

Increasing dietary breadth through allometry: bite forces in sympatric Australian skinks

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Abstract. Ecomechanical measures of performance such as bite force may function as an indirect measure of niche. This study proposes that allometric changes in performance may contribute to niche separation, especially in a group where the specific mechanism(s) remains unclear. We surveyed the bite force and morphology of 5 wild caught, sympatric skink species in the Kimberley region of Western Australia. Skinks were collected from trapline fences, weighed, photographed, and maximum bite force was measured with a piezoresistive force sensor. Morphological metrics were derived from photographs of the dorsum. Normalized morphological traits indicate interspecific variability in form, particularly in forelimb length, which may be a result of habitat separation. Bite force showed strong, significantly positive, allometric scaling against most morphological traits. Tail length was the only morphological trait that scaled isometrically. Allometric changes in bite force may increase dietary breadth, allowing larger skinks to supplement their diet with larger, more durable prey. This study reveals that ecologically relevant traits may be explained by allometric differences coupled with size variation. Future work should focus on (1) an increase in sample size, (2) long-term measurement of diet selection, and (3) accessibility of prey items to our focal animals.

Keywords: Ecomechanics; Morphology; Niche separation; Scincomorpha; Western Australia

Introduction

Assessing variation in ecologically relevant traits to better understand niche dates back to Hutchinson (1959). Since then a multitude of studies have examined niche separation in numerous vertebrate taxa, including family level studies such as Anolidae (Schoener, 1970; Roughgarden, 1995), Fringillidae (Zeng and Lu, 2009), Muridae (Millien-Parra and Loreau, 2000), and

Varanidae (Pianka, 1986). Concerning ecomechanical traits (Wainwright, 1991), bite force has received widespread attention with respect to dietary niche. Maximum bite force is expected to relate causally to food type (D'Amore et al., 2011), maximum size (Wroe et al., 2005), or hardness (McCurry et al., 2015). Studies have looked at how increases in bite force allow species to occupy different, usually durophagous, niches (Mara et al., 2010; Schaerlaeken et al., 2012). Bite force has also been used as a dimension to facilitate niche partitioning between sympatric species (Herrel et al., 2001a; Verwaijen et al., 2002; Measey et al., 2011).

Bite force functions as an ideal ecomechanical variable to explore concerning systems where the explanations for niche separation are unresolved. Western Australian skinks (Infraorder Scincomorpha) are an excellent example of this. Over 420 species of skinks occur in Australia alone (Wilson and Swan, 2013; Cogger, 2014). Several skink species often co-occur in their respective environments, and one can find up to 40 species occurring together in the deserts of Australia (Pianka, 1969a). Several hypotheses have been put forward to explain how skinks achieve such high levels of sympatric diversity there. Place, food, and time are

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potentially the most substantial niche dimensions, allowing for minimal ecological distances between sympatric species (Pianka, 1969a,b). Others have stated that the nature of spinifex (genus: *Triodia*) grasslands is ideal for lizards to flourish and diversify (Morton and James, 1988). Skinks are often seen as opportunistic generalists, and any dietary differentiation is often subtle and distinguishable only at the prey’s generic level (James, 1991a). These unspecialized diets, compounded with variable juvenile mortality and reproductive success (James, 1991b; Read, 1998), may reduce niche overlap to the point of eliminating competition. Some argue the food supply may be ‘super abundant’ and eliminate any need for dietary niche separation (Twigg *et al.*, 1996). On the other hand, niche separation may be primarily facilitated by habitat/microhabitat use (often attributed to increased environmental heterogeneity) and variation in peak foraging times (Goodman, 2007; Goodman *et al.*, 2008; Pianka, 1969a; Twigg *et al.*, 1996).

