

Parental behavior drives large bite force in an insular skink population

H.-Y. Tseng¹ , C.-P. Liao^{1,2}, J.-Y. Hsu¹, L.-Y. Wang³  & W.-S. Huang¹ 

¹ Department of Biology, National Museum of Natural Science, Taichung, Taiwan

² Department of Life Science, Tunghai University, Taichung, Taiwan

³ Functional Morphology and Biomechanics, Institute of Zoology, Kiel University, Kiel, Germany

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Correspondence

Wen-San Huang, Department of Biology, National Museum of Natural Science, 1, Guancian Rd., Taichung 40453, Taiwan
Email: wshuang.380@gmail.com

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Abstract

Different environments may drive the evolution of morphological traits due to selection on organismal performance. In lizards, bite force plays an important role both for inter- and intra-specific interactions, such as prey preference, resource competition, predatory defense, and courtship behavior. Individuals with large bite force may benefit from a high reproductive success through territorial defense or predatory deterrence. Under extremely high predation risk from the oophagic kukri snake (*Oligodon formosanus*), long-tailed skinks (*Eutropis longicaudata*) on Orchid Island exhibit an exclusive post-ovipositional parental care, not found in any other populations. In this study, we tested the assumption that Orchid Island skinks exhibit higher bite force than two other populations without egg-guarding behavior. We investigated the three hypotheses that best explain this adaptation: (1) Orchid Island skinks have different parental care than Green Island and Taiwan skinks, which may drive larger bite force; (2) in the three populations, male–male competition and mating bites enhance bite force, leading males to present higher bite force than females; (3) head traits are indicators of bite force. Our results show for the first time that Orchid Island skinks exhibit larger bite force than the other populations do, which may be shaped by a higher egg-predation pressure and the consequent parental behavior. Males exhibit stronger bite force likely due to a stronger sexual selection. Bite force of long-tailed skink is positively correlated with larger body weight and head length, and the larger head can further enhance bite force for males in sexual selection.

Introduction

Phenotypic performance, usually related to survival and fitness, is affected and modified by selection forces and trait differences across populations. Such performance may reflect local adaptation to various selection pressures, originating from either abiotic environments (Dudley, 1996) or biotic factors (e.g. species community composition) (Reznick, Bryga & Endler, 1990; Reznick, Butler & Rodd, 2001). Therefore, morphological traits, such as cryptic or conspicuous coloration for predator recognition (Ruxton, Sherratt & Speed, 2004; Chouteau & Angers, 2011), feeding apparatus for food competition (Herrel *et al.*, 2001; Grant & Grant, 2006), and songs or colors for mate choice (Jiggins *et al.*, 2001; Seddon, 2005), evolve as an adaptation strategy. One of the most famous examples of morphological trait adaptation is the astonishing coloration of poison frogs, which functions as an aposematic and mating signal display, offering the locally adapted advantages of warning predators (Saporito *et al.*, 2007; Noonan & Comeault,

2009) and attracting mates (Summers *et al.*, 1999; Reynolds & Fitzpatrick, 2007).

Insularity has been shown to influence different aspects of organisms, including morphological traits (Clegg & Owens, 2002; Lomolino, 2005), behavior (Huang, 2006b; Cooper, Dimopoulos & Pafilis, 2015), reproduction strategies and life history (Covas, 2012; Novosolov, Raia & Meiri, 2013). In lizards, some insular populations display larger bite forces than their mainland counterparts do, possibly due to the adaptation to specific prey species or population density (Sagonas *et al.*, 2014). Bite force varies to match ecologically relevant challenges and, therefore, is regarded as an indicator of adaptation. In addition, bite force is a functional trait, associated with inter- and intraspecific competition. The former including prey composition (Herrel *et al.*, 2001; Measey *et al.*, 2011) and predator defense (Herrel *et al.*, 2009; de Barros *et al.*, 2010), while the latter is closely related with sexual selection (Lailvaux *et al.*, 2004; Huyghe *et al.*, 2005; Husak *et al.*, 2006; Cameron, Wynn & Wilson, 2013). Numerous studies have

demonstrated that a larger bite force enhances food handling efficiency (Verwajen, Van Damme & Herrel, 2002), territoriality (Lappin & Husak, 2005), and defense from predators (de Barros *et al.*, 2010). Moreover, sexual selection (e.g. male–male combat or mating bite) is common in lizards, and bite force is critical for territory defense and mate choice. Individuals with larger bite force have a better chance to mate and breed successfully (Lappin & Husak, 2005; Lailvaux & Irschick, 2007; Husak, Lappin & Van Den Bussche, 2009). Usually, the males have a stronger bite force than the females do, due to different tradeoffs under differential selective pressures (Herrel *et al.*, 2010; Vanhooydonck *et al.*, 2010; Cameron *et al.*, 2013). Although numerous studies have focused on the variation in bite performance among different populations or species, none of them has examined how parental care influences it.

