Ontogenetic Scaling of Bite Force in Lizards and Turtles*

Anthony Herrel[1],[†]
James C. O'Reilly[2]
[1]Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Antwerp, Belgium; [2]Department of Organismal Biology and Anatomy, University of Chicago, 1027 East 57th Street, Chicago, Illinois 60637

ABSTRACT

Because selection on juvenile life-history stages is likely strong, disproportionately high levels of performance (e.g., sprint speed, endurance, etc.) might be expected. Whereas this phenomenon has been demonstrated with respect to locomotor performance, data for feeding are scarce. Here, we investigate the relationships among body dimensions, head dimensions, and bite force during growth in lizards and turtles. We also investigate whether ontogenetic changes in bite performance are related to changes in diet. Our analyses show that, for turtles, head dimensions generally increase with negative allometry. For lizards, heads scale as expected for geometrically growing systems. Bite force generally increased isometrically with carapace length in turtles but showed significant positive allometry relative to body dimensions in lizards. However, both lizards and turtles display positive allometric scaling of bite force relative to some measures of head size throughout ontogeny, suggesting (1) strong selection for increased relative bite performance with increasing head size and (2) intrinsic changes in the geometry and/or mass of the jaw adductors during growth. Whereas our data generally do not provide strong evidence of compensation for lower absolute levels of performance, they do show strong links among morphology, bite force, and diet during growth.

Introduction

That the dimensions of organisms are of enormous importance in biology and have major consequences on nearly all aspects of an organism's biology has been stressed by numerous researchers (e.g., Hill 1950; Schmidt-Nielsen 1984; La Barbera 1989). Studies examining the effects of body dimensions on physiology and kinematics have demonstrated that younger life-history stages typically show lower absolute levels of performance (e.g., Garland 1984; Katz and Gosline 1993; O'Reilly et al. 1993; Nauen and Shadwick 1999; Quillin 2000; Wilson et al. 2000). Consequently, juveniles may be at a competitive disadvantage because of their absolute smaller dimensions. Moreover, because juveniles often are faced with the same predators and have to forage in the same environments, strong selection for relatively high levels of locomotor performance at these early life-history stages can be expected (see review in Carrier 1996). However, juveniles of some species appear to have compensated for their smaller body dimensions and actually show levels of burst locomotor performance that are relatively high and in some cases similar to those of adults (e.g., Emerson 1978; Jayne and Bennet 1990; Carrier 1996; Trillmich et al. 2003).

Despite these observations, little attention has been given to the effects of changing dimensions on the function and performance of the feeding apparatus (but see Osenberg and Mittelbach 1989; O'Reilly et al. 1993; Richard and Wainwright 1995; Herrel et al. 1999a, 2001a, 2001b; Meyers et al. 2002; Hjelm et al. 2003). Because juveniles often forage in the same environments as adults, they will have to compete for the same trophic resources. However, because of their absolute smaller dimensions, they are likely to have smaller gapes and bite forces, which might in turn put them at a competitive disadvantage when compared with adults. Moreover, size differences may affect components of feeding such as handling time (e.g., Preest 1994; Verwaijen et al. 2002), energy expenditure during feeding (Andrews et al. 1987; Preest 1991, 1994), and consequently also the optimal prey size and type selected by an organism (e.g., Hoyle and Keast 1987). Those studies examining feeding or foraging behavior show that juveniles often perform at levels that are much lower on an absolute scale than those observed for adults (e.g., Richard and Wainwright 1995; Herrel et al. 1999a; Irschick 2000; Irschick et al. 2000; Meyers et al. 2002), suggesting that they are indeed at a competitive disadvantage compared with adults. Alternatively, juveniles and/or adults might avoid competition by selecting nonoverlapping resources, in which case no compensation for lower absolute levels of performance would be expected.

Ectothermic vertebrates appear to be a particularly interesting group to investigate the consequences of changes in body dimensions during ontogeny on feeding performance. Not only do they have to function autonomously from the day they are

---

born, but they often also grow several orders of magnitude, which may lead to dramatic changes in performance. Given that ectotherms tend to grow isometrically (O'Reilly et al. 1993; Richard and Wainwright 1995; Meyers et al. 2002; Robinson and Motta 2002; Toro et al. 2003), juveniles are predicted to perform differently than adults because of the differential scaling of force (proportional to length to the second power) and mass (proportional to length to the third power). Thus, whereas larger individuals will be able to bite harder, juveniles will have a higher capacity for acceleration. On the basis of these simple theoretical arguments, it can be predicted that larger animals should eat bigger and harder but generally less elusive prey. Juveniles, on the other hand, are expected to select more agile but softer prey.

In this article, we examine the scaling of body dimensions, head dimensions, and bite force for ontogenetic series of ectothermic vertebrates. First, we investigate turtles because they increase in mass by several orders of magnitude during their life span and because bite force has been shown to be ecologically relevant in these animals (Herrel et al. 2002). We selected three turtles (*Trachemys scripta*, *Chelydra serpentina*, and *Staurotypus* sp.) on the basis of their availability, considerable growth, and ecological differences. Second, we focus on two species of lizards that show considerable growth during their life and were accessible for dietary analyses (*Anolis equestris* and *Anolis garmani*). Specifically, the goals of this article were to (1) examine ontogenetic scaling of morphology and bite force in these species, (2) investigate the correlation of ontogenetic changes in morphology and performance to diet, and (3) examine whether juveniles show relatively high levels of performance when compared with adults to compensate for their absolutely smaller body dimensions.