Niche separation is often facilitated by divergence in one or more specific, ecologically relevant physical or behavioral trait(s) (Brown and Wilson, 1956; Losos, 2000). It is also possible that consistent allometric growth patterns may achieve a similar end. Size differences within sympatric species could facilitate disproportionate character changes in a consistent, predictable fashion, and these allometric character changes would result in niche separation. This has been seen ontogenetically in a number of species where allometric changes in bite force allow for niche transition with age and size (Binder and Valkenburgh, 2000; Erickson *et al.*, 2003; Herrel *et al.*, 2006; Pfaller *et al.*, 2011).

The purpose of this study is to determine if changes in body size correlated to bite performance could function as a mechanism for niche separation within a sympatric group of vertebrates. We determine if bite force potentially allows for niche partitioning

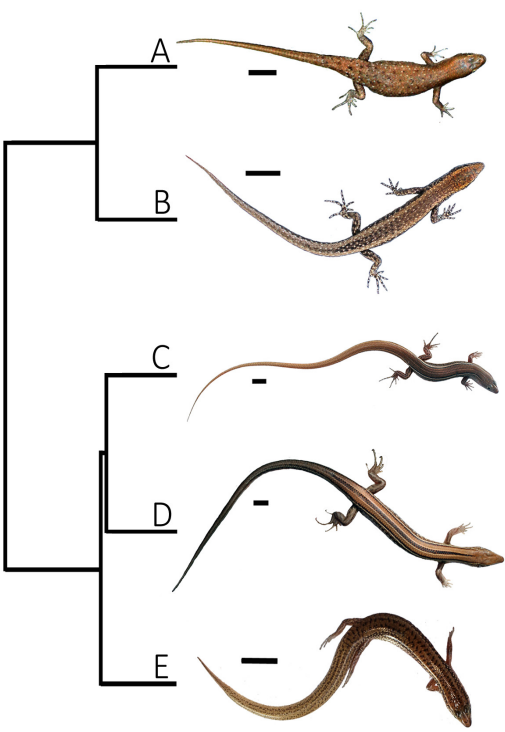


Figure 1. Phylogeny of skink species captured in this study. Branches are scaled based on branch lengths modified from Pyron *et al.* (2013). Species include (A) *Carlia triacantha*, (B) *Cryptoblepharus metallicus*, (C) *Ctenotus inornatus*, (D) *Ctenotus robustus*, and (E) *Eremiascincus isolepis*. Scale = 1 cm. Photos by D. Meadows.

Table 1. Number of skink individuals that were caught, and those that produced usable bite force data.

Skink species	Number caught	Number bit
<i>Carlia triacantha</i>	2	2
<i>Cryptoblepharus metallicus</i>	11	8
<i>Ctenotus robustus</i>	15	12
<i>Ctenotus inornatus</i>	10	9
<i>Eremiascincus isolepis</i>	5	5

through allometric change across sympatric species. We surveyed the bite forces of wild caught skinks from the Kimberley region of Western Australia, along with masses and a number of morphological measurements. We hypothesize that bite force, when scaled against body size and morphological traits, will display a significant, positively allometric trend. We also provide description of skink morphological variability. This pilot study will allow researchers to better test the role of bite force in niche partitioning within complex multispecific communities in the future.

Materials and Methods

Location and Measurements.—Fieldwork was conducted during June, 2013 at the El Questro Wilderness Park in the East Kimberley region of Western Australia. A total of 43 individuals of 5 species

of skink were captured in a two-week period, and 36 produced usable bite force data (Table 1). Species captured were all members of Lygosominae (Pyrone et al., 2013), comprising of *Carlia triacantha* (Mitchell, 1953), *Cryptoblepharus metallicus* (Boulenger, 1887), *Ctenotus inornatus* (Gray, 1845), *Ctenotus robustus* (Storr, 1970), and *Eremiascincus isolepis* (Boulenger, 1887) (Fig. 1). Skinks were collected from four isolated trapline fences located throughout the park in areas of variable moisture and shade-cover, in concert with an ongoing study of the herpetofauna in this region (Doody et al., 2014, 2015a,b,c). Each fence consisted of both pit and funnel traps located equidistant along both sides of an upright tarp, and were checked and cleared daily at dawn. Upon capture, we field identified each skink to species and brought them back to the campsite for data collection. Body size was a proxy for age, and sex was not determined due to a lack of field adequate probing equipment. After all data collection was completed, we released each skink at its capture location.