Several morphological characters, especially head size and shape, are tightly associated with bite force (Kaliontzopoulou *et al.*, 2012; Sagonas *et al.*, 2014; Žagar *et al.*, 2017). In some rock-dwelling lizards, head shape may vary because of adaptation to microhabitat use (e.g. narrow crevices) and predation pressure (Žagar *et al.*, 2017). Larger and taller heads are associated with stronger bite force than flatter heads are. Head height is related to bite force due to the increased available space for jaw adductor muscles and physiological cross-sectional area. In contrast, bite performance may be constrained by other morphological traits of head in other lizards (Kaliontzopoulou *et al.*, 2012; Broeckhoven & Mouton, 2014).

The long-tailed skink (*Eutropis longicaudata*) is distributed across south China, Vietnam, Laos, Cambodia, Thailand and Taiwan (Das, 2010). The diet of skink consist of diverse insect groups, such as orthopterans, coleopterans and hemipterans (Huang, 2006a). About half of individuals were found in the holes of concrete walls, because the temperature inside the holes is higher than outsides (Huang, 2006a). Violent chasing between two skinks can be occasionally observed in the field. One single population inhabiting Orchid Island, located in southeastern offshore of Taiwan, displays a unique parental care behavior to protect their eggs from the predation of oophagic kukri snake (*Oligodon formosanus*) (Huang, 2006b; Huang & Wang, 2009). When a kukri snake intrudes into the nest of a long-tailed skink, the female skink will defend the eggs by attacking the intruder with strong bites until it retreats (Video S1). This egg-guarding behavior efficiently enhances the egg survival rate (Huang, 2006b), and is likely driven by a high predation pressure of the island habitat (Huang *et al.*, 2013).

This study aims to compare the morphological traits and bite capacity of three long-tailed skink populations inhabiting mainland Taiwan (Kenting), Green Island (Ludao), and Orchid Island (Lanyu). We hypothesized that the unique maternal care displayed by the Orchid Island population facilitates a larger bite force than that exhibited by the Green Island and Kenting populations. Moreover, we hypothesized that, for all the three populations, the males exhibit a stronger bite force than the females do, due to intra- and intersexual competition. Finally, we hypothesized that bite force is positively correlated with head traits, and we investigated which morphological characters predominantly affect bite force.

Materials and methods

Field sampling

Long-tailed skinks use concrete holes to hide during the night and to lay eggs (Huang, 2006a). From 1997 to 2001 the long-tailed skink populations were surveyed with the purpose of comparing the population density among islands. Within each island, the population density was estimated by visually recording the number of lizards in one transect and dividing it by the transect area. Each transect's width was 2 m, while the lengths were 1.5, 0.5 and 2 km in Orchid Island, Green Island and Kenting, respectively. Each population was surveyed once a year. The concrete walls were established before 1997, and the surrounding environments did not change a lots during the 20 years.

During 2014–2016, we visited the concrete walls in the early morning and evening, and caught skinks from the holes in Orchid Island (N 22° 2'2.15", E 121°33'53.02"), Green Island (N 22°39'59.66", E 121°30'22.50") and Kenting (southern Taiwan) (N 121°30'22.50", E 120°38'49.86") which are geographically close to each other (Fig. 1). The skinks were brought back to the laboratory, and all the measurements were conducted within 24 hours of capture. After the measurements and the sex identification, all the skinks were marked and were released back into their original places.

Bite force and morphological measurement

Bite force was measured at 28°C using a piezo high-sensitivity force transducer (range: –500–500N) (type 9203, Kistler Inc., Winterthur, Switzerland), mounted on a holder and attached to a handheld charge amplifier (type 5995A, Kistler) (See Herrel *et al.*, 1999 for detailed description of the equipment setup). The distance between two biting plates was fixed to 0.80 mm. Each individual underwent a series of five consecutive bite force measurements, with an inter-measurement interval of at least five minutes. For each lizard, the maximal bite force corresponded to the maximal obtained value (Herrel *et al.*, 2001).

