

Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard *Anolis lineatopus*

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It has been documented extensively that body size affects the physiology and musculoskeletal function of organisms. However, less well understood is how body size affects the ecology of organisms through its effects on physiology and performance. We explored the effects of body size on morphology and performance in different ontogenetic classes and sexes of a common *Anolis* lizard (*A. lineatopus*). Next, we tested whether these morphological and performance differences may affect functional aspects of the diet such as prey size and prey hardness. Our data showed that males, females and juveniles differ significantly in head size, head shape and bite force. Multiple regression models indicated that head shape and bite force are significantly correlated to prey size and hardness. Yet juveniles had relatively large heads and bit disproportionately hard for their size, allowing them to eat prey as large as those of females. However, for a given prey size, males and females ate more robust prey than did juveniles. Additionally, males ate relatively harder prey than did juveniles. These data suggest that: (1) body size affects the dietary ecology of animals through its effect on head size and bite force; (2) changes in head morphology independent of changes in overall size also have important effects on performance and diet. © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, 89, 443–454.

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INTRODUCTION

That body size may have important consequences for the biology of an organism because of its effects on organismal physiology and the functioning of musculoskeletal systems has long been noted (e.g. Hill, 1950; McMahon, 1973; Schmidt-Nielsen, 1984). Beyond these direct effects, body size may also affect processes further downstream, such as the ecology (e.g. Hoyle & Keast, 1987; Irschick *et al.*, 2000; Lukoschek & McCormick, 2001) and behaviour (e.g. Irschick, 2000; Cooper & Lemos-Espinal, 2001) of organisms. Because of the profound effects of body size on many aspects of the biology of organisms, it has been suggested that body size in itself may be an important factor in struc-

turing animal communities (Werner & Gilliam, 1984; Lima & Magnusson, 1998). Often, changes in ecology and behaviour associated with body size can be linked directly to the effects of size on physiological performance (e.g. Carrier, 1996; Mackessy, Williams & Ashton, 2003). For example, whereas small animals face high energy requirements to allow for rapid growth, larger animals typically have a lower body-mass-specific metabolism. This may in turn affect foraging ecology, and larger animals may display a dietary shift towards less nutritious but more readily obtainable food items, such as plants (e.g. Clark & Gibbons, 1969; Durtsche, 2000).

Besides changes in metabolic rate and other physiological processes, musculoskeletal performance (e.g. running speed, jump distance) is also expected to be affected by changes in size throughout ontogeny. Theoretical scaling models (e.g. Hill, 1950; Richard &

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Wainwright, 1995), for example, predict that whereas larger size classes benefit from relatively high force-generation capacity, juveniles are expected to be relatively faster, which may allow them to exploit more agile prey. Experimental data for lizards confirm this partially and show that bite force generally increases with body size, resulting in larger lizards biting relatively harder (Herrel *et al.*, 1999, 2001). Moreover, behavioural and ecological data show that at least in some lizards, animals with higher bite force take less time to process prey and include larger and harder prey in their diet (Herrel *et al.*, 2001; Verwajen, Van Damme & Herrel, 2002). However, such changes in diet throughout ontogeny are not always present, and animals may decide to exploit abundant prey sources throughout their growth period (e.g. Teixeira-Filho, Rocha & Ribas, 2003).

In many vertebrates intersexual differences in body size also exist. Such a sexual size dimorphism has also been documented in lizards (e.g. Olsson & Madsen, 1998; Fox, McCoy & Baird, 2003). Among *Anolis* lizards, there are well-documented differences in body size between males and females (e.g. Schoener, 1967, 1968; Hebrard & Madsen, 1984; Fox *et al.*, 2003). Previous research on *Anolis* lizards has demonstrated that intersexual differences in body size can be related to intersexual differences in habitat use (Schoener, 1967, 1968; Schoener & Schoener, 1971), home ranges (Schoener & Schoener, 1982) and diet (Schoener, 1967, 1968; Schoener & Gorman, 1968). However, few studies have examined how intersexual differences in body size may result in differential performance (i.e. the ability to execute an ecologically relevant task; see Huey & Stevenson, 1979), a crucial step in explaining how morphological differences may affect resource partitioning. The few studies that have examined this issue have demonstrated some differences in performance (i.e. locomotor performance), but the relationships with underlying morphological traits often remain unclear (Macrini & Irschick, 1998).

Body-size effects, however, may be circumvented by shape changes during growth (e.g. juveniles with disproportionately big heads or long legs) or changes in mechanics that allow young individuals to perform as well as adults (see review of Carrier, 1996). Juvenile black-tailed jackrabbits, for example, have relatively stronger leg extensor muscles and longer moment arms of these muscles than do adults, resulting in escape accelerations that are as large as or larger than those of adults (Carrier, 1983, 1995). Similarly, sexual dimorphism is often not restricted to differences in body and head size; head shape differences and even the differences in the distribution of jaw-closing muscles that may affect bite performance have been observed (e.g. Herrel, Van Damme & De Vree, 1996; Herrel *et al.*, 1999). This could allow members of the

smaller sex or age classes to perform relatively well and thus allow them to exploit similar resources. However, often the ecological data needed to assess the potential effects of differences in size and shape are lacking. Thus it remains unclear whether, for example, shape differences could allow animals to compensate for their lower performance levels arising as a consequence of their smaller body size (but see Carrier, 1983, 1995; Trillmich *et al.*, 2003).

We tested whether different age/sex classes of an abundant trunk-ground *Anolis* species from Jamaica (*A. lineatopus* Gray 1840) differed in their head size and shape, bite force and diet. We chose this species for the following reasons: it is abundant, males differ from females in body size, and although microhabitat differences are present between different sex and age classes (Macrini & Irschick, 1998), there appears to be considerable overlap in temporal and spatial aspects of foraging (Andrews, 1971; pers. observ.). We chose to examine bite force as a performance trait as it is affected directly by changes in head dimensions (Herrel *et al.*, 1999, 2001) and affects diet composition in some lizard species (Herrel *et al.*, 2001; Verwajen *et al.*, 2002). Rather than focusing on differences in taxonomical composition of the diet, we specifically expected functional aspects of diet, such as prey size and hardness, to be affected by size-induced differences in head size and bite performance (see also Aguirre *et al.*, 2003).