We collected bite force (BF) data on the day the animal was captured within the same two-hour period to avoid variability in duration between capture and sampling. We measured BF with a Flexiforce sensor (Tekscan Inc., South Boston, MA.), which is a piezoresistive force sensor that fit into the skink's mouth. There were two separate sensors; with or without a wooden brace glued to the underside. The wooden brace was for the larger skinks. Lappin and Jones (2014) showed that the substrate of the transducer may bias the force produced. Unfortunately, there was no way to produce a uniform substrate in the field; small skinks could not fit the wooden brace in their mouth, and large skinks bit directly through a transducer without a brace. Each sensor was calibrated separately. The instruments recorded data at eight times per second, and all force measurements are in Newtons (N). BF was collected by holding the animal and approaching it with the transducer. Care was taken to ensure that the rostrum of the animal made

direct contact with the center of the transducer during all trials. Many skinks were eager to bite when approached with the transducer, whereas others were encouraged to bite with gentle taps on the nose that readily induced defensive bites. Consecutive attempts were made to induce a single specimen to bite, until five usable bite force measures were collected from each. The maximum value out of these was used as BF.

Body Mass (BM) was measured using Pesola scales to the nearest 0.5 grams. Euclidean linear measurements included Body Length (BL), Head Length (HL), Head Width (HW), Forelimb Length (FLL), Hindlimb Length (HLL), and Tail Length (TL) (*sensu* Herrel et al., 1999a; Herrel et al., 2001a, 2002; Irschick et al., 2005; Lappin et al., 2006; Tulli et al., 2011, 2012). Multiple dorsal-perspective pictures were taken of each skink in a clear container (with a scale) with a Canon EOS Rebel T3 with an 18-55 mm lens. Lines were drawn on the dorsal-perspective photographs using the "draw curves" tool in the landmark software TpsDig2.6 (Rohlf, 2010). We then resampled the lines to 15 equidistant points, and the final measure was the sum distance between these points. BL was measured from the tip of the rostrum, along the midline to the caudal-most point where the hind legs meet the body. Note that BL approximates the standard measurement snout-vent length (SVL), but is measured on the dorsal surface (SVL is measured on the ventral surface). FLL and HLL were measured from the proximal-most point of the limb to the distal-most point on the longest digit (digits III and IV respectively). HL is defined as the midsagittal distance from the tip of the rostrum to the junction between the parietal/interparietal scales and the nuchal scales on the dorsal head shield (see Wilson and Swan, 2013). HW was the widest part of the head. TL started from where BL ceased to the tip of the tail. Skinks autotomize their tails to elude predators (for a review see Bateman and Fleming, 2009). The variable size of regrown tails could influence the results, so tails that were clearly regrown (indicated by

Table 2. Mean (and standard deviation) of skink morphology and performance. BM = Body Mass; BL = Body Length; FLL = Forelimb Length; HLL = Hindlimb Length; HW = Head Width; HL = Head Length; TL = Tail Length; BF = Bite Force.

Skink species	BM (g)	BL (mm)	FLL (mm)	HLL (mm)	HL (mm)	HW (mm)	TL (mm)	BF (N)
<i>Carlia triacantha</i>	2.75 (1.06)	44.81 (6.19)	11.84 (0.82)	19.20 (0.96)	8.92 (0.37)	7.81 (1.05)	—	0.41 (0.41)
<i>Cryptoblepharus metallicus</i>	1.00 (0.50)	35.70 (6.93)	10.63 (1.96)	14.15 (3.06)	7.91 (1.44)	5.19 (0.94)	46.36 (10.51)	0.12 (0.10)
<i>Ctenotus robustus</i>	16.60 (15.94)	90.53 (33.74)	19.99 (6.21)	32.44 (9.91)	15.04 (4.82)	11.64 (4.06)	176.11 (82.46)	3.74 (3.09)
<i>Ctenotus inornatus</i>	5.40 (2.49)	63.99 (9.49)	14.93 (2.32)	24.51 (3.03)	12.42 (1.85)	8.84 (1.37)	138.83 (36.36)	1.26 (0.60)
<i>Eremiascincus isolepis</i>	3.00 (1.84)	53.11 (9.91)	10.76 (2.52)	15.91 (4.23)	9.68 (1.80)	7.23 (1.48)	89.11 (54.05)	0.32 (0.23)

abrupt tapering and color changes) were omitted from statistical analyses.