Morphological traits were measured to the nearest 0.01 mm using a digital caliper, and included snout-vent length (SVL, from the tip of snout to the cloaca), head length (HL, from the tip of snout to the posterior edge of ear opening), head width (HW, the widest part of the head), and head height (HH, the highest part of the head). Body weight (BW) was measured to the nearest 0.01 g using an electronic scale.

Ethical notes

All the work was performed in accordance with the animal ethics protocols approved by the Taiwanese Wildlife Conservation Act by the Forestry Bureau, Council of Agriculture, Taiwan, and the Taiwanese National Museum of Natural Science (approval NMNSHP14-02).

Statistical analyses

Population densities were compared by fitting the number of lizards with a mixed-effect Poisson regression. Population

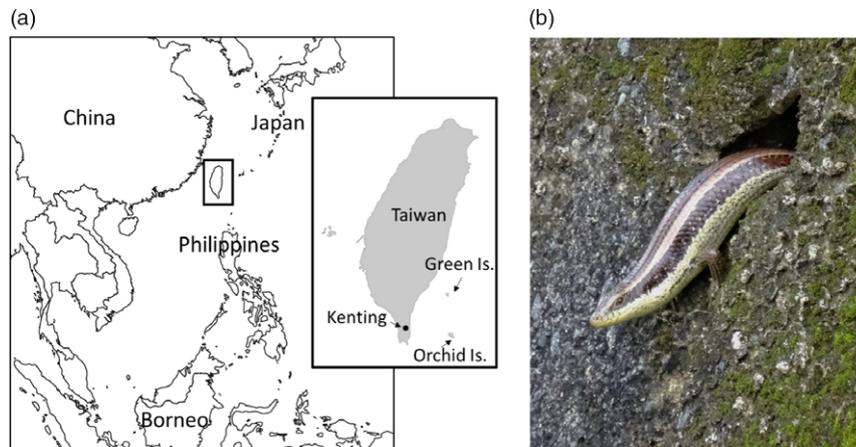


Figure 1 (a) Study locations of Kenting (south Taiwan), Green Island, and Orchid Island. (b) Long-tailed skink (*Eutropis longicaudata*) staying at the entrance of a concrete hole. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

category was considered as a fixed factor, survey year was considered as a random factor, and natural log transformed transect area was given as an offset term. To compare the bite force variation between the sexes and among the three populations, first, we used a general linear model to compare bite force against lizard sex, location, and their interaction. Then, we fitted bite force again but involved five morphological variables and their quadric terms as covariates.

Permutational multivariate analysis of variance (PERMANOVA) was performed to compare five morphological variables against sex, location and their interaction; then, each morphological variable was fitted separately using general linear models with Holm–Bonferroni method to adjust *P*-values, thus, avoiding multiple testing problems because the dependent variables were highly correlated. All the standard errors in the general linear models were estimated based on heteroskedasticity-consistent estimations (Long–Ervin HC3) of the covariance matrix to avoid potential heteroskedasticity. Insignificant (marginal *P*-value >0.05) quadric terms and interaction terms were eliminated. We used a series of Shapiro’s test and Bartlett’s test to confirm the residual normality and homoscedasticity, respectively; and confirmed all the variance inflation factors of each parameter <10 to avoid multicollinearity.

Results

Skink density across the three populations

During 1997–2001, no significant differences were found in the average population densities (type III Wald test, $\chi^2 = 1.590$, d.f. = 2, *P* = 0.452) of Kenting (mean \pm SD, 0.0138 ± 0.00160 #/m²; *n* = 5), Orchid Island (0.00149 ± 0.00146 #/m²; *n* = 5) and Green Island (mean \pm SD, 0.0160 ± 0.002 #/m²; *n* = 5). The survey year as a random factor did not significantly affect population density (type III Wald test, $\chi^2 = 1.770$, d.f. = 1, *P* = 0.183).

Variation in bite force between sexes and among populations

A total of 44 (27 females and 17 males), 66 (36 females and 30 males) and 48 (32 females and 16 males) skinks were captured in Orchid Island, Green Island and Kenting, respectively. Significant differences were found between the sexes and among the populations regarding bite force. After eliminating insignificant interaction terms [sex \times location, $F_{2,152} = 0.082$, *P* = 0.921], the marginal difference in bite force between males and females was about 5.787 N (male > female, *P* < 0.001; Table 1a; Fig. 2a), indicating that, in all the populations, the males have a stronger bite force than the females do. Multiple comparisons among locations showed that Orchid Island lizards exhibited significantly stronger bite force than those in Kenting and Green Island did. No bite force difference was found between lizards from Kenting and Green Island (Table 1a; Fig. 2a).