MATERIAL AND METHODS

STUDY ANIMALS

Individuals of *A. lineatopus* were caught by noose or by hand at the Discovery Bay Marine Laboratory (DBML), Discovery Bay, Jamaica between 21 January 2002 and 2 February 2002. In total, we captured 122 *A. lineatopus*. The snout–vent length (SVL) of all individuals was measured from the tip of the snout to the posterior edge of the anal scale; head length was measured from the back of the parietal bone to the tip of the upper jaw; head width was measured at the widest part of the head (at the level of the jugal bones); head height was measured just posterior to the orbits; lower jaw length was measured from the back of the retroarticular process to the tip of the lower jaw. Bony elements used to delineate morphological segments could be detected easily through palpation. Additionally, three morphological variables reflecting the biomechanics of the jaw system were estimated by measuring (1) the distance from the jaw articulation to the tip of the lower jaw and (2) the distance from the coronoid bone (estimated by the posterior edge of the jugal) to the tip of the lower jaw. By subtracting distance (1) from the lower jaw length we calculated the length of the jaw in-lever for opening (i.e. distance from the

articulation to the back of the retroarticular process where the jaw-opener muscles insert). Subtracting distance (2) from distance (1) gave the in-lever for jaw closing (i.e. the distance from the articulation to the coronoid where the jaw-closing muscles attach). The distance from the articulation to the tip of the jaw (1) is the jaw out-lever. All measurements were taken using digital callipers (Mitutoyo CD-20DC, Sakato, Japan; precision, 0.01 mm).

MEASUREMENT OF BITE CAPACITY

We measured *in-vivo* bite force for all individuals using an isometric Kistler force transducer (type 9203) mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5995, Kistler Inc., Winterthur, Switzerland; see Herrel *et al.*, 1999 for a detailed description of the set-up). When needed, we induced the *A. lineatopus* to bite the force transducer by tapping them on the side of the mouth. The tapping readily resulted in a characteristic threat response in which the jaws are opened maximally. The free ends of the holder (the bite plates) were then placed between the jaws, which resulted immediately in prolonged biting. As body temperature is known to affect performance capacity in lizards, we placed the *A. lineatopus* outside in the shade in individual bags at least half an hour prior to experimentation and in between trials. In doing so, they attained body temperatures equal or close to the environmental temperature at which they were typically active ($29 \pm 2^\circ\text{C}$). At least five vigorous bites were obtained for each *A. lineatopus*. As an estimate of maximum bite capacity, we used the highest bite force of the five bites for each individual.

STOMACH-CONTENT ANALYSIS

Anolis lineatopus were stomach-flushed directly after capture using a syringe with a ball-tipped steel needle attached. The size of the syringe and needle was adjusted to the size of the animal. Animals were tapped gently on the sides of the jaw, resulting in a threat response, in which the jaws are opened widely. A small plastic ring was inserted between the jaws to allow unhindered flow of water and food out of the digestive tract. The needle was gently inserted into the pharynx and pushed further down the digestive tract to the end of the stomach (the position of the needle could be detected by palpation). Next, water was gently squeezed out of the syringe while massaging the stomach of the lizard. Water was added until the food was regurgitated or pushed out with the water. Stomach contents were placed in individual vials with 70% ethanol and labelled. Animals were marked with a nontoxic marker and allowed to recover from stomach flushing for at least 12 h before being returned to

their exact site of capture. Stomach contents were analysed down to the lowest possible taxonomic order (for animal prey), and measured. Length and width of all intact food items was determined using digital callipers (Mitutoyo CD-20DC; precision, 0.01 mm). The mass of each intact food item was determined using an electronic balance (M220, Denver Instruments, Denver, CO, USA; precision, 0.01 mg). Average prey dimensions and prey number were calculated for each individual and used in subsequent analyses.

PREY AVAILABILITY

To get an indication of prey availability at the DBML fieldsite, seven pitfalls 15 cm in diameter and 10 cm deep were used. Pitfalls were dug into the ground at or near sites where *A. lineatopus* individuals were observed foraging, and were left for 48 h. An aqueous formaldehyde (5%) solution with a little soap added (to reduce surface tension) was poured into each pitfall. All invertebrates were removed from the pitfalls after 24 h and again after 48 h. All invertebrates captured were stored in a 70% aqueous ethanol solution. All invertebrates retrieved from the pitfalls were taken back to the lab, identified, counted, measured (length and width; Mitutoyo CD-20DC; precision, 0.01 mm) and weighed (M220; precision, 0.01 mg).

ESTIMATION OF PREY HARDNESS

Each prey item was classified as being either hard (Coleoptera, Isopoda, bees and wasps, Mollusca), of intermediate hardness (ants, Orthoptera, Odonata, fruit) or soft (all other prey) based on previous measurements of prey hardness for a large sample with great diversity of arthropod prey (Herrel *et al.*, 1999, 2001; unpubl.; Aguirre *et al.*, 2003). Next, prey hardness was estimated for all intact prey (i.e. prey items for which the length could be determined) based on previously established relationships between prey hardness and prey length (see Herrel *et al.*, 1999, 2001; unpubl.; Aguirre *et al.*, 2003), using the following regressions:

$$\begin{aligned} \text{soft: } & \text{Log}_{10}[\text{prey hardness (in N)}] = 0.997 \\ & \times \text{Log}_{10}[\text{prey length (in mm)}] - 1.379; \\ \text{intermediate: } & \text{Log}_{10}[\text{prey hardness (in N)}] = 1.780 \\ & \times \text{Log}_{10}[\text{prey length (in mm)}] - 1.942; \\ \text{hard: } & \text{Log}_{10}[\text{prey hardness (in N)}] = 1.582 \\ & \times \text{Log}_{10}[\text{prey length (in mm)}] - 1.365. \end{aligned}$$

Finally, an average prey hardness value was calculated for each individual and used in subsequent analyses.

STATISTICAL ANALYSES

All morphological and performance data were \log_{10} -transformed before analysis. After \log_{10} transforma-

tion all variables displayed a normal distribution. Ordinary least squares regressions were used throughout. To investigate ontogenetic changes in head size, head dimensions were regressed against SVL. Multivariate analyses of variance (MANOVAs) were used to test for absolute differences in body size, head dimensions and bite force between juveniles, adult females and adult males. Due to nonoverlapping ranges (e.g. between juveniles and adults), residuals of the regression of morphometric variables against SVL were calculated. These were then used in MANOVAs to test for differences in relative head dimensions and bite performance between groups.