Material and Methods

Animals

The *Chelydra serpentina* used in this study were trapped in the vicinity of Amherst, Massachusetts (Commonwealth of Massachusetts, Division of Fisheries and Wildlife scientific collecting permit 15.00SCRA to A. Richmond), or obtained from commercial dealers. The other species of turtles used were obtained from zoos or commercial dealers (see also Herrel et al. 2002). All wild-caught animals were released the same or the next day at their exact site of capture after measuring bite forces and body dimensions. The lizards used in this study were captured in Miami, Dade County, Florida (*Anolis equestris* and *Anolis garmani*), or at the Discovery Bay Marine Lab, Discovery Bay, Jamaica (*A. garmani*). After stomach flushing and measurement of bite forces and body and head dimensions, lizards were released at their exact site of capture. Sample sizes for each species are listed in Tables 1 and 2. All procedures were approved by the Institutional Animal Care and Use Committee at the University of Antwerp.

Bite Forces

In vivo bite forces were measured using isometric Kistler force transducers (types 9203, range ± 500 N, and 9311B, range ± 5,000 N, Kistler, Switzerland) mounted on purpose-built holders and connected to a Kistler charge amplifier (type 5058A5, Kistler, Switzerland; see Herrel et al. 1999*a*, 2001*a*, 2001*b* for a more detailed description of the setup). When the free end of the holder was placed between the jaws of the animal, prolonged and repeated biting resulted. The place of application of bite forces was standardized by mounting acrylic stops (small animals) or metal shields onto the free end of the holder. Gape angle was standardized by moving the bite plates away from each other for larger animals. Measurements were repeated five times for each animal, with an intertrial interval of at least 30 min. The maximal value obtained during such a recording session was considered to be the maximal bite force for that animal.

Morphometrics

Immediately after the performance trials, the following morphological measurements were taken from each animal where applicable: mass, carapace length, carapace width, snout-vent length, head length, lower jaw length, head width, head height, the distance between the quadrate bone and the tip of the lower jaw (=jaw outlever), and the distance between the back of the jugal bone and the tip of the lower jaw (see Tables 1, 2). Head length was measured from the anterior end of the premaxillary to the posterior edge of the parietal lower jaw length from the anterior end of the dentary bone to the posterior edge of the retroarticular process. Head width was measured at the widest part of the skull and includes potential bulging of the jaw muscles, and head height was measured at the highest part of the skull just posterior to the orbita (see Herrel et al. 1999*a*, 2002). The inlever for jaw opening was calculated by subtracting the length of the jaw outlever from the lower jaw length; the inlever for jaw closing was calculated by subtracting the distance from the back of the jugal to the jaw tips from the jaw outlever. For small animals, measurements were taken using digital callipers (Mitutoyo CD-20DC); the largest and more aggressive turtles were filmed in lateral and dorsal views using a digital camera (Sony DCR-TRV120E). An object of known size (1-m ruler) was kept in the field of view for scaling purposes. Lateral and dorsal images of the animals were analyzed using the public domain National Instiues of Health (NIH) image program (ver. 1.61; developed at the NIH and available on the Internet at http://rsb.info.nih.gov/nih-image/default.html).

Table 1: Summary morphometrics and bite forces for turtles

Species	Average ± SD		Minimum	Maximum
Chelydra serpentina ($N = 11$):				
Carapace length (mm)	197.30 ±	124.84	67.31	386.09
Carapace width (mm)	167.55 ±	103.54	57.47	344.00
Mass (g)	3,940.32 ±	5,805.46	19.42	16,650.00
Head length (mm)	65.45 ±	32.15	27.32	118.28
Head width (mm)	51.26 ±	30.76	18.96	101.16
Head height (mm)	34.80 ±	19.11	14.39	65.76
Lower jaw length (mm)	46.80 ±	24.64	17.99	95.18
Bite force (N)	208.98 ±	226.10	9.39	656.81
Staurotypus sp. ($N = 12$):				
Carapace length (mm)	134.78 ±	86.20	40.43	360.00
Carapace width (mm)	87.51 ±	40.86	33.17	175.90
Mass (g)	636.09 ±	1,029.40	10.08	3,775.00
Head length (mm)	52.40 ±	30.26	14.08	106.27
Head width (mm)	34.19 ±	17.49	12.68	74.70
Head height (mm)	25.34 ±	12.24	10.02	52.09
Lower jaw length (mm)	33.13 ±	17.45	11.23	74.20
Bite force (N)	167.25 ±	144.20	15.99	491.21
Trachemys scripta ($N = 32$):				
Carapace length (mm)	89.62 ±	53.88	28.92	245.00
Carapace width (mm)	74.94 ±	37.56	28.37	178.56
Mass (g)	241.04 ±	416.27	5.46	2,132.00
Head length (mm)	25.20 ±	11.50	11.66	52.08
Head width (mm)	16.47 ±	6.98	8.54	38.04
Head height (mm)	13.07 ±	5.22	7.21	27.60
Lower jaw length (mm)	17.78 ±	8.42	8.74	46.62
Bite force (N)	14.83 ±	19.01	1.02	104.14

Analyses

To examine intraspecific scaling in bite performance, we selected two species of turtles for which a full size range from hatchling to adults was available (*Trachemys scripta* and *C. serpentina*). Additionally, we pooled the data for two species of *Staurotypus* (*Staurotypus triporcatus* and *Staurotypus salvini*) to obtain a full size range. Given their close phylogenetic position and similarity in overall size, shape, and diet (Pritchard 1979), we considered this approach valid. For all species (turtles and lizards), morphological and performance variables were logarithmically transformed ($\log_{10}$) before analyses. Scaling was examined using reduced major axis regressions given the potential for measurement error on both X and Y variables. For the scaling analysis, we considered deviations from predicted slopes significant if the predicted slopes fell outside of the 95% confidence intervals of the observed slope. In reporting the results of our regression analyses, we follow Schmidt-Nielsen (1984) and use the terms "isometry" and "geometric similarity" interchangeably. Allometry is used when slopes are deviating from the predictions of geometric similarity. When discussing the

scaling of forces, isometry refers to a slope of two relative to linear dimensions, based on the prediction that force scales proportional to the physiological cross-sectional area of a muscle.