Considering the effect of morphological traits on bite force, all the five morphological covariates were involved in the model. After eliminating insignificant interaction and quadric terms, the marginal differences between sexes and among locations were similar to the model with no covariates (Table 1b; Fig. 2b). Furthermore, the model revealed that both BW and HL were positively correlated with bite force and contributed to explain variance by 29%, whereas sex and location contributed by 18% (Table 1b; Fig. 2c,d). Lizard’s SVL and HH were marginally insignificantly correlated with bite force (~13% totally; Table 1b; Figure 2e,f). In addition, we found that the quadric term of HW was significant, indicating that an extreme HW may contribute to additional bite force (Table 1b; Fig. 2g).

Morphological differences between sexes and among the three populations

After eliminating the insignificant interaction terms [sex \times location, $F_{2,152} = 0.082$, *P* = 0.921], the results from

Table 1 Results of the general linear model fitting bite force (N) in long-tailed skinks (a) against sex and location, and (b) against additional morphological covariates. Relative importance (RI) describes the total F^2 partitioned by variable

Parameters/Comparisons	Estimate	95% CIs	SE	<i>T</i>	<i>P</i>	RI
(a)						
Intercept	16.811	(15.34, 18.28)	0.743	22.628	<0.001	–
Sex (male – female)	5.787	(3.954, 7.619)	0.928	6.237	<0.001	0.201
Location	Type III test: $F_{2,154} = 20.193$				<0.001	0.174
KT–GI	–1.104	(–3.130, 0.922) ^a	0.859	–1.285	0.402 ^a	–
OI–GI	5.308	(2.626, 7.990) ^a	1.137	4.667	<0.001 ^a	–
OI–KT	6.412	(4.028, 8.797) ^a	1.011	6.340	<0.001 ^a	–
(b)						
Intercept	17.00	(15.98, 18.02)	0.516	32.950	<0.001	–
Sex (male – female)	2.342	(0.513, 4.172)	0.926	2.531	0.012	0.068
Location	Type III test: $F_{2,148} = 18.662$				<0.001	0.111
KT–GI	1.107	(–0.614, 2.828) ^a	0.728	1.520	0.282 ^a	–
OI–GI	4.437	(2.717, 6.158) ^a	0.728	6.095	<0.001 ^a	–
OI–KT	3.330	(1.316, 5.345) ^a	0.852	3.907	<0.001 ^a	–
Body weight (g)	0.274	(0.154, 0.394)	0.061	4.519	<0.001	0.155
SVL (mm)	–0.045	(–0.196, 0.105)	0.076	–0.597	0.551	0.056
Head length (mm)	0.921	(0.311, 1.532)	0.309	2.982	0.003	0.130
Head width (mm)	0.715	(–0.024, 1.453)	0.374	1.913	0.058	0.115
(Head width) ² (mm ²)	0.372	(0.183, 0.560)	0.095	3.897	<0.001	0.033
Head height (mm)	–0.016	(–0.759, 0.727)	0.376	–0.044	0.965	0.070

GI, Green Island; KT, Kenting; OI, Orchid Island.

^aFamily-wise error rates for multiple comparisons were controlled to 0.05 using the single-step method.

morphological comparisons using PERMANOVA showed significant differences among locations and between sexes (Table 2a). Univariate models showed that BW and SVL did not differ significantly between sexes (Table 2b–c; Fig. 3a,b). However, a sexual dimorphism was found regarding head shape (length, width, height), with males exhibiting a larger head than females (Table 2d–f; Fig. 3c–e).

Orchid Island's lizards had a higher BW than those of Kenting did, whereas those from Green Islands did not differ significantly from the other two populations (Table 2b; Fig. 3a). SVL and head length, width and height showed a general trend to differ among locations, with Kenting's lizards exhibiting a smaller head than the other two populations did (Table 2c–f; Fig. 3b–e).