Next, we regressed prey dimensions, prey number and prey hardness against *A. lineatopus* SVL to investigate ontogenetic changes in diet. To test for differences between juveniles, females and males in absolute prey dimensions, prey number and prey hardness, MANOVAs coupled to subsequent univariate *F*-tests were used. Relationships between head shape and prey dimensions were examined by extracting the residuals of the regressions of head dimensions against SVL, and introducing them into a stepwise multiple regression model with the prey dimensions and prey hardness as dependent variables.

Relationships between bite force and prey dimensions were assessed by regression analysis. To test whether relative bite force also explained variation in prey dimensions, we calculated the residuals of the regression of bite force against SVL and regressed this against prey dimensions and prey hardness.

Finally, we tested whether sex and age classes differed in the relative dimensions of prey eaten by

regressing prey dimensions (width, mass and hardness) against prey length, extracting the residuals and entering them into a MANOVA.

RESULTS

HEAD SIZE AND SHAPE

A MANOVA indicated significant differences in body and head size among groups ($F_{20,222} = 19.47$; $P < 0.001$). Posthoc tests showed that: (1) males were larger than females and juveniles in all body and head dimensions, and (2) females were also significantly larger than juveniles in all dimensions (see also Table 1). Although body mass scaled isometrically with SVL, most head dimensions (with the exception of the jaw out-lever and the in-lever for jaw opening) scaled with slight but significant negative allometry across individuals (Table 2, Fig. 1). Interestingly, the jaw-closing in-lever scaled with significant positive allometry, suggesting that as animals grow, the biomechanics of the jaw system change to enhance bite-force generation. Analyses of residuals demonstrated that groups also differed significantly in head shape [MANOVA (Wilk's lambda): $F_{18,224} = 5.05$; $P < 0.01$]. Subsequent univariate analyses indicated that differences were significant for all variables (all $P = 0.01$) with the exception of body mass ($F_{2,120} = 0.084$; $P > 0.05$) and the in-lever for jaw opening ($F_{2,120} = 1.38$; $P > 0.05$). Post-hoc tests on the residual data showed that whereas females had significantly smaller heads for their SVL (with the exception of the in-lever for jaw closing, which was not significantly different between

Table 1. Summary of head dimensions, prey dimensions and bite force for *Anolis lineatopus*

	Males ($N = 58$)	Females ($N = 45$)	Juveniles ($N = 21$)
SVL (mm)	51.60 ± 5.87	44.02 ± 2.24	31.34 ± 5.04
Mass (g)	3.11 ± 1.15	1.86 ± 0.47	0.69 ± 0.30
Head length (mm)	15.86 ± 2.06	13.00 ± 0.58	10.10 ± 1.05
Head width (mm)	8.39 ± 1.10	6.79 ± 0.32	5.38 ± 0.52
Head height (mm)	6.34 ± 0.83	5.12 ± 0.32	4.22 ± 0.44
Lower jaw length (mm)	16.19 ± 2.21	13.14 ± 0.62	10.04 ± 1.18
Jaw out-lever (mm)	14.82 ± 2.06	12.00 ± 0.61	9.16 ± 1.03
Opening in-lever (mm)	1.38 ± 0.24	1.14 ± 0.28	0.87 ± 0.20
Closing in-lever (mm)	2.34 ± 0.51	1.76 ± 0.28	1.30 ± 0.25
Bite force (N)	3.40 ± 1.42	1.66 ± 0.30	0.90 ± 0.23
Prey length (mm)	7.26 ± 5.62	4.20 ± 4.27	7.49 ± 18.23
Prey width (mm)	2.77 ± 1.48	1.89 ± 0.91	1.46 ± 0.78
Prey mass (g)	0.02 ± 0.04	0.05 ± 0.22	0.01 ± 0.02
Prey number (N)	1.41 ± 1.15	1.52 ± 0.99	1.95 ± 1.52
Prey hardness (N)	0.40 ± 0.41	0.17 ± 0.18	0.29 ± 0.76

Data are presented as mean ± standard deviation. Prey dimensions are individual averages based on intact prey only. Sample sizes for prey dimensions were: males: 47; females: 36; juveniles: 18. SVL, snout–vent length.

Table 2. Relationships between snout–vent length, head dimensions, prey dimensions and bite force in *Anolis lineatopus*

	R^2	Slope	Intercept
Body mass (g)	0.87	3.0	-4.67
Head length (mm)†	0.93	0.89	-0.34
Head width (mm)†	0.91	0.88	-0.60
Head height (mm)†	0.86	0.83	-0.62
Lower jaw length (mm)†	0.94	0.96	-0.44
Jaw out-lever (mm)	0.94	0.96	-0.48
Opening in-lever (mm)	0.53	0.97	-1.53
Closing in-lever (mm)†	0.64	1.18	-1.67
Bite force (N)†	0.83	2.54	-3.88
Prey length (mm)	0.11	1.47	-1.81
Prey width (mm)	0.19	1.31	-1.87
Prey mass (g)	0.17	4.53	-9.84
Prey number (N)*	0.04	-2.74	6.06
Prey hardness (N)	0.18	2.52	-4.94

All regressions significant at $\alpha = 0.01$. *Regression not significant ($P = 0.06$). †Variables had slopes differing significantly from the predicted slope of 1 for linear dimensions and 2 for bite force.

females and juveniles, $P = 0.069$), males and juveniles did not differ in head shape.

BITE FORCE

Bite force was related significantly to overall animal size and scaled with significant positive allometry (see Table 2, Fig. 1). Consequently, bite force was significantly different between groups ($F_{2,123} = 121.27$; $P < 0.01$), with males biting harder than females, and juveniles having the lowest absolute bite force (see Table 1). An analysis of the residuals of bite force against SVL indicated that differences among groups remained, even when taking into account differences in overall body size ($F_{2,120} = 22.67$; $P < 0.001$). Post-hoc tests, however, showed that whereas females had significantly lower bite force for their body size, males and juveniles did not differ in relative bite force. A stepwise multiple regression analysis with residual head dimensions as independent and residual bite force as dependent variables extracted a significant model with residual head length and residual head width as the only variables ($r^2 = 0.45$; $P < 0.01$), indicating that *A. lineatopus* with relatively longer and wider heads bite relatively harder.