To investigate which elements of morphology were the strongest determinants of bite force, we performed a stepwise multiple regression analysis with bite force as the dependent variable and the morphological traits as independent variables. Next, bite force was regressed against the major morphological determinant of bite force to examine scaling relationships further.

Quantitative analyses of diet were possible for *A. garmani* only because the sample size for *A. equestris* was too small. All prey recovered from the stomachs of *A. garmani* were determined to order, measured (length, width, and mass), and classified as soft, of intermediate hardness, or hard on the basis of published and unpublished prey hardness data (see also Verwaijen et al. 2002). Next, the average prey length was calculated for each individual, and an average prey hardness was calculated on the basis of the following regression equations (for soft,

Table 2: Summary morphometrics and bite forces for lizards

Species	Average ± SD	Minimum	Maximum
Anolis equestris (N = 13):			
Snout-vent length (mm)	116.03 ± 41.96	60.11	166.42
Mass (g)	43.89 ± 39.95	3.50	120.00
Head length (mm)	35.81 ± 12.27	19.42	50.98
Head width (mm)	20.48 ± 7.73	10.56	31.11
Head height (mm)	15.99 ± 5.81	9.03	24.01
Lower jaw length (mm)	36.05 ± 13.06	18.76	52.82
Jaw outlever	33.39 ± 11.96	17.65	49.01
Opening inlever	2.65 ± 1.14	1.11	4.42
Closing inlever	5.76 ± 2.76	2.67	9.62
Bite force (N)	37.09 ± 39.97	3.96	112.91
Anolis garmani (N = 39):			
Snout-vent length (mm)	84.05 ± 22.62	26.52	117.66
Mass (g)	16.71 ± 11.52	.42	38.00
Head length (mm)	23.92 ± 6.27	8.99	33.65
Head width (mm)	13.38 ± 3.70	5.85	19.94
Head height (mm)	10.58 ± 3.07	4.38	15.72
Lower jaw length (mm)	25.22 ± 6.60	8.90	35.52
Jaw outlever	22.82 ± 6.24	8.00	32.38
Opening inlever	2.16 ± .67	.82	3.22
Closing inlever	4.26 ± 1.53	.89	6.85
Bite force (N)	11.05 ± 8.90	.70	32.79

intermediate, and hard, respectively) relating prey length to hardness:

$$\log_{10}[\text{prey hardness (N)}] = 0.997 \times \log_{10}[\text{prey length (mm)}] - 1.379,$$

$$\log_{10}[\text{prey hardness (N)}] = 1.780 \times \log_{10}[\text{prey length (mm)}] - 1.942,$$

$$\log_{10}[\text{prey hardness (N)}] = 1.582 \times \log_{10}[\text{prey length (mm)}] - 1.365.$$

These regressions are based on regressions of prey length to prey hardness for previously published data for a wide array of invertebrate prey (see Herrel et al. 1999a, 1999b, 2001b; Aguirre et al. 2003). The individual averages for prey size and hardness were $\log_{10}$ transformed before further analyses. To investigate which aspects of an animal's morphology or bite force determined prey size, a stepwise multiple regression analysis was run with prey length as the dependent variable and all morphological and performance traits as independent variables. Next, a similar analysis was performed using average prey hardness as a dependent variable. All analyses were performed using SPSS (ver. 11.5).

Results

Our data spanned at least two orders of magnitude in body mass for the turtles and almost two orders of magnitude in the two species of lizards examined (see Tables 1, 2). Regression of head measures and bite force against carapace length or snout-vent length revealed highly significant and positive correlations (Tables 3, 4; Figs. 1, 2). In *Chelydra serpentina*, carapace width, head width, body mass, and bite force scaled as expected for geometrically similar systems relative to carapace length (slopes not significantly different from 1, 3, or 2, respectively). All other head dimensions scaled with a slope slightly lower than but significantly different from 1 (Table 3). For *Staurotypus* individuals, body mass, head length, and bite force scaled with isometry, and all other measures showed slight negative allometry (Table 3). For *Trachemys scripta*, all body and head dimensions showed significant negative allometries against carapace length. Bite force scaled with negative allometry as well (Table 3). In the *Anolis* lizards, most traits scaled as expected for geometrically growing systems (Table 4). Notable exceptions are head length scaling with significant negative allometry in both species and the jaw closing inlever and bite force both scaling with significant positive allometry (Table 4). Body mass in *Anolis garmani* and the opening inlever in *Anolis equestris* also scale with significant positive allometry.

Stepwise multiple regression models retained head length ($R^2 = 0.98$; $P < 0.01$), head height ($R^2 = 0.98$; $P < 0.01$), and carapace length ($R^2 = 0.91$; $P < 0.01$) as the only predictors of bite force for *Chelydra*, *Staurotypus*, and *Trachemys*, respectively. When excluding body dimensions, a significant model was retained for *Trachemys*, with head width as the only pre-

Table 3: Regressions of morphometric data and bite force against carapace length for turtles