Discussion

Parental care behavior shapes bite force in long-tailed skinks

When confronting predators, bite force plays an important role that determines the outcome of aggressive interactions, where individuals with more powerful bite force may be more aggressive toward potential threats (Herrel *et al.*, 2009). Our results show that Orchid Island skinks exhibit stronger bite forces than those from Green Island and Kenting, which exhibit similar bite force. Parental care behavior is very common among endothermic vertebrates, but extremely rare in reptiles (Somma, 1990), with only a few species displaying egg-guarding behavior (Greene *et al.*, 2002; Huang, 2006b). In

long-tailed skinks, predator deterrence is crucial for egg survival. Since the abundance of kukri snakes is 9–20 times higher on Orchid Island compared to Green Island and Kenting (Huang *et al.*, 2013), lizards on Orchid Island face a stronger predation risk than the other two populations do, displaying parental care behavior to increase the offspring survival rate. This unique behavior may trigger selection for larger bite force against the high density of oophagic predators than in the case of the other populations. Considering the predation pressure to adult skinks, only one lizard predator was discovered on Orchid Island, *Elaphe carinata*, whereas many other predators inhabit on Taiwan, such as *Protobothrops mucrosquamatus*, *Trimeresurus stejnegeri*, *Bungarus multicinctus* and *Naja atra* (Huang *et al.*, 2013). Therefore, bite force of skink on Orchid Island is less likely driven by predation pressure. Although only female on Orchid Island display egg-guarding behavior, the males with larger bite force than populations from Green Island and Kenting may due to maternal inheritance.

The difference in bite force between populations may also be related to population density, since a higher population density may increase intraspecific competition for resources or mates (Knell, 2009), thus, enhancing bite force capacity (Donihue *et al.*, 2016). Our study demonstrated that the Orchid Island population exhibits a larger bite force, despite the three populations showing similar density, thus, failing to support the prediction that population density affects bite force in long-tailed skinks. However, the unique parental care exhibited by Orchid Island skinks has shaped the evolution of bite force.