DIET COMPOSITION

The diet of *A. lineatopus* consisted of a wide variety of invertebrate prey (Table 3). Whereas Hymenoptera,

spiders and insect larvae were relatively common, fruit and seeds were uncommon in the diet. Taxonomic differences among males, females and juveniles were generally minor. Noteworthy was a juvenile *Anolis* lizard in the stomach of a male *A. lineatopus*. For male *A. lineatopus*, ants, spiders and bees were numerically the most common items in the diet. However, when expressed relative to the total mass of the prey, Lepidoptera, their larvae, and other insect larvae were the most important food items in the diet of male *A. lineatopus* (see Table 2). For females, ants, spiders and insect larvae were the most common prey in the diet based on prey counts. However, as in males, lepidopteran and other larvae were the most important food items when expressed relative to the total prey mass consumed. For juveniles, spiders, ants and bees were the most common prey, while when expressed by mass, ants, larval lepidopterans and phasmids became the most important prey in the diet (Table 3). It should be noted, however, that the importance of phasmids was due to a single very large specimen retrieved from the stomach of a juvenile *A. lineatopus*.

A comparison of the actual diet samples with information on prey availability (Table 4) suggested that *A. lineatopus* did not eat prey randomly in accordance to their availability. Insect larvae (relatively heavy prey) were especially abundant in the diet of *A. lineatopus* when compared with the prey available (Table 4).

PREY DIMENSIONS AND HARDNESS

Prey dimensions and prey hardness were significantly and positively correlated with *A. lineatopus* SVL (Table 2, Fig. 2). The average number of prey in the stomach showed a negative, but nonsignificant, trend with SVL ($P = 0.06$; see Table 2), suggesting that larger *A. lineatopus* eat fewer, but larger, prey. The dimensions of prey in the diet of males, females and juveniles were significantly different (MANOVA: $F_{8,190} = 3.60$; $P = 0.001$). Subsequent univariate tests showed that these differences were significant for all prey dimensions and prey hardness (all $P = 0.02$). Differences in prey number, however, were not significant ($P = 0.12$). Post-hoc tests demonstrated significant differences in prey mass among all groups. Differences in prey length, prey width and prey hardness were only significant for males compared with females and juveniles (all $P < 0.01$). Differences between females and juveniles were not significant (all $P > 0.05$). An analysis of prey shape using residual prey dimensions (relative to prey length) indicated significant differences among groups ($F_{6,192} = 2.38$; $P = 0.03$). Subsequent univariate tests coupled to posthoc tests showed that males and females differed significantly from juveniles (but not from one another) in residual prey

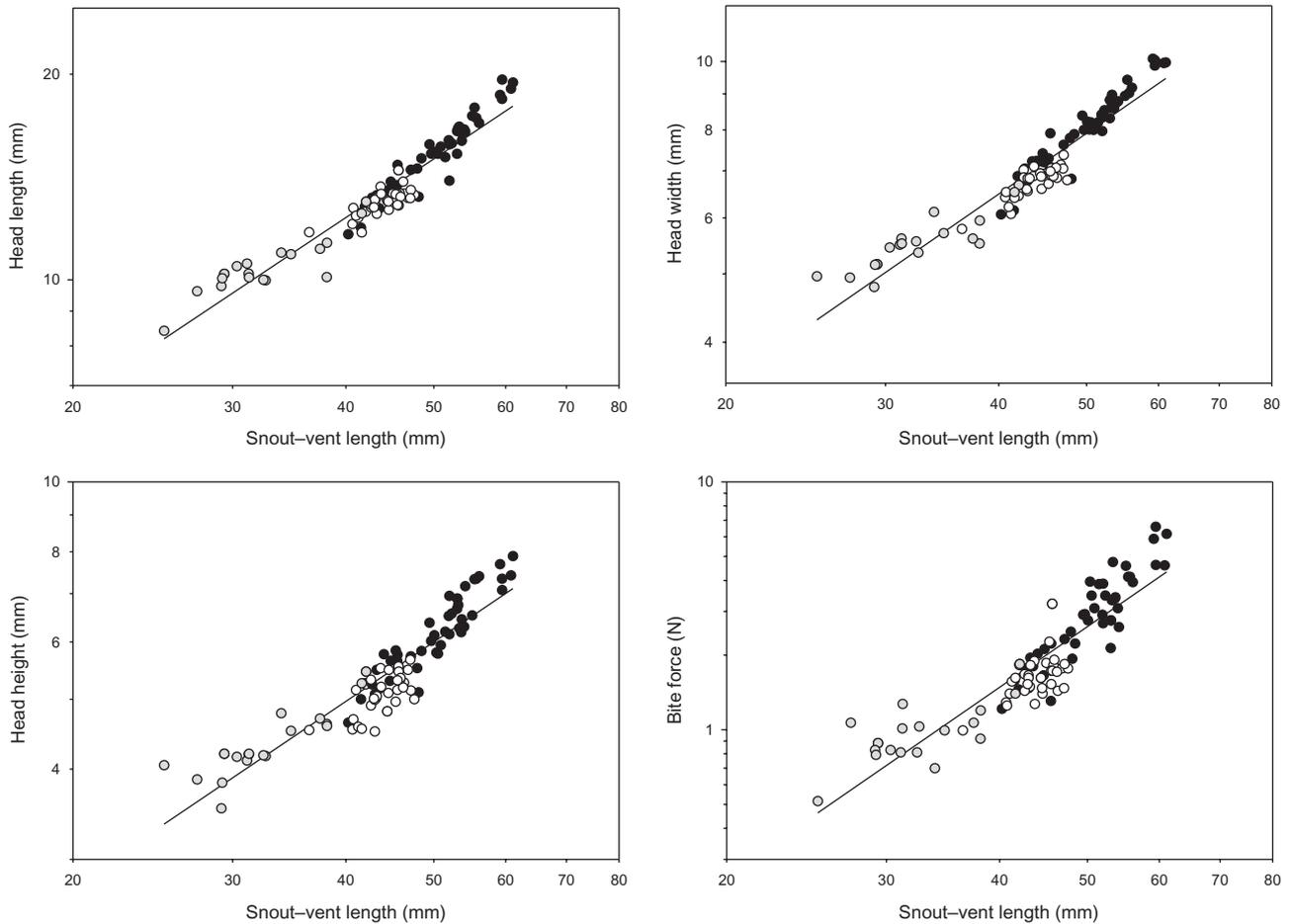


Figure 1. Graphs depicting the relationships between body size (snout-vent length) and head dimensions in *Anolis lineatopus*. Note how both juveniles (○) and males (●) have relatively larger heads for a given body size compared with females (○).

mass and residual prey width, indicating that males and females eat prey that are relatively wider and heavier for a given prey length. Males also differed significantly from juveniles in residual prey hardness, indicating that they eat relatively harder prey.

