C. Y. (2009). Sexual size and shape dimorphism in an agamid lizard, *Japalura swinhonis* (Squamata: Lacertilia: Agamidae). *Zoological Studies.* 48(3): 351-361.

Lappin, A. K., & Husak, J. F. (2005). Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *The American Naturalist* . 166(3): 426-436.

Lappin, A. K., Hamilton, P. S., & Sullivan, B. K. (2006). Bite-force performance and head shape in a sexually dimorphic crevice-dwelling lizard, the common chuckwalla [*Sauromalus ater* (= obesus)].*Biological Journal of the Linnean Society* . 88(2): 215-222. doi:10.1111/j.1095-8312.2006.00615.x.

McBrayer, L. D., & Anderson, R. A. (2007). Sexual size dimorphisms and bite force in the northern alligator lizard, *Elgaria coerulea* .*Journal of Herpetology* . 41(4): 554-559. doi:10.1670/07-045.1.

Mitani, J. C., Gros-Louis, J., & Richards, A. F. (1996). Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. *The American Naturalist* . 147(6): 966-980. doi:10.2307/2463187.

Naretto, S., Cabezas-Cartes, F., López Juri, G., & Chiaraviglio, M. (2022). Intraspecific variability of bite force in Achala copper lizards in a sexual selection context: who bites harder and when and why?.*Biological Journal of the Linnean Society* . 136(2): 282-292. doi:10.1093/biolinnean/blac034.

Noble, G. K., & Bradley, H. T. (1933). The mating behavior of lizards; its bearing on the theory of sexual selection. *Annals of the New York Academy of Sciences* . 35(1): 25-100. doi:10.1111/j.1749-6632.1933.tb55365.x.

Olsson, M., Shine, R., Wapstra, E., Ujvari, B., & Madsen, T. (2002). Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution* . 56(7):1538-1542. doi: 10.1111/j.0014-3820.2002.tb01464.x.

Pafilis, P., Meiri, S., Foufopoulos, J., & Valakos, E. (2009). Intraspecific competition and high food availability are associated with insular gigantism in a lizard.*Naturwissenschaften* . 96(9): 1107-1113. doi:10.1007/s00114-009-0564-3.

Pincheira-Donoso, D., & Hunt, J. (2017). Fecundity selection theory: concepts and evidence. *Biological Reviews* . 92(1): 341-356. doi:10.1111/brv.12232.

Pincheira-Donoso, D., Tregenza, T., Butlin, R. K., & Hodgson, D. J. (2018). Sexes and species as rival units of niche saturation during community assembly. *Global Ecology and Biogeography* . 27(5): 593-603. doi:10.1111/geb.12722.

Rand, A. S. (1967). Ecology and social organization in Anolis lineatopus. *Proceedings of the United States National Museum* . 122, 1-79.

Rodda G. H. (1992). The mating behavior of *Iguana iguana* .*Smithsonian Contributions to Zoology* . 534: 1-40.

Sagonas, K., Pafilis, P., Lymberakis, P., Donihue, C. M., Herrel, A., & Valakos, E. D. (2014). Insularity affects head morphology, bite force and diet in a Mediterranean lizard. *Biological Journal of the Linnean Society* . 112(3): 469-484. doi:10.1111/bij.12290.

Schoener, T. W. (1967). The ecological significance of sexual size di-morphism in the lizard *Anolis conspersus* . *Science* . 155(3761): 474-477. doi:10.1126/scien ce.155.3761.474.

Schauble, C. S. (2004). Variation in body size and sexual dimorphism across geographical and environmental space in the frogs*Limnodynastes tasmaniensis and L. peronii* . *Biological Journal of the Linnean Society* . 82(1): 39-56. doi:10.1111/j.1095-8312.2004.00315.x.

Schwarzkopf, L. (2005). Sexual dimorphism in body shape without sexual dimorphism in body size in water skinks (*Eulamprus quoyii*).*Herpetologica* . 61(2): 116-123. doi:10.1655/04-66.

Taverne, M., King-Gillies, N., Krajnović, M., Lisičić, D., Mira, Ó., Petricioli, D., Sabolić, I., Štambuk, A., Tadić, Z., & Vigliotti, C. (2020). Proximate and ultimate drivers of variation in bite force in the insular lizards *Podarcis melisellensis* and *Podarcis sicula* . *Biological Journal of the Linnean Society* . 131(1): 88-108. doi:10.1093/biolinnean/blaa091.

Wang, K., Ren, J. L., Wu, J. W., Jiang, K., Jin, J. Q., Hou, S. B.,Zheng, P, Y., Xie, F., Siler, C. D., & Che, J. (2021). Systematic revision of Mountain Dragons (Reptilia: Agamidae: Diploderma) in China, with descriptions of six new species and discussion on their conservation. *Journal of Zoological Systematics and Evolutionary Research* . 59(1): 222-263. doi:10.1111/jzs.12414.