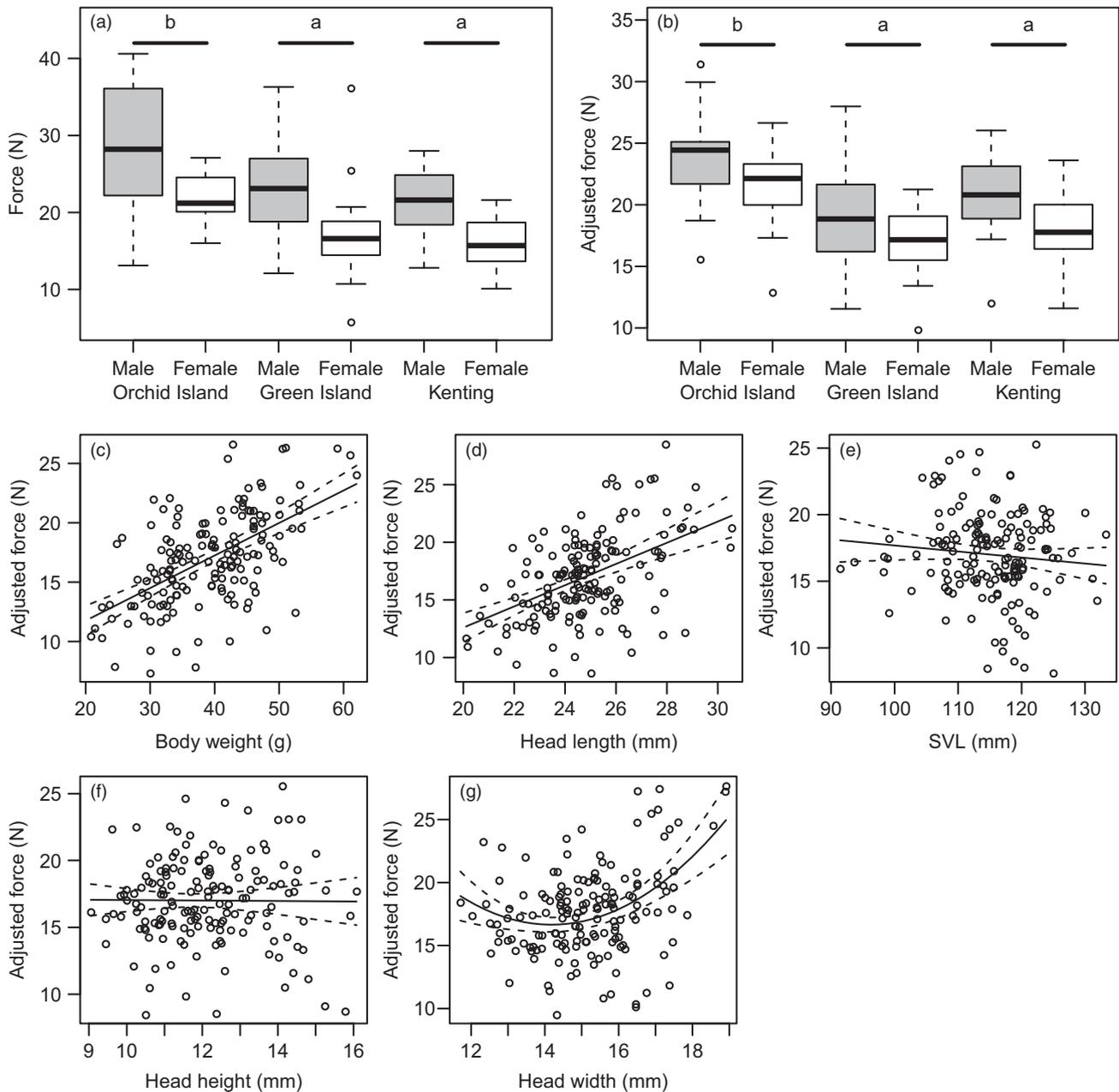


Figure 2 Differences in bite force between sexes and among the three locations, in long-tailed skinks (*Eutropis longicaudata*). (a) Original bite force between sexes and among locations. Partial-residual plots demonstrating the marginal effects of (b) population and sex, (c) body weight, (d) head length, (e) snout-vent length (SVL), (f) head height, and (g) head width. Lowercase letters in panel a and b show the results of multiple comparisons when morphological covariates are excluded and involved to fit bite force, respectively.

Sexual selection affects bite force in all populations

Our results show that, in all the three populations, the males exhibit stronger bite force than the females do, which may represent different selection pressures between males and females. There are two possible explanations for such sexual dimorphism: sexual selection (intrasexual male–male competition or intersexual mating bite) and

food niche partitioning. Regarding sexual selection, many lizard species display male dominance in territory defense and mating success (Lappin & Husak, 2005; Herrel *et al.*, 2010), whereupon confrontations are typically won by males with harder bite force (Lailvaux *et al.*, 2004; Huyghe *et al.*, 2005; Husak *et al.*, 2006). In long-tailed skinks, the violent chases between skinks can be observed in the field. This shows that long-tailed skinks display competitive or agonistic behaviors.

Table 2 Results of permutational multivariate analysis of variance comparing: (a) five morphological dependent variables between sexes and among locations, and general linear models with corresponding post hoc tests fitted for three locations, (b) body weight, (c) SVL, (d) head length, (e) head width, and (f) head height in long-tailed skinks. Relative importance (RI) describes the total R^2 partitioned by variables

Comparisons	Estimate	95% CIs	SE	T(154)	P	RI
(a) Sex		Type III test: $F_{1,154} = 24.537$			<0.001	0.148
Location		Type III test: $F_{1,154} = 14.809$			<0.001	0.151
(b) Body weight						
Sex (male – female)	1.921	(–0.770, 4.613)	1.362	1.410	0.321	0.015
Location		Type III test: $F_{1,154} = 9.39$			<0.001	0.111
KT–GI	–3.157	(–6.586, 0.274)	1.451	–2.176	0.078 ^a	–
OI–GI	3.905	(0.104, 7.706)	1.607	2.430	0.213 ^a	–
OI–KT	7.063	(3.205, 10.921)	1.631	4.329	<0.001 ^a	–
(c) SVL						
Sex (male – female)	–0.878	(–3.286, 1.531)	1.219	–0.720	0.473	0.002
Location		Type III test: $F_{1,154} = 7.61$			<0.001	0.089
KT–GI	–5.010	(–8.072, –1.948)	1.295	–3.869	<0.001 ^a	–
OI–GI	–1.371	(–4.669, 1.928)	1.395	–0.983	1.000 ^a	–
OI–KT	3.639	(0.073, 7.205)	1.508	2.413	0.044 ^a	–
(d) Head length						
Sex (male – female)	2.035	(1.487, 2.582)	0.277	7.341	<0.001	0.280
Location		Type III test: $F_{1,154} = 10.15$			<0.001	0.098
KT–GI	–1.293	(–1.987, –0.599)	0.293	–4.408	<0.001 ^a	–
OI–GI	–0.279	(–1.030, 0.472)	0.318	–0.879	1.000 ^a	–
OI–KT	1.014	(0.218, 1.810)	0.337	3.012	0.017 ^a	–
(e) Head width						
Sex (male – female)	1.115	(0.706, 1.523)	0.207	5.390	<0.001	0.158
Location		Type III test: $F_{1,154} = 10.02$			<0.001	0.113
KT–GI	–1.010	(–1.573, –0.448)	0.238	–4.246	<0.001 ^a	–
OI–GI	–0.073	(–0.645, 0.498)	0.242	–0.303	1.000 ^a	–
OI–KT	0.937	(0.306, 1.568)	0.267	3.509	0.005 ^a	–
(f) Head height						
Sex (male – female)	1.246	(0.837, 1.655)	0.207	6.022	<0.001	0.184
Location		Type III test: $F_{1,154} = 36.93$			<0.001	0.250
KT–GI	–1.680	(–2.160, –1.201)	0.203	–8.276	<0.001 ^a	–
OI–GI	–0.350	(–0.953, 0.254)	0.256	–1.369	1.000 ^a	–
OI–KT	1.330	(0.738, 1.923)	0.251	5.301	<0.001 ^a	–