INTERACTIONS AMONG HEAD SHAPE, BITE FORCE AND DIET

Regression analyses showed that bite force was significantly correlated with prey dimensions and prey hardness across individuals (Table 5, Fig. 3). Residual bite force was also significantly and positively related to residual prey length, indicating that animals with relatively larger bite force eat longer prey (Table 5). Stepwise multiple regression models with residual head dimensions and residual bite force as independent variables and prey dimensions and hardness as dependent variables retained significant models for prey length ($P = 0.008$), prey width ($P = 0.03$) and prey

hardness ($P = 0.03$), with residual head width as the only variable (Fig. 4). Prey mass, on the other hand, was not correlated with residual head dimensions or residual bite force ($P > 0.05$).

DISCUSSION

DIET OF *ANOLIS LINEATOPUS*

Anolis lineatopus appears to be a generalist, eating a variety of invertebrate prey (see also Schwartz & Henderson, 1991). The preliminary availability data, however, suggest that individuals do not eat prey randomly according to their availability. For instance, cockroaches were relatively uncommon in the diet but abundant in the environment and insect larvae were more common in the diet than would be expected according to our arthropod sampling. As insect larvae are nutritious, slow, and soft prey, *A. lineatopus* are indeed expected to exploit these prey when possible. Our data also suggest a rather similar resource

Table 3. Taxonomical composition of diet in *Anolis lineatopus*

Dietary component	Males (N = 55)			Females (N = 43)			Juveniles (N = 19)		
	Number	Mass	relative (%)	Number	Mass	relative (%)	Number	Mass	relative (%)
	absolute	absolute (mg)	relative (%)	absolute	absolute (mg)	relative (%)	absolute	absolute (mg)	relative (%)
Acari	3	0.0005	0.03				1	0.0001	0.04
Aranea	16	0.0237	1.4	23	0.0083	13.5*	17	0.0118	12.1*
Coleoptera	9	0.0553	3.3	9	0.0061	5.3	10	0.0085	7.1
Collembola				1	0.0081	0.6			
Dermaptera	4	0.04	2.4	10	0.0407	5.9	2	0.0006	1.4
Dictyoptera	3	0.1537	9.1	7	0.0548	4.1	1	0.0102	0.7
Diplopoda				1	0.0181	0.6			
Diptera	2	0.002	0.1				7	0.0197	5.0
Larvae	1	0.0389	2.3						
Ephemeroptera	1	0.0126	0.7						
Hemiptera	5	0.0313	1.9	3	0.0011	1.8			
Hymenoptera	8	0.0518	3.1						
Formicidae	58	0.0737	4.4	144	0.0132	84.2*	32	0.0235	22.9*
Vespidae	1	0.0025	0.2				27	0.0018	19.3*
Bees	12	0.0036	0.2	2	0.0078	1.2	1	0.0007	0.7
Isopoda									
Isoptera	1	0.0007	0.04	2	0.0027	1.2			
Lepidoptera	1	0.2795	16.5*	2	0.0014	1.2			
Larvae	5	0.2413	14.2*	1	0.0854	0.6	4	0.0917	2.9
Mollusca	1	0.0026	0.2	4	0.002	2.3			
Odonata	1	0.0321	1.9	1	0.0072	0.6			
Orthoptera	4	0.1605	9.5	1	0.0302	0.6			
Phasmidae							1	0.0736	29.93*
Thysanoptera				2	0.0009	1.2			
Unidentified insect larvae	11	0.1924	11.4*	14	0.2045	8.2*			
Lizard	1	0.0674	4.0						
Skin	2	0.0387	2.3	2	0.0253	1.2	1	0.0001	0.7
Fruit	2	0.0769	4.5	2	0.0042	1.2			
Seeds	5	0.0118	0.7				1	0.0001	0.7
Stone	1	0.0039	0.2	1	0.0064	0.6			
Unidentified	14	0.0966	5.7	11	0.036	6.4	34	0.0066	24.3
Total	171	1.694		243	0.5644		140	0.2459	

Invertebrate prey were identified to the lowest taxonomical level possible. *The three most important dietary categories for males, females and juveniles, in terms of relative number and relative mass.

Table 4. *Anolis lineatopus* prey availability as determined by pitfall sampling: number and mass of prey in pitfalls

Order	Family	Number		Mass	
		absolute	relative (%)	absolute (mg)	relative (%)
Coleoptera	Scarabidae	1	1.28	468.00	20.20*
Coleoptera		1	1.28	0.37	0.02
Dictyoptera		19	24.36*	1383.39	59.72*
Diptera		14	17.95*	2.44	0.11
Hymenoptera		3	3.85	9.10	0.39
Homoptera		1	1.28	14.03	0.61
Arachnida		3	3.85	16.90	0.73
Hymenoptera	Formicidae (trap jaw ants)	9	11.54	105.17	4.54
Hymenoptera	Formicidae, other	23	29.49*	309.14	13.35*
Orthoptera	Gryllidae	2	2.56	1.31	0.06
Lepidoptera		2	2.56	6.66	0.29
Total		78		2316.52	

Invertebrate prey were identified to the lowest taxonomical level possible. *The three most important dietary categories, in terms of relative number and relative mass.

Table 5. Relationships between bite force and prey dimensions in *Anolis lineatopus*

	R^2	Slope	Intercept	P
Absolute bite force as dependent				
Prey length (mm)	0.16	0.64	0.44	< 0.001
Prey width (mm)	0.19	0.47	0.15	< 0.001
Prey mass (g)	0.19	1.69	-2.87	< 0.001
Prey hardness (N)	0.20	0.96	-1.07	< 0.001
Residual bite force as dependent				
Prey length (mm)	0.06	0.87	0.62	0.02

Regressions based on intact prey only.

utilization among male, female and juvenile *A. lineatopus* based on prey taxonomy (Table 3). However, a more in-depth analysis demonstrated clear differences in functional aspects of the prey eaten, including prey size, shape, and hardness.

Previous studies have demonstrated that males, females and juveniles use slightly different microhabitats (mainly perch height and diameter; see Macrini & Irschick, 1998), suggesting that the observed differences in diet might be the result of differences in the availability of prey in these microhabitats. Although this might indeed be partially responsible for the observed differences in diet, two lines of evidence suggest that this is probably not the only explanation: (1) animals of different size and sex classes were observed foraging in similar microhabitats (i.e. males will come down to the ground to forage in the same areas in which females and juveniles forage), and (2) the taxonomic distribution of prey in the diet was very similar.

Clearly, data on the availability of the different functional prey groups in the different microhabitats occupied by juveniles, females and males are essential to resolve this in more detail.