Morphological and Bite Force Allometry.—Bivariate plots and linear regressions were generated using Microsoft Excel (v. 2010, Microsoft Inc. Redmond, WA.), using natural logarithm (ln) scaling. We performed all statistical analyses using SPSS (v. 17.0, SPSS Inc., Chicago, IL), and all regressions were reduced major axis (*sensu* Clarke, 1980).

General morphological description of body dimensions of each species were depicted as standardized residuals for the purpose of comparison. The BL of each individual was regressed against the five remaining morphological variables similar to da Silva *et al.* (2014) where SVL was used as the standard. The resultant residuals were compared using a Multivariate Analysis of Variance (MANOVA) to determine if these relative differences were significant. *Carlia triacantha* had an $n = 2$ (Table 1) and was omitted from this statistical test. TL was also excluded due to the high frequency of autotomy observed.

BF of all species was separately plotted against all morphological variables. In order to determine if there is a multispecific allometric relationship, the slope (m) of each bivariate regression was compared to an isometric coefficient similar to previous studies (Huxley, 1924; Thomason, 1991; Meyers *et al.*, 2002; Erickson *et al.*, 2003). Isometric coefficients were based on the nature of the variables analyzed, and compared to these allometric coefficients. BM is a three-dimensional measure due to its dependence on *volume*, BF is a product of jaw muscle two-dimensional cross-sectional *area*, and all *linear* morphometrics are one-dimensional. Therefore, BF vs. BM would have an isometric coefficient of 2/3, and BF vs. BL would have 2/1. A heterogeneity of slopes test, in the form of a modified *t*-test (as shown by Clarke, 1980), was used to determine if the observed slope was significantly different from the relevant isometric coefficient. A significant difference ($P < 0.05$) was taken to indicate allometry.

Results

Masses for all species ranged from 0.5 to 44.0 grams, and the mean mass of *C. robustus* was an order of magnitude greater than all the other skinks (Table 2). All skinks had greater mean HLL than FLL, and greater HL than HW. TL was highly variable, and complete tails were unavailable for many individuals and all within *C. triacantha*. *Eremiascincus isolepis* showed a noticeable reduction in limb dimensions (Fig. 2). HL was closely

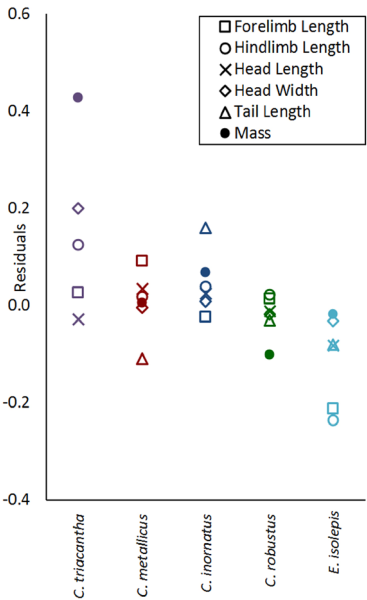


Figure 2. Residuals of morphological variables for *Carlia triacantha*, *Cryptoblepharus metallicus*, *Ctenotus inornatus*, *Ctenotus robustus*, and *Eremiascincus isolepis*. Morphological variables were regressed against Body Length.

linked to HW in most species, except *C. triacantha* whose head was relatively short. *Carlia triacantha* also had the longest relative HLL and greatest relative mass for its length. *Cryptoblepharus metallicus* had the longest relative forelimbs. *Ctenotus robustus*, although largest in absolute mass, was smallest in relative mass. When normalized for by BL, morphological traits showed significant differences according to MANOVA [$F(15, 91.50) = 3.458; P = 0.0001$; Wilk’s $\Lambda = 0.289$].