GI, Green Island; KT, Kenting; OI, Orchid Island.

^aType I error rates for multiple comparisons among locations were controlled to 0.05 using the single-step method.

Regarding food niche partitioning, some studies focused on the relationship between bite force and feeding apparatus, showing that prey composition affected lizard bite force (Verwajen *et al.*, 2002; Measey *et al.*, 2011; Sagonas *et al.*, 2014). Within the same habitat, the diet may differ between sexes, since males can handle harder prey than females can due to their larger bite force (Verwajen *et al.*, 2002; Sagonas *et al.*, 2014). Although the different bite force of both sexes may be affected by diet differentiation, the diet of long-tailed skinks is composed of a wide range of prey, including soft prey (e.g. crickets, cicadas, bugs) and some hard insects (e.g., beetles) (Huang, 2006a). Comparing the width and hardness of potential prey with HW and bite force revealed that the prey are significantly softer than the bite force of both male and female long-tailed skinks (Herrel *et al.*, 2001; Wang,

2017) (Figure S1 and Table S1). Therefore, in this study, prey hardness may not be the main factor related to the bite capacity of male and female skinks.

Contribution of morphological traits for bite force

In some lizard species, bite force is positively correlated with head features (Herrel, Van Damme & De Vree, 1996; Herrel *et al.*, 1999). In this study, BW and HL predominantly affected the bite force of the long-tailed skink. BW may reflect the total mass of muscles that directly affect bite force. However, in terms of head morphology, our results show that in long-tailed skinks, the bite force is positively correlated with HL, rather