Whereas our data show that it is important to examine functional aspects of the diet, such as prey size, shape and hardness, other prey properties, such as caloric content and evasiveness, may also be important functional prey characteristics that may affect prey selection. Whereas predators should try to consume prey with a high caloric value, the evasiveness or 'escape ability' of a prey may prevent a predator from catching prey. Morphological differences among animals resulting in functional differences of the feeding or locomotor systems (e.g. longer jaws resulting in faster jaw closing or longer legs resulting in longer and faster jumps) may allow certain animals to exploit more evasive prey. Whether all of these functional prey properties or only a subset of them play a role in diet selection is currently unknown, but crucial to our understanding of predator-prey interactions and dietary resource partitioning. Quantitative estimates of jaw-closing speeds, escape speeds of different prey types, and acceleration capacity of *A. lineatopus* should shed further light on this issue.

THE EFFECTS OF SIZE AND SHAPE ON PERFORMANCE AND DIET

That size has a profound effect on the functioning of the feeding system is apparent by examining our results. Larger *A. lineatopus* had larger heads and consequently also larger bite force. However, bite force scaled disproportionately to body size despite

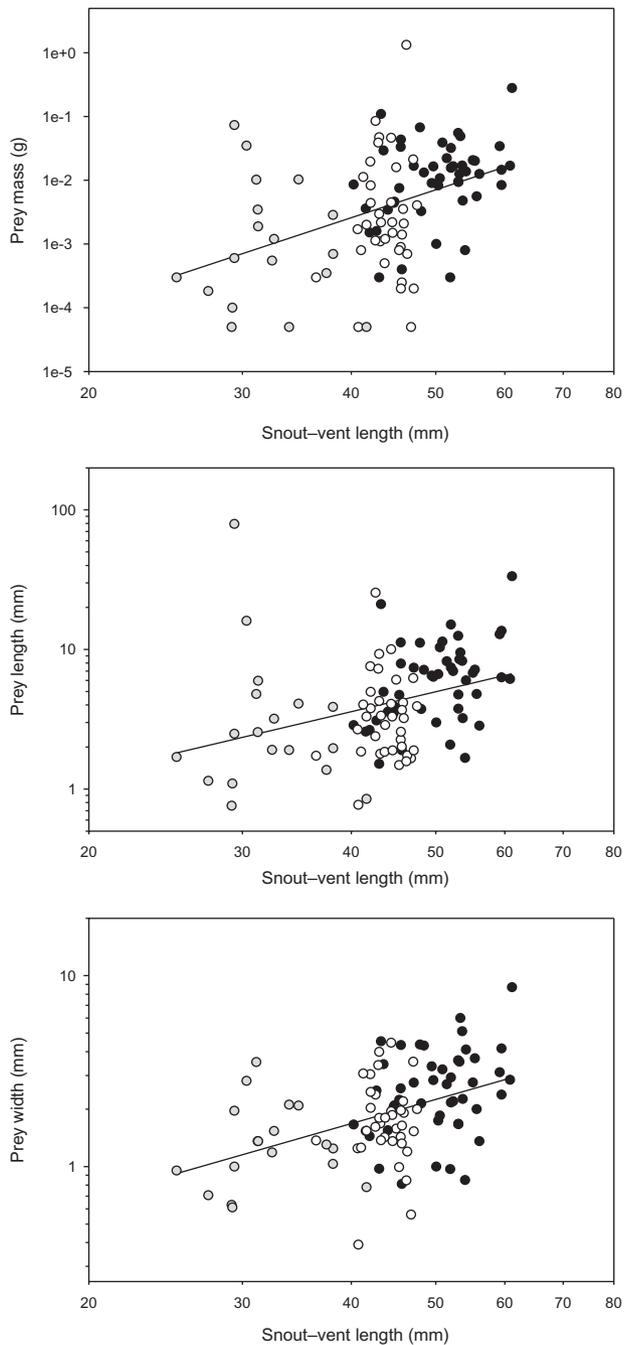


Figure 2. Graphs depicting the relationships between body size in *Anolis lineatopus* and prey dimensions. Only data for intact prey were included. All relationships between body size and prey dimensions were significant. ○, juveniles; ○, females; ●, males.

the negative allometry of head size to body size (Table 2). Thus, larger *A. lineatopus* bite hard but have relatively small heads for their body size. One element that can potentially explain this, at first sight paradoxical, result is the positive allometry of

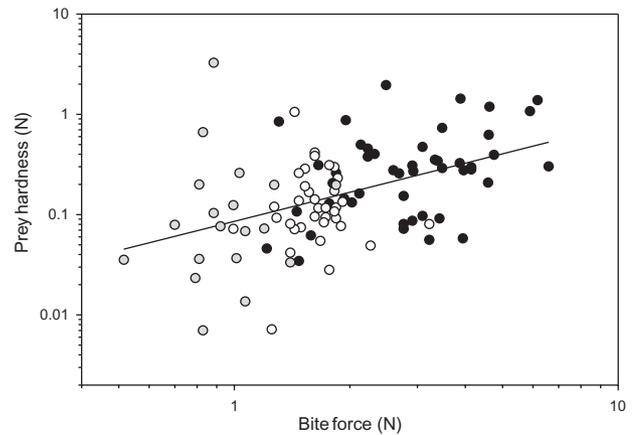


Figure 3. Graph illustrating the relationship between maximum bite force capacity in *Anolis lineatopus* and prey hardness. Animals with higher bite forces also eat larger prey. ○, juveniles; ○, females; ●, males.