	R^2	Intercept	Slope	Confidence Limits
Chelydra serpentina:				
Carapace width	.99	−.01	.97	.88–1.07
Mass	.95	−4.29	3.28	2.59–3.96
Head length	.98	.01	**.79**	.72–.87
Head width	.99	−.42	.93	.85–1.01
Head height	.99	−.39	**.84**	.80–.89
Lower jaw length	.96	−.22	**.83**	.74–.93
Bite force	.95	−2.94	2.23	1.78–2.68
Staurotypus sp.:				
Carapace width	.99	.22	**.81**	.74–.88
Mass	.99	−3.46	2.82	2.53–3.12
Head length	.87	−.56	1.07	.84–1.30
Head width	.99	−.23	**.83**	.77–.89
Head height	.99	−.27	**.79**	.74–.84
Lower jaw length	.99	−.30	**.86**	.78–.95
Bite force	.96	−1.56	1.75	1.47–2.03
Trachemys scripta:				
Carapace width	.99	.26	**.83**	.82–.85
Mass	.99	−3.38	**2.79**	2.75–2.83
Head length	.95	−.05	**.75**	.70–.79
Head width	.98	−.05	**.66**	.60–.71
Head height	.98	−.10	**.63**	.60–.66
Lower jaw length	.95	−.13	**.71**	.65–.77
Bite force	.91	−2.30	**1.73**	1.53–1.93
Scaling of bite force to head dimensions:				
C. serpentina:				
Head length[a]	.98	−2.98	**2.82**	2.50–3.14
Head width	.95	−1.94	2.40	1.95–2.85
Head height	.94	−1.92	**2.64**	2.13–3.15
Staurotypus sp.:				
Head length	.88	−.64	**1.63**	1.40–1.87
Head width	.98	−1.08	2.10	1.82–2.38
Head height[a]	.98	−.96	1.94	2.01–2.48
T. scripta:				
Head length	.85	−2.19	**2.31**	2.02–2.96
Head width[a]	.91	−2.17	**2.63**	2.35–2.91
Head height	.89	−2.02	**2.73**	2.31–3.15

Note. Reduced major axis regression equations of carapace length against morphometric and performance variables. Bold variables have slopes deviating significantly from predictions of geometric similarity. All regressions are based on $\log_{10}$-transformed data.

[a] Best predictor of bite force based on stepwise multiple regression analyses with bite force as the dependent variable and all morphological traits as independent variables. Note that expected slopes are 1 for linear dimensions, 2 for forces, and 3 for masses when regressed against a linear dimension such as carapace length.

dictor ($R^2 = 0.91$; $P < 0.01$). Bite force scaled with significant positive allometry in *Chelydra* when regressed against head length (Table 3). Similarly, bite force scaled with significant positive allometry in *Trachemys* when regressed against head width (Table 3). For *Staurotypus*, however, variation in bite force is fully explained by changes in head height during growth (Table 3; Fig. 3A). For the *Anolis* lizards, stepwise multiple regressions retained a significant model with head height ($R^2 = 0.96$; $P < 0.01$) and head width ($R^2 = 0.94$; $P < 0.01$) for *A. equestris* and *A. garmani*, respectively (Table 4). Regressions

Table 4: Regressions of morphometric data and bite force against snout-vent length for lizards

	r	Intercept	Slope	Confidence Limits
Anolis equestris:				
Mass	.98	−4.88	3.09	2.84–3.34
Head length	.99	−.40	**.95**	.91–.98
Head width	.98	−.83	1.04	.91–1.17
Head height	.98	−.82	.98	.90–1.07
Lower jaw length	.99	−.51	1.00	.98–1.02
Jaw outlever	.99	−.51	.99	.95–1.02
Opening inlever	.95	−2.08	**1.21**	1.05–1.36
Closing inlever	.94	−1.98	**1.32**	1.11–1.53
Bite force	.94	−5.59	**3.37**	2.93–3.80
Anolis garmani:				
Mass	.99	−4.93	**3.15**	3.01–3.29
Head length	.98	−.38	**.91**	.86–.96
Head width	.95	−.64	.92	.77–1.06
Head height	.94	−.84	.97	.81–1.12
Lower jaw length	.96	−.37	.92	.83–1.00
Jaw outlever	.91	−.48	.95	.89–1.02
Opening inlever	.81	−1.77	1.09	.86–1.32
Closing inlever	.90	−1.96	**1.34**	1.19–1.49
Bite force	.86	−4.14	**2.65**	2.23–3.07
Scaling of bite force to head dimensions:				
A. equestris:				
Head length	.93	−4.17	**3.56**	3.10–4.02
Head width	.94	−2.89	**3.24**	2.74–3.75
Head height[a]	.96	−2.76	**3.43**	2.98–3.87
A. garmani:				
Head length	.88	−3.05	**2.90**	2.60–3.20
Head width[a]	.90	−2.30	**2.89**	2.57–3.20
Head height	.88	−1.85	**2.74**	2.49–3.00

Note. Reduced major axis regression equations of snout-vent length against morphometric and performance variables. Bold variables have slopes deviating significantly from predictions of geometric similarity. All regressions are based on $\log_{10}$-transformed data.

[a] Best predictor of bite force based on stepwise multiple regression analyses with bite force as the dependent variable and all morphological traits as independent variables. Note that expected slopes are 1 for linear dimensions, 2 for forces, and 3 for masses when regressed against a linear dimension such as snout-vent length.

of bite force against head dimensions still showed significant positive allometry (Fig. 3B).

Dietary analyses showed that *A. garmani* eats a variety of invertebrates and fruits. *Anolis equestris* consumed vertebrates in addition to invertebrates and fruits (Table 5; see also Bracht 1976; Dalrymple 1980). Stepwise multiple regression analyses (*A. garmani* only) with prey length as the dependent variable retained a significant model with the jaw outlever as the only predictor ($R^2 = 0.17$; $P = 0.03$; see Fig. 4). A stepwise multiple regression analysis with prey hardness as the dependent variable, however, retained a significant model with bite force as the only predictor ($R^2 = 0.16$; $P = 0.04$; Fig. 5).