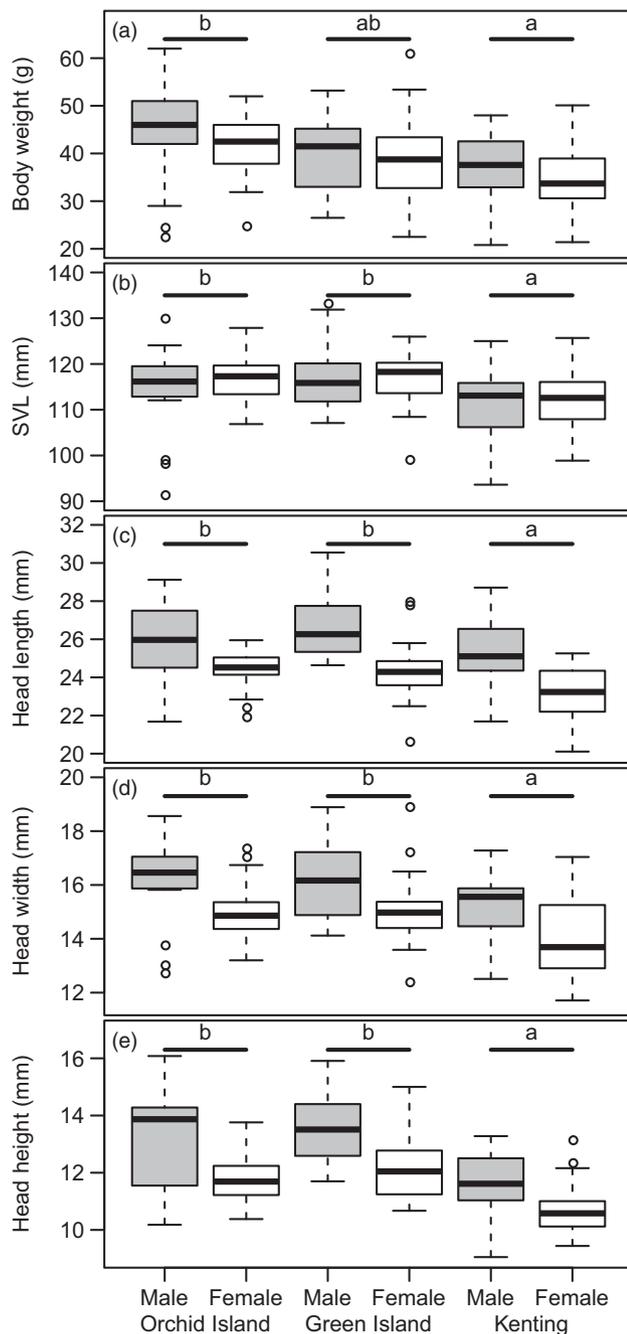


Figure 3 Comparison of morphological variables between sexes and among three locations, in long-tailed skinks (*Eutropis longicaudata*). The variations of (a) body weight, (b) snout-vent length (SVL), (c) head length, (d) head width, and (e) head height between sexes and among populations are shown in box plots. Lowercase letters show the results of post hoc tests comparing the marginal differences among the populations.

than with the HW and HH. This result is consistent with the findings for female tuataras (*Sphenodon punctatus*), where HL partly explained the pattern of bite force (Herrel *et al.*, 2010),

but contradicted other studies, according to which HH and HW are the best predictors of bite force in lizards (Herrel, Vanhooydonck & Van Damme, 2004; Lappin, Hamilton & Sullivan, 2006). Longer HH can increase the biting distance between upper and lower jaws, and may enhance the ability to deter predators. Bite force is not merely determined by head shape. Many other muscular factors (e.g. muscle-skeleton connection, muscle mass and distribution of muscle fiber types) also affect the strength of bite force in different species (Herrel *et al.*, 1999; Anderson, McBrayer & Herrel, 2008). However, the cranial system and behavior may constrain head shape; thus, further studies on long-tailed skinks focused on other systems are needed.

Morphological differences between sexes and among populations

Morphological sexual dimorphism is common in many species (Herrel *et al.*, 1996, 1999, 2010; Sagonas *et al.*, 2014; Thomas *et al.*, 2015). In long-tailed skinks, head morphology, including HL, HW and HH differs between the sexes. However, SVL and BW are similar between males and females. This result shows that the sexual dimorphism of long-tailed skinks lies in the head, and larger head may enhance the bite force of male lizards to increase fitness (e.g. male–male competition, mating success and territory defense). Comparisons among Kenting, Orchid and Green Islands populations indicate that the Kenting population is smaller in most of the investigated characteristics except in terms of BW. The island rule and island syndrome hypotheses represent the changes of phenotypic or life-history traits between mainland and island relatives (Lomolino, 2005; Novosolov *et al.*, 2013). Body gigantism on island may due to ecological release, such as lower intraspecific competition, resources competition or predation pressure (Li *et al.*, 2011; Runemark, Sagonas & Svensson, 2015). The larger body size in Orchid Island and Green Island may fit the island syndrome compared to the small size in Kenting population. Besides, large body size on Orchid Island might be a consequence of the highest *Oligodon formosanus* population density (Huang *et al.*, 2013).

In conclusion, following head and body size corrections, our study provides, for the first time, strong evidence that parental care behavior under intense predation pressure may drive the evolution of bite force in lizards. Male–male competition and mating bites may play an important role for the sex difference in bite force. Therefore, males have a larger bite force than females in all the populations. In terms of morphological traits, the larger head observed in males may enhance bite capacity in competition. Our results also show that HL and BW are reliable bite force indicators in long-tailed skinks. Although we tried to inter-cross the three populations (i.e. mating 40 Orchid Island females with 20 Kenting and 20 Green Island males) F1 survival and growth in the laboratory were quite low (only two females survived in each location). The biting forces of the four F1 females were close to that of Orchid Island population, reaching 21 N. This indicates that the larger bite force may have a genetic basis. However, the small sample size limits this conclusion and further cross-mating studies are required to test this genetic-based hypothesis.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Video S1. The video showed the parental care behavior of the long-tailed skink in Orchid Island.

Figure S1. The prey hardness, head width and bite force of the long-tailed skinks. The potential prey were recorded from Huang (2006). The prey hardness is based on Wang (2017). The vertical and horizontal lines represent head width and bite force of the skinks, respectively. Different type of line shows the male or female from different populations.

Table S1. Independent sample Wilcoxon rank sum tests were used to test whether (a) head width and (b) bite force of the long-tailed skink was greater than the body width and hardness of potential preys, respectively. *P*-values were adjusted based on Holm–Bonferroni method to control the family-wise error rate.