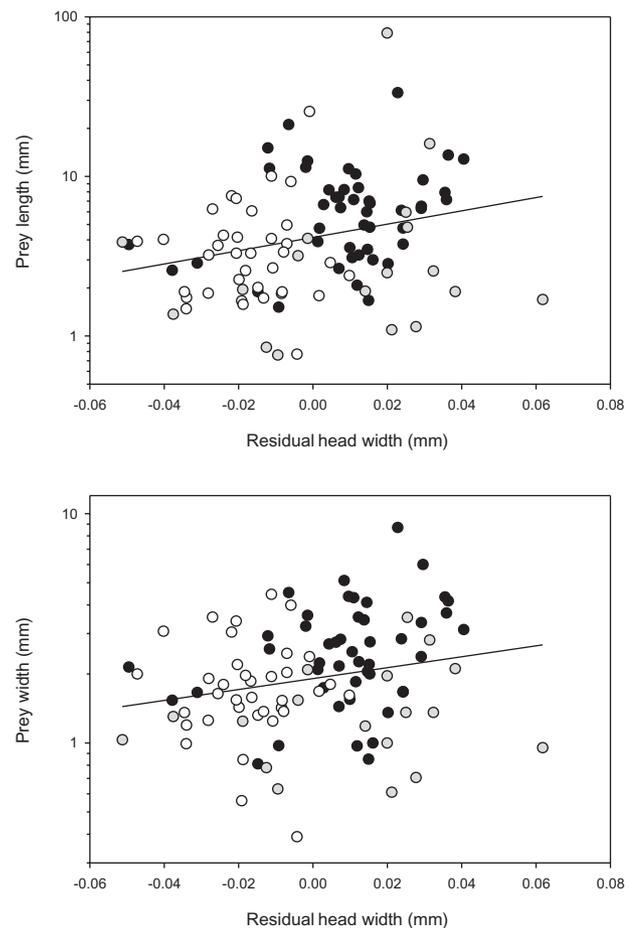


Figure 4. Graphs showing that *Anolis lineatopus* with relatively wider heads eat longer and wider prey. Note how males (●) and juveniles (○) have relatively wide heads for their size and thus eat long and wide prey. ○, females.

jaw-closing in-lever during growth. Yet the results from the multiple regression analysis (retaining head width and length as variables best explaining the variation in bite force) suggest that the changes in bite force throughout ontogeny cannot be explained by changes in lever mechanics alone. Other traits, such as jaw muscle mass, pennation angle and orientation of the jaw-closing muscles, are likely important in generating the positive allometry of bite force during ontogeny.

Ontogenetic changes in body size, however, do not only affect head size and bite force, but also result in differences in diet among animals of different size classes (Fig. 2). In general, larger *A. lineatopus* eat prey that are longer, wider, heavier and harder than do smaller individuals. Whereas this might be purely a function of larger individuals having larger head sizes, our data suggest that this is mediated through changes in performance (i.e. bite force) as well. Bite force was significantly correlated to prey dimensions and prey hardness, indicating that individuals with larger bite force generally eat both bigger and harder prey (Fig. 3). For a given body size, animals with relatively larger bite force also eat larger prey. Head width also appears to play a major role in determining the size of prey eaten. This is likely because of the dual effect of head width on maximum prey size, because (1) it directly limits passage of food items to the oesophagus, and (2) it is positively correlated with bite force.

Surprisingly, and contrary to the general trends noted above, juveniles ate prey that were just as heavy, long, wide and hard as did females, despite their smaller size. Our data suggest that this is at least partly due to the fact that juveniles have relatively big heads and high bite force. Why they have relatively big heads and bite force remains unclear, but we suggest that this might be related to the availability of prey in the environment. Our preliminary availability data do indeed suggest that very small prey might be relatively uncommon (Fig. 5), thus forcing juveniles to eat relatively large prey. Additionally, as food availability in insular environments can be low and unpredictable (Andrews, 1979), having a wide potential prey spectrum (facilitated by large heads and bite force) might be an important evolutionary strategy. Clearly, a more in-depth assessment of prey availability is needed to assess these hypotheses.

SEXUAL SIZE DIMORPHISM

Our data on sexual size and head size dimorphism are consistent with previously published accounts and indicate strong differences in body size between the sexes (Schoener, 1967, 1968; Schoener & Schoener, 1971; Preest, 1994). Yet in addition to differences in

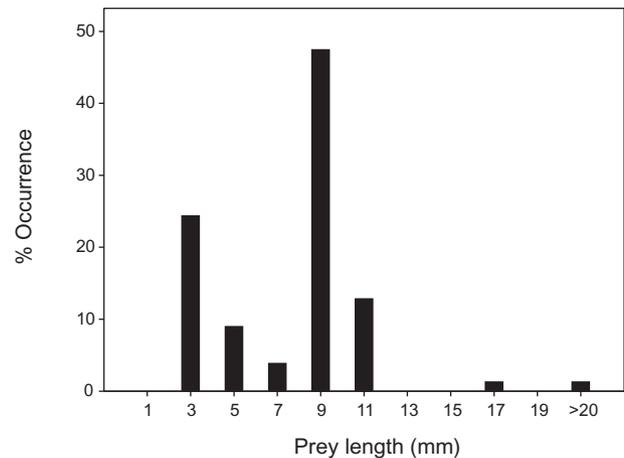


Figure 5. Histogram showing the proportion of *Anolis lineatopus* prey of different length classes available in the environment. Note, however, that these data are based on a limited sample only (seven pitfalls for 48 h).

body size, male and female *A. lineatopus* differed in head shape, with males having bigger heads for a given SVL compared with females. As differences in head shape between sexes resulted in differential performance, and as performance was related to functional aspects of diet (size, shape and hardness of prey), dietary differences are functionally related to the observed sexual head size/shape dimorphism. Although this is consistent with the idea that the observed dimorphism is caused by natural selection resulting in reduced intraspecific competition, sexual selection would also be expected to lead to differences in head size and shape between males and females, as large heads and high bite force are likely important in male–male combat (McMann, 1993; Stamps & Krishnan, 1997). If this is so, then the observed differences in diet could be an epiphenomenon of sexual selection acting on head size and bite force in relation to male–male combat. Currently, we cannot tease apart the potential contributions of both selection pressures and further comparative data will be crucial in understanding the evolution of sexual head size and shape dimorphism in *Anolis* lizards. A comparison of head size, head shape and bite force, including nonterritorial species (e.g. twig anoles), or nondimorphic species (e.g. species such as *A. vermiculatus* or *Polychrus* species) in an evolutionary context might shed light on the selective pressures that gave rise to sexual differences in diet among anoles.

In conclusion, our data suggest that ontogenetic changes in body size affect the morphology and performance of the jaw system in *A. lineatopus*. Moreover, through its effect on performance, body size also affects feeding ecology. Juvenile *A. lineatopus*, however, have relatively large heads and bite relatively

hard, which might be linked to the relative scarcity of small prey in the environment. Finally, sexual differences in head size and shape result in differences in bite force and ultimately diet in *A. lineatopus*. Although consistent with a niche-divergence hypothesis, the origin of the dimorphism (i.e. sexual or natural selection) cannot be determined based on our data.