Regression analysis demonstrates that BF was significantly correlated with all morphological parameters, but was best correlated with BM and BL (Fig. 3). All morphological variables had a relatively high $r^2 (> 0.7186)$ and significant P -values (< 0.0001). Limb lengths were most weakly correlated with BF. Heterogeneity of slopes confirmed positive allometry in all regressions except for TL (Table 3), with significant differences indicated between the coefficients and the isometric model. The largest *C. robustus* individuals bit harder than all other skinks, but the other species overlapped with the smaller individuals. Larger *C. inornatus* individuals bit harder than *C. triacantha* and *E. isolepis*, and the latter two these species were overlapped by larger *C. metallicus* individuals.

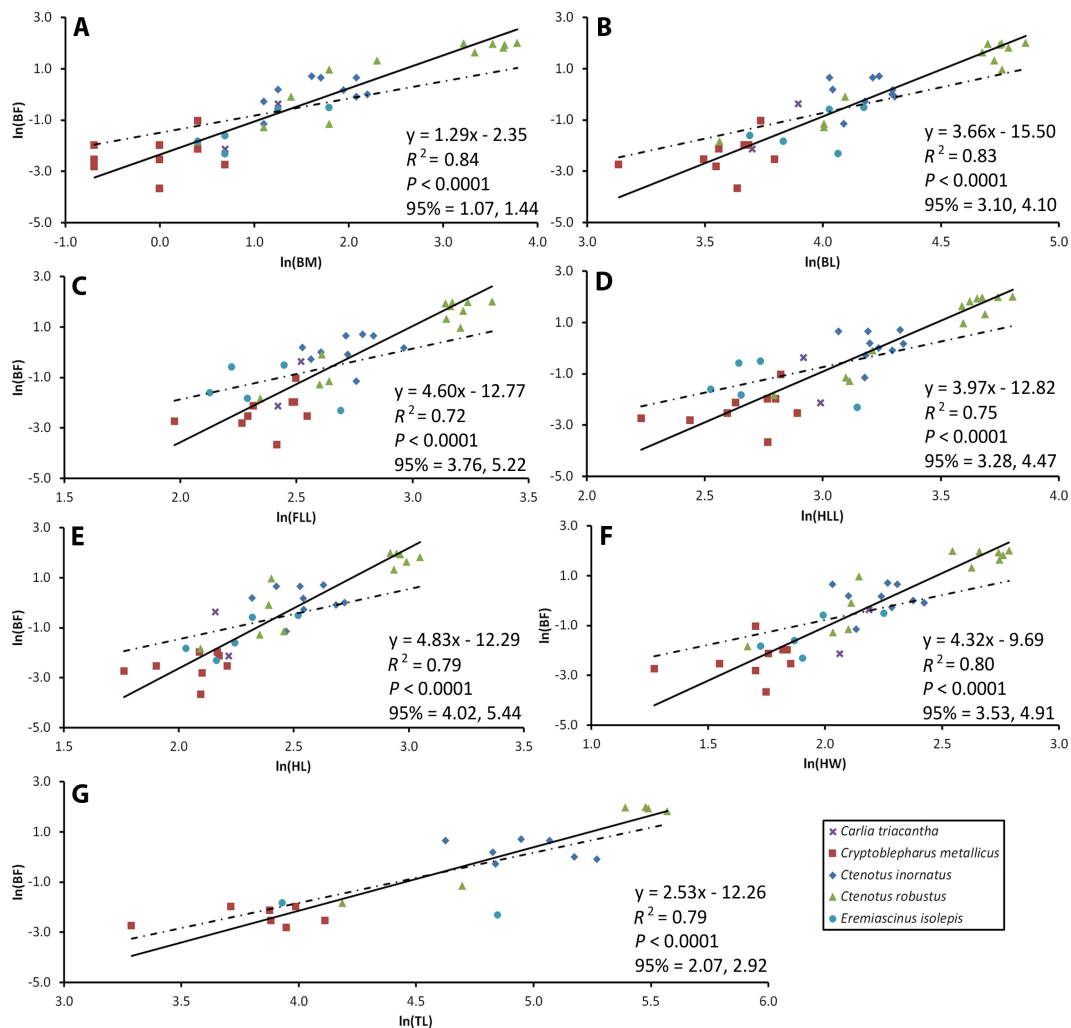


Figure 3. $\ln$ Bite Force (BF) plotted against $\ln$ of (A) Body Mass (BM), (B) Body Length (BL), (C) Forelimb Length (FLL), (D) Hindlimb Length (HLL), (E) Head Length (HL), (F) Head Width (HW), and (G) Tail Length (TL). The solid line indicates the reduced major axis regression for the observed data, and the broken line indicates the isometric model.

Discussion

Bite force and feeding in Kimberley skinks.—Bite force in sympatric Western Australian skinks displayed significant positive allometry when scaled with most morphometric measures across species. We therefore fail to reject our hypothesis. Because body size varied between these skinks, allometric scaling exaggerated differences in BF between several species along this size gradient. This resulted in more separation than would be allowed for through isometry. The low sample size did not allow for any between-species comparisons, but,

as a whole, bite force for these skinks was comparable to that of vertebrates of similar masses found in the literature (7–45g). These included several species of bats, fish, birds, and other lizards (Clifton and Motta, 1998; Herrel et al., 2001b; Van der Meij and Bout, 2004; Santana and Dumont, 2009).

Allometric changes in bite force may allow for an increase in dietary breadth, potentially resulting in niche differentiation across both an ontogenetic and interspecific gradient. Australian skinks are often described as dietary generalists, with a fair degree