Discussion

Ontogenetic Changes in Morphology and Performance

In this study, we examine how changes in size affect the performance of the feeding system in lizards and turtles. More specifically, we examine how head dimensions and bite force are affected by changes in overall size. Surprisingly, our intraspecific analyses for turtles indicated that nearly all head measures scaled with negative allometry to carapace length with the exception of head length in *Staurotypus* (scaling isometrically with carapace length). Given that ectothermic vertebrates typically grow nearly geometrically (O'Reilly et al. 1993; Richard
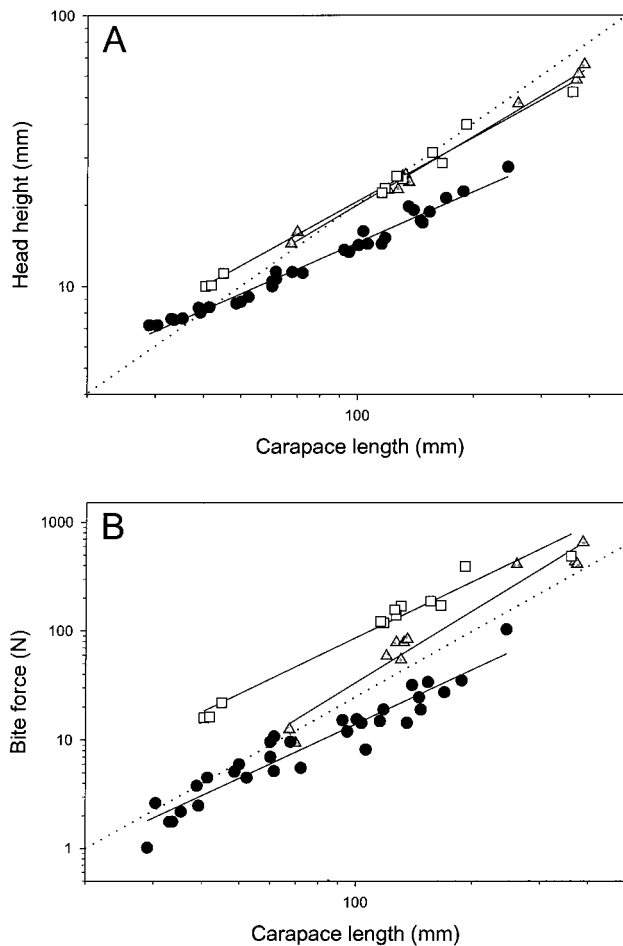
An obvious explanation for the difference in scaling of bite force versus body size when comparing lizards and turtles is that differential scaling of head size to body size occurs in lizards and turtles, respectively. While the majority of head dimensions scale with strong and significant negative allometry to body size in turtles, head dimensions generally scale isometrically relative to overall size in lizards. Thus, when examining scaling of performance traits, overall body size might not always be the relevant independent variable. Which aspects of head size or shape are good indicators of bite force in the animals examined here? Whereas for *Chelydra* head length is the main predictor of bite force, in *Staurotypus* only head height had any explanatory power. In *Trachemys*, overall body size was the main predictor of bite force throughout ontogeny. Growth pat-
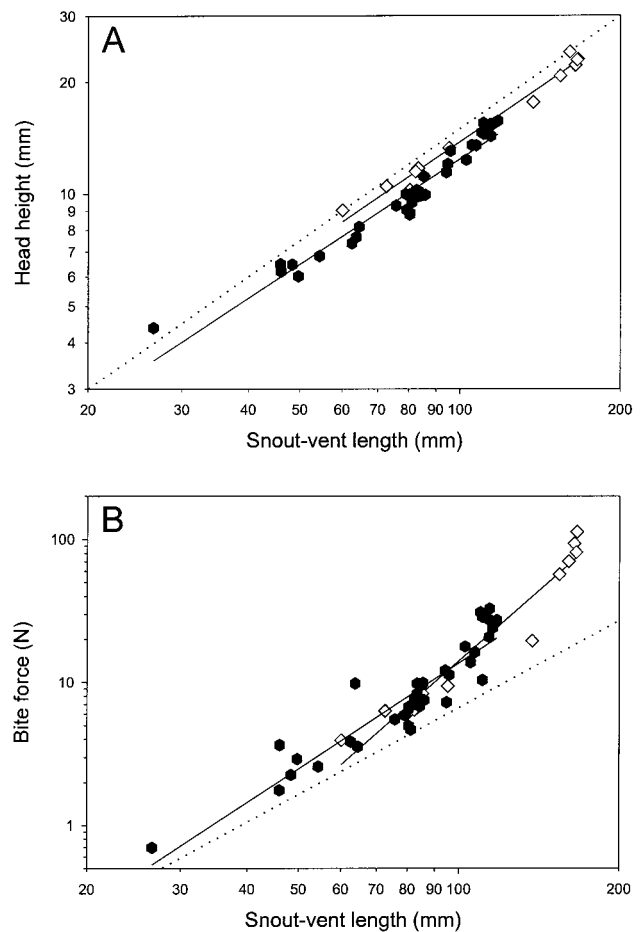

Figure 1. *A*, Scaling of head height on carapace length in the three species of turtles examined in this study. Head height scales with significant negative allometry in all species. *B*, Scaling of bite force on carapace length. Bite force scales isometrically in both *Staurotypus* sp. and *Chelydra serpentina* but scales with significant negative allometry in *Trachemys scripta*. Note that both plots are expressed on a log-log scale. The dotted line indicates the predicted slope according to geometric similarity. See Table 3 for the regression equations. *Filled circles = T. scripta, open squares = Staurotypus* sp., *gray triangles = C. serpentina.*

and Wainwright 1995; Robinson and Motta 2002) and that muscle force is proportional to the physiological cross-sectional area of the muscle, we predicted that bite force should increase to length to the second power (Hill 1950). The data gathered here indicate that in two out of three species of turtles, bite force did indeed increase to the second power relative to carapace length as predicted. For the other species (*Trachemys*), bite force scaled with slight negative allometry (note, however, that head measures scaled negatively allometrically in this species as well). In accordance with previously published data (Herrel et al. 1999*a*; Meyers et al. 2002), bite force scaled with strong and significant positive allometry to body size in the lizards examined (see also Table 4).