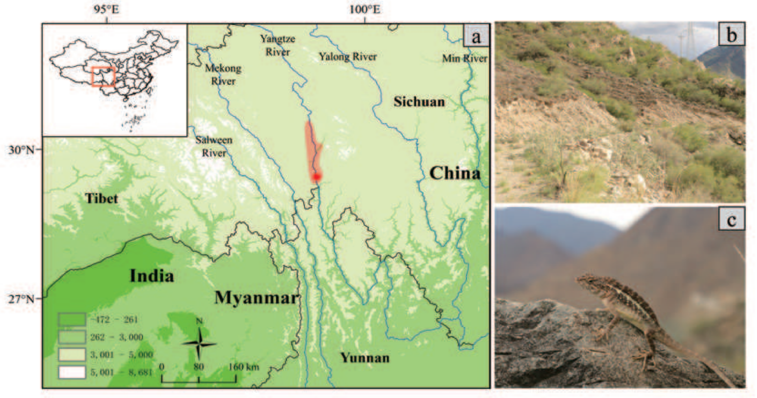
Wegener, J. E., Mulder, K. P., Pringle, R. M., Losos, J. B., & Kolbe, J. J. (2019). Head size of male and female lizards increases with population density across island populations in the Bahamas.*Breviora* . 566(1): 1-9. doi:10.3099/0006-9698-566.1.1.

Wittorski, A., Losos, J. B., & Herrel, A. (2016). Proximate determinants of bite force in *Anolis* lizards. *Journal of Anatomy* . 228(1): 85-95. doi:10.1111/joa.12394.

Xiong, J., Bai, Y., Li, G., & You, Z. (2022). Sexual dimorphism in the mountain dragon, *Diploderma micangshanensis* (Squamata: Lacertilia: Agamidae) from central China.*Animal Biology* . 1(aop): 1-10. doi:10.1163/15707563-bja10085.

Zhong, G. H., Liu, Q., Li, C., Peng, P., & Guo, P. (2017). Sexual dimorphism and geographic variation in the asian lance-headed pitviper *Protobothrops mucrosquamatus*in the mainland china. *Asian Herpetological Research* . 8(2): 118-122. doi:10.16373/j.cnki.ahr.160011.

Zhu, F., Chen, L., Guo, P., Xu, Y., & Liu, Q. (2022). Sexual Dimorphism and Geographic Variation of the White-lipped Pit Viper (*Trimeresurus albolabris*) in China. *Current herpetology* . 41(1): 24-34. doi:10.5358/hsj.41.24.



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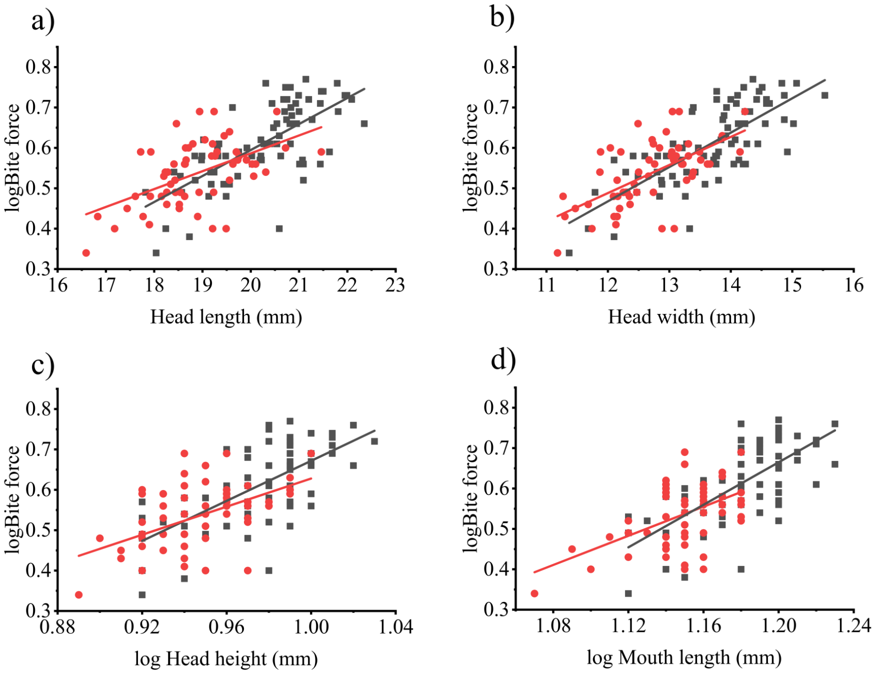

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