Table 3. Heterogeneity of slopes test, including both *t*-value and significance (*P*) values for observed ln-bite force versus ln-morphological variables. BM = Body Mass; BL = Body Length; FLL = Forelimb Length; HLL = Hindlimb Length; HL = Head Length; HW = Head Width; TL = Tail Length.

	BM	BL	FLL	HLL	HL	HW	TL
<i>t</i> =	4.358	3.929	4.144	3.631	4.920	4.488	1.032
<i>P</i> =	<0.0001	0.0002	<0.0001	0.0004	<0.0001	<0.0001	0.1591

of overlap in prey type as noted in the literature. The genera considered here eat a broad diet of similar types of arthropod food items, with a seasonal focus on Isoptera (Pianka, 1969b; Taylor, 1986; James, 1991a; Pough et al., 1997). Other major foods noted in the literature include Arachnida, Blattaria, Chilopoda, Coleoptera, Hemiptera, Isopoda, Orthoptera, and Thysanura (Twigg et al., 1996; Pianka and Harp, 2011; Manicom and Schwarzkopf, 2011). Jaw morphology influences several ecologically relevant behaviors in skinks, including prey selection (Pough and Andrews, 1985; Andrews et al., 1987). As prey size increases, often so does durability and handling time of said prey (Pough et al., 1997; Herrel et al., 1999b; Meyers et al., 2002). This usually requires a disproportionately larger biting mechanism, resulting in positive allometry with growth (Herrel et al., 2002; Herrel and Gibb, 2006). Prey items that were considered too ‘difficult’ to acquire now become accessible.

Allometric bite force in skinks may play less of a role in increasing typical prey size, and instead function to increase the overall range of potential prey available. This has been seen in skinks outside the Kimberley. *Niveoscincus* increases maximum prey size as head length increases, however this upper extreme is only rarely exploited (Wapstra and Swain, 1996). We suspect that the Kimberley skinks may be similar; strong dietary overlap is typical, but larger individuals are able to supplement their diet with larger/more durable prey if necessary. For example, larger *Ctenotus* species are capable of eating relatively larger prey items (Pianka, 1969b). In particular, adult *C. robustus* consumes larger prey than both juveniles and smaller co-occurring congenics (Archer et al., 1990).