Figure 2. *A*, Scaling of head height on snout-vent length in the two species of *Anolis* lizards examined in this study. Head height scales isometrically in both species. *B*, Scaling of bite force on carapace length. Bite force scales with significant positive allometry in both species. Note that both plots are expressed on a log-log scale. The dotted line indicates the predicted slope according to geometric similarity. See Table 4 for the regression equations. *Filled hexagons = Anolis garmani, open diamonds = Anolis equestris.*
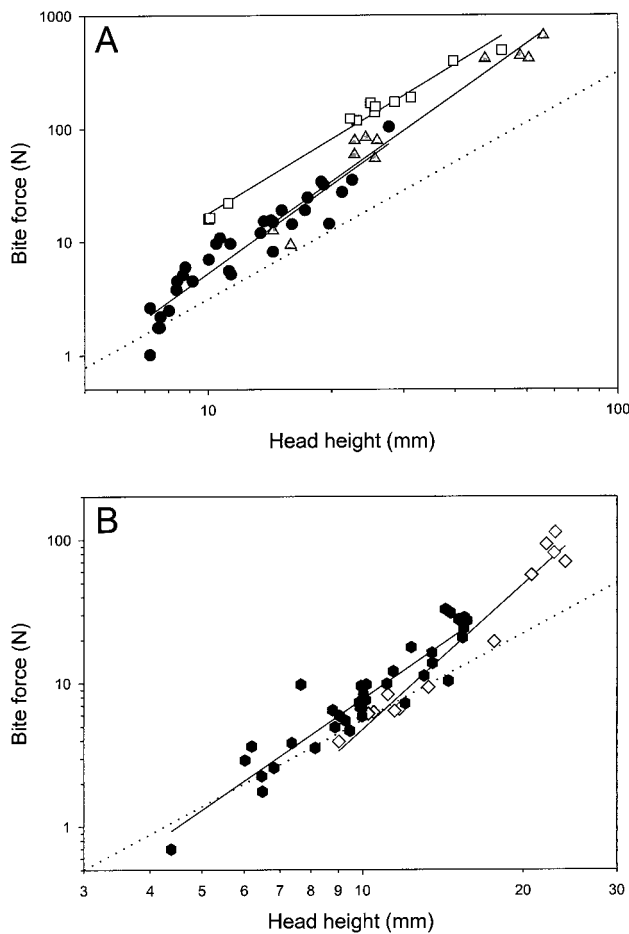
Figure 3. *A*, Scaling of bite force against head height in the three turtle species. Note that both *Trachemys scripta* and *Chelydra serpentina* show significant positive allometry. Turtles of the genus *Staurotypus* display isometry of bite force against head height. *B*, Scaling of bite force against head height in *Anolis equestris* and *Anolis garmani*. Both species show significant positive allometry of bite force against head height. The dotted line indicates the predicted slope according to geometric similarity. See Tables 3 and 4 for regression equations. Note that both plots are expressed on a log-log scale. Symbols as in figures 1 and 2.

terns thus seem to be different for different species of turtles and may be correlated with the trophic ecology and food availability of the species (Dalrymple 1977; Lindeman 2000). Similarly, for the two species of lizards examined here, distinctly different aspects of head shape (head height for *Anolis equestris* and head width for *Anolis garmani*) appear to be major predictors of bite force throughout ontogeny. Whereas head width likely reflects the larger absolute size of the jaw adductors (positioned at the side of the head), head width likely reflects a more favorable position of the jaw adductors (more perpendicular to the lower jaw), allowing them to generate larger closing moments (see also Herrel et al. 1999*a*, 2001*a*, 2001*b*).

Surprisingly, however, changes in head dimensions during

ontogeny cannot explain the observed changes in bite force in both lizards and turtles. In both groups, bite force increases with significant positive allometry with respect to head dimensions (Tables 3, 4). This suggests significant changes in the size, geometry (e.g., the degree of pennation), or physiology of the jaw adductor muscles throughout ontogeny in these species. Whereas in the lizards examined here the observed increase in bite force might also be partially explained by the positively allometric scaling of the inlever for jaw closing (Table 4), this clearly cannot explain the entire change in bite force observed. Further studies quantifying muscle masses, muscle architecture, and muscle physiology throughout ontogeny would be especially insightful in understanding how these animals increase their bite forces disproportionately as they grow.

Ecological Correlates of Ontogenetic Changes in Bite Performance

Why do the animals examined here show a disproportionate increase in bite force as they grow? Our analyses of diet in *A. garmani* may shed some light on this issue. Not only do our data demonstrate a significant increase in prey size as lizards get bigger, but larger lizards also eat harder prey (Fig. 4). Moreover, our data suggest that whereas overall prey size is tightly correlated with the jaw outlever, prey hardness is correlated with lizard bite force, thus suggesting that lizards with larger jaw outlevers (i.e., reflecting a larger gape) eat bigger prey and lizards with stronger bite forces eat harder prey. Although these trends are suggestive of a tight correlation between the morphology and performance of the feeding system and the ecology of the animals examined, they do not allow us to assess the nature of the scaling relationships between bite force and prey hardness. Nevertheless, our data do clearly demonstrate that the larger and harder prey accessible to adults are likely excluded from the diet in small lizards (either because of the increased costs associated with handling larger prey or because of prey hardness being directly limiting), while larger lizards still eat soft and small prey items. Because the cost of chasing and capturing small, evasive prey gets disproportionately high for larger animals (e.g., Ballinger et al. 1977; Hoyle and Keast 1987; Paulissen 1987), they should select larger prey whenever possible. The fact that arthropods tend to get harder with increasing size (Herrel et al. 2001*b*; Aguirre et al. 2003) might explain why larger animals show disproportionately larger bite forces. Moreover, higher bite forces may also result in decreased handling times (Pough et al. 1997; Verwaijen et al. 2002), making larger or harder prey especially profitable for larger animals. Unfortunately, our sample for *A. equestris* was too small to determine whether the trends observed for *A. garmani* are generally applicable for large species of *Anolis* lizards. Clearly, more quantitative data on prey size and hardness are needed to test the generality of our findings.