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REFERENCES

- Aguirre LF, Herrel A, Van Damme R, Mathysen E. 2003.** The implications of food hardness for diet in bats. *Functional Ecology* **17**: 201–212.
- Andrews RM. 1971.** Structural habitat and time budget of a tropical *Anolis* lizard. *Ecology* **52**: 262–270.
- Andrews RM. 1979.** Evolution of life histories: a comparison of *Anolis* lizards from matched island and mainland habitats. *Breviora, Museum of Comparative Zoology* **454**: 1–51.
- Carrier DR. 1983.** Postnatal ontogeny of the musculo-skeletal system in the Black-tailed jack rabbit (*Lepus californicus*). *Journal of Zoology, London* **201**: 27–55.
- Carrier DR. 1995.** Ontogeny of jumping performance in the black tailed jack rabbit, (*Lepus californicus*). *Zoology* **94**: 309–313.
- Carrier DR. 1996.** Ontogenetic limits on locomotor performance. *Physiological Zoology* **69**: 467–488.
- Clark DB, Gibbons JW. 1969.** Dietary shift in the turtle *Pseudemys scripta* (Schœpff) from youth to maturity. *Copeia* **1969**: 82–105.
- Cooper WE, Lemos-Espinal JA. 2001.** Coordinated ontogeny of food preference and response to chemical food stimuli by a lizard *Ctenosaura pectinata* (Reptilia: Iguanidae). *Ethology* **107**: 639–653.
- Durtsche RD. 2000.** Ontogenetic plasticity of food habits in the Mexican spiny-tailed iguana, *Ctenosaura pectinata*. *Oecologia* **124**: 185–195.
- Fox SF, McCoy JK, Baird TA. 2003.** *Lizard social behavior*. Baltimore: The Johns Hopkins University Press.
- Hebrard JJ, Madsen T. 1984.** Dry season intersexual habitat partitioning by flap necked chameleons (*Chamaeleo dilepis*) in Kenya. *Biotropica* **16**: 69–72.
- Herrel A, Spithoven L, Van Damme R, De Vree F. 1999.** Sexual dimorphism of head size in *Gallotia galloti*; testing the niche divergence hypothesis by functional analyses. *Functional Ecology* **13**: 289–297.
- 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**: 253–262.
- Herrel A, Van Damme R, Vanhooydonck B, De Vree F. 2001.** The implications of bite performance to diet in two species of lacertid lizards. *Canadian Journal of Zoology* **79**: 662–670.
- Hill AV. 1950.** The dimensions of animals and muscular dynamics. *Science Progress* **38**: 209–230.
- Hoyle JA, Keast A. 1987.** The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). *Canadian Journal of Zoology* **65**: 1972–1977.
- Huey RB, Stevenson RD. 1979.** Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *American Zoologist* **19**: 357–366.
- Irschick DJ. 2000.** Effects of behavior and ontogeny on the locomotor performance of a West Indian lizard *Anolis lineatopus*. *Functional Ecology* **14**: 438–444.
- Irschick DJ, Macrini TE, Koruba S, Forman J. 2000.** Ontogenetic differences in morphology, habitat use, behavior and sprinting capacity in two West Indian *Anolis* lizard species. *Journal of Herpetology* **34**: 444–451.
- Lima AP, Magnusson WE. 1998.** Partitioning seasonal time: interactions among size, foraging activity and diet in leaf-litter frogs. *Oecologia* **116**: 259–266.
- Lukoschek V, McCormick MI. 2001.** Ontogeny of diet changes in a tropical benthic carnivorous fish, *Parupeneus barberinus* (Mullidae): relationship between foraging behaviour, habitat use, jaw size and prey selection. *Marine Biology* **138**: 1099–1113.
- Mackessy SP, Williams K, Ashton KG. 2003.** Ontogenetic variation in venom composition and diet of *Crotalus oreganus concolor*: a case of venom paedomorphosis? *Copeia* **2003**: 769–782.
- Macrini TE, Irschick DJ. 1998.** An intraspecific analysis of trade-offs in sprinting performance in a West Indian lizard (*Anolis lineatopus*). *Biological Journal of the Linnean Society* **63**: 579–591.
- McMahon T. 1973.** Size and shape in biology. *Science* **179**: 1201–1204.
- McMann S. 1993.** Contextual signalling and the structure of dyadic encounters in *Anolis carolinensis*. *Animal Behaviour* **46**: 657–668.
- Olsson M, Madsen T. 1998.** Sexual selection and sperm competition in reptiles. In: Birkhead TR, Moller AP, eds. *Sperm competition and sexual selection*. San Diego: Academic Press, 503–564.
- Preest MR. 1994.** Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: why do females take smaller prey than males? *Journal of Herpetology* **28**: 292–298.
- Richard BA, Wainwright PC. 1995.** Scaling of the feeding mechanism of large mouth bass (*Micropterus salmoides*): kinematics of prey capture. *Journal of Experimental Biology* **198**: 419–433.
- Schmidt-Nielsen K. 1984.** *Scaling: why is animal size so important?* Cambridge: Cambridge University Press.

- Schoener TW. 1967.** The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* **155**: 474–477.
- Schoener TW. 1968.** The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49**: 704–726.
- Schoener TW, Gorman GC. 1968.** Some niche differences in three lesser Antillean lizards of the genus *Anolis*. *Ecology* **49**: 819–830.
- Schoener TW, Schoener A. 1971.** Structural habitats of West Indian *Anolis* lizards I. Lowland Jamaica. *Breviora, Museum of Comparative Zoology* **368**: 1–53.
- Schoener TW, Schoener A. 1982.** Intraspecific variation in home-range size in some *Anolis* lizards. *Ecology* **63**: 809–823.
- Schwartz A, Henderson RW. 1991.** *Amphibians and reptiles of the West Indies*. Gainesville: University of Florida Press.
- Stamps JA, Krishnan VV. 1997.** Functions of fights in territory establishment. *American Naturalist* **150**: 393–405.
- Teixeira-Filho PF, Rocha CFD, Ribas SC. 2003.** Relative feeding specialization may depress ontogenetic, seasonal and sexual variations in diet: the endemic lizard *Cnemidophorus littoralis* (Teiidae). *Brazilian Journal of Biology* **63**: 321–328.
- Trillmich F, Bieneck M, Geissler E, Bischof H-J. 2003.** Ontogeny of running performance in the wild guinea pig (*Cavia aperea*). *Mammalian Biology* **68**: 214–223.
- Verwajen D, Van Damme R, Herrel A. 2002.** Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Functional Ecology* **16**: 842–850.
- Werner EE, Gilliam JF. 1984.** The ontogenetic niche and species interactions in size-structured populations. *Annual Reviews in Ecology and Systematics* **15**: 393–425.