Other influences on morphology and dietary niche—Although bite force scaled allometrically with most morphological traits, TL was the only one that was isometric. This may indicate that TL also increased allometrically along a similar trajectory. This was further supported by the fact that TL showed a clear

allometric slope of 1.451 ($r^2 = 0.9015$, $P < 0.0001$) when plotted against a body size metric such as BL (as opposed to the predicted isometric slope of 1.00). This trajectory may be a response to increased dietary needs of larger skinks, or a display of maturity. Interestingly, head dimensions did not scale in such a way to suggest an allometric enlargement of the jaw apparatus. Bite force is often correlated with certain head dimensions, especially widths, because they are generally linked to jaw adductor size (Herrel et al., 2002; Huyghe et al., 2009; Marshall et al., 2012). Not only did HW not scale isometrically with BF, it was slightly negatively allometric with BL ($m = 0.886$, $r^2 = 0.9644$, $P < 0.0001$). There are several explanations for this. First, head dimensions may be heavily influenced by phylogeny, as seen in other Australian lygosomines (Poughe et al., 1997). Alternatively, some selection pressure outside of feeding may antagonistically influence head sizes (Lappin et al., 2006). The degree of ossification of joints may also play a role as suggested for primates (Greaves, 1988).

Even with allometric scaling of bite force, overlap still exists between certain species. Other factors most likely facilitate niche separation in these sympatric taxa. For example, *C. triacantha* and *E. isolepis* occupy a similar size range and therefore have a similar bite forces. But, these species rarely forage in similar habitats in the Kimberley and would not compete for prey. *Eremiascincus isolepis* is a sand-swimmer that forages in leaf litter (Wilson and Swan, 2013). On the other hand, *Carlia* species have an arboreal arthropod-based diet (Manicom and Schwarzkopf, 2011). Because there is no need to exploit prey in similar habitats, there is no need for a deviation in performance to partition said prey. Limb lengths may facilitate this spatial division, as short limbs (as seen in *Eremiascincus*) are often associated with a fossorial lifestyle (Wilson and Swan, 2013). Limb lengths also correlated the least with bite force, indicating they are influenced by factors other than size and bite performance.

Previous researchers have argued being fossorial may restrict the biting apparatus in skinks (Andrews et al., 1987). This appears to not apply to *E. isolepis*, as bite force plots similarly to the other skink taxa of similar sizes. This may be an influence of a similar diet, as *Eremiascincus* preys upon mostly beetles like most other skinks in the Kimberley (James and Losos, 1991). Other Australian sand-swimmers of the genus *Lerista* have reduced heads and jaws, and are limited to eating small, soft-bodied prey such as subterranean larvae (Pough et al., 1997; Greer, 1987; Greer, 1990; Lee et al., 2013).

Increasing resource axes and future work.—The data reported here add bite force to the list of potential traits that influence the breadth of dietary niche in these skinks. Improving our understanding of this further requires; (1) an increase in sample to allow for between-species effects and the consideration of phylogeny; (2) long-term measurement of diet selection for each species across size classes and (3) sampling of prey items that are spatially, temporally, and physically accessible to our focal animals. This will determine to what degree resource overlap occurs in these skinks, as well as determine to what extent they form a true guild. Traits of interest need to be measured for all species in the taxocene, allowing for a more thorough analysis of character displacement if present. It is possible that bite force is associated with a head dimension that was not measured here (e.g. head height, relative rostral length). This creates a need to collect more fine-scaled, 3D morphometric data on head shape in these skinks in the future (*sensu* McHenry et al., 2006; McHenry, 2009; Walmsley et al., 2013). Finally, the potential role of discrete morphological variation (e.g., sexual dimorphism) in traits relevant to niche use requires investigation (for examples in lizards see Vitt and Cooper, 1985; Vitt and Cooper, 1986; Lappin et al., 2006).

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