Although no quantitative dietary data were obtained for the

Table 5: Summary of stomach content analysis for *Anolis equestris* and *Anolis garmani*

Food Type	No. Stomachs		No. Items	
	Absolute	%	Absolute	%
Anolis equestris ($N = 5$):				
Leaves or other plant material	1	20	3	7.5
Fruits (*Ficus*)	1	20	1	2.5
Hymenoptera:				
Vespidae	1	20	19	47.5
Formicidae	2	40	3	7.5
Orthoptera	2	40	2	5
Zygoptera	1	20	2	5
Diptera	1	20	1	2.5
Isoptera	1	20	2	5
Araneae	1	20	1	2.5
Vertebrata (*Anolis distichus*)	2	40	2	5
Shed skin	4	80	4	10
Anolis garmani ($N = 31$):				
Leaves or other plant material	4	12.9	4	2.23
Seeds	2	6.45	2	1.12
Fruits (*Ficus*)	2	6.45	2	1.12
Fruits	6	19.35	6	3.35
Hymenoptera:				
Vespidae	9	32.25	10	5.59
Formicidae	15	48.39	100	55.87
Hemiptera	1	6.45	2	1.12
Orthoptera	1	3.23	1	.56
Coleoptera	6	19.35	7	3.91
Lepidoptera:				
Adult	2	6.45	3	1.68
Larval	2	6.45	2	1.12
Zygoptera	2	6.45	2	1.12
Diptera	8	25.81	12	6.70
Isoptera	1	3.23	1	.56
Blattoidea	1	3.23	1	.56
Crustacea (Isopoda)	1	3.23	1	.56
Unidentified arthropods	4	12.9	4	2.23
Araneae	4	12.9	4	2.23
Mollusca	1	3.23	1	.56
Shed skin	1	3.23	1	.56
Parasites:				
Nematoda	3	6.45	7	3.91
Cestoda	1	3.23	2	1.12
Rocks	3	6.45	4	2.23

turtles examined here, previously published data on growth patterns and ontogenetic changes in diet in *Trachemys scripta* (Cagle 1950; Clark and Gibbons 1969) might help explain some of the patterns we observed. These studies show that *T. scripta* switches from a predominantly insectivorous to an almost exclusively herbivorous diet when it reaches a plastron length of about 60 mm. A closer inspection of the bite force data gathered for this species suggests a very interesting pattern of rapid increases in bite force up to this size (slope = 2.4; $R^2 = 0.78$), after which the slope of bite force against carapace length changes dramatically to a significantly lower slope (slope = 1.54; $R^2 = 0.80$; see Fig. 5). Because plants are extremely tough and require fairly large bite forces to be processed (Herrel et al. 1999b), this pattern suggests that selection has led to a rapid
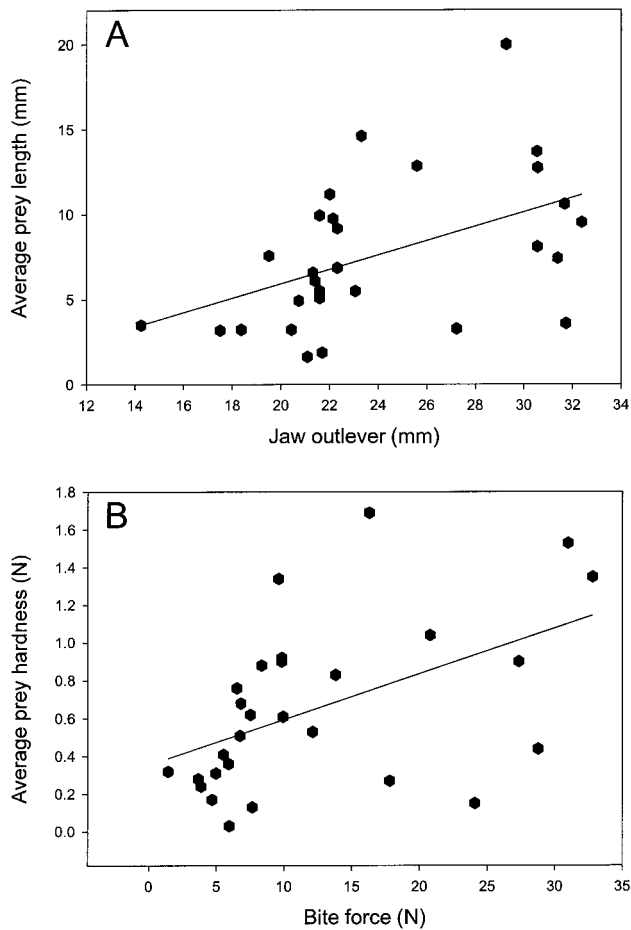
Figure 4. *A*, Scaling of prey size against the jaw outlever length in *Anolis garmani*. Lizards with longer jaw outlevers, and thus larger gapes, eat larger prey on average. *B*, Average prey hardness is significantly correlated to lizard bite as demonstrated by multiple regression analyses (see "Results"), suggesting that increased bite forces allow larger *A. garmani* to eat not only larger but also harder prey.

increase in bite force up to a threshold where plant matter can be reduced efficiently, at which point the animals can switch to a very abundant food source for which competition is likely low (Clark and Gibbons 1969).

Bite force appears to be ecologically relevant for turtles, supporting previous results based on comparative data on bite force that suggested that animals that generally consume hard prey exhibit higher bite forces (Herrel et al. 2002). Interestingly, whereas the evolutionary changes in bite force across species were closely associated with evolutionary changes in head height, our ontogenetic data suggest that head height is not the only predictor of bite force. Whereas the two turtles in our data set that specialize on large and/or hard prey (*Chelydra* and *Staurotypus*) bite much harder than the omnivorous *Trachemys* (Fig. 1), this cannot fully be explained by differences in head size. Whereas the difference between *Trachemys* and *Chelydra*

is indeed a pure consequence of the latter having a bigger head, *Staurotypus* has a different design of the jaw system and consequently bites much harder than the other two species for a given head size (Fig. 3). The extreme nature of the diet of kinosternid turtles such as *Staurotypus*, which include mostly hard prey (including other turtles in the case of *Staurotypus*; see Herrel et al. 2002), has presumably led to this disproportionate performance. How these animals achieve such high levels of performance is currently unknown and should be investigated by means of detailed examinations of the morphology and physiology of the jaw adductors and the design of the jaw system.

Although we find fairly strong and direct correlations among morphology, performance, and diet in both lizards and turtles, our data do not appear to support the notion that younger life-history stages compensate for their lower absolute levels of performance, in contrast to previously published data for locomotor systems (e.g., see Carrier 1996; Trillmich et al. 2003). Only in *Trachemys* does there appear to be a rapid increase in performance up to a level where plants can be included in the diet. All other species examined illustrate a pattern in which larger individuals have disproportionately higher levels of bite force. This raises the question, Why don't juveniles exhibit increased performance levels? One possibility is that they are limited by developmental or design constraints limiting the amount of jaw adductor muscle that can be developed during early ontogeny or the design of the head and the jaw system. Alternatively, there might be no direct selection for increased performance in juveniles (see Meyers et al. 2002). Although data to support either hypothesis are scarce, studies examining prey availability do generally show a disproportionately large
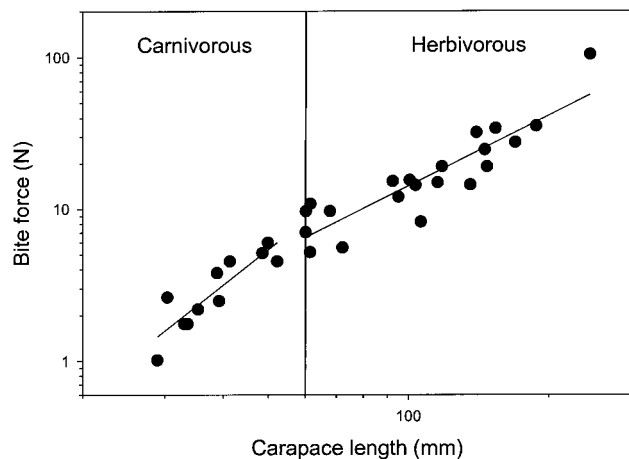

Figure 5. Ontogenetic scaling of bite force against carapace length in *Trachemys scripta*. At a size of about 60 mm carapace length, animals switch from a carnivorous to an almost fully herbivorous diet (Clark and Gibbons 1969). Note that until that size, a rapid increase in bite force takes place. After the switch to herbivory, the slope of bite force against carapace length decreases considerably.

percentage of small prey available in the environment (Paulissen 1987; J. Meyers, personal observation). Large prey, on the other hand, tend to be rare. Given that prey hardness increases rapidly with prey size for some prey types (Aguirre et al. 2003), selection for improved bite performance is likely greater for adults rather than juveniles. Further studies examining ontogenetic change in performance, diet, and prey availability are needed to test the validity of this hypothesis.

Acknowledgments

Literature Cited

Aguirre L.F., A. Herrel, R. Van Damme, and E. Matthysen. 2003. The implications of food hardness for diet in bats. Funct Ecol 17:201–212.

Andrews R.M., F.H. Pough, A. Collazo, and A. de Queiroz. 1987. The ecological cost of morphological specialization: feeding by a fossorial lizard. Oecologia 73:139–145.

Ballinger R.E., M. Newlin, and S. Newlin. 1977. Age-specific shift in the diet of the crevice spiny lizard *Sceloporus poinsetti* in southwestern New Mexico. Am Midl Nat 97:482–484.

Bracht V. 1976. Habits and food of *Anolis equestris* in Florida. Copeia 1976:187–189.

Cagle F.R. 1950. The life history of the slider turtle, *Pseudemys scripta troosti*. Ecol Monogr 20:31–54.

Carrier D.R. 1996. Ontogenetic limits on locomotor performance. Physiol Zool 69:467–488.

Clark D.B. and J.W. Gibbons. 1969. Dietary shift in the turtle *Pseudemys scripta* (Schoepff) from youth to maturity. Copeia 1969:82–105.

Dalrymple G.H. 1977. Intraspecific variation in the cranial feeding mechanism of turtles of the genus *Trionyx*. J Herpetol 11:255–285.

———. 1980. Comments on the density and diet of a giant anole, *Anolis equestris*. J Herpetol 14:412–415.

Emerson S.B. 1978. Allometry and jumping in frogs: helping the twain to meet. Evolution 32:551–564.

Garland T., Jr. 1984. Physiological correlates of locomotory performance in a lizard: an allometric approach. Am J Physiol 247:806–815.

Herrel A., E. De Grauw, and J.A. Lemos-Espinal. 2001a. Head shape and bite performance in xenosaurid lizards. J Exp Zool 290:101–107.

Herrel A., J.C. O'Reilly, and A.M. Richmond. 2002. Evolution of bite performance in turtles. J Evol Biol 15:1083–1094.

Herrel A., L. Spithoven, R. Van Damme, and F. De Vree. 1999a. Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. Funct Ecol 13:289–297.

Herrel A., R. Van Damme, B. Vanhooydonck, and F. De Vree. 2001b. The implications of bite performance for diet in two species of lacertid lizards. Can J Zool 79:662–670.

Herrel A., M. Verstappen, and F. De Vree. 1999b. Modulatory complexity of the feeding repertoire in scincid lizards. J Comp Physiol A 184:501–518.

Hill A.V. 1950. The dimensions of animals and muscular dynamics. Sci Prog 38:209–230.

Hjelm J., G.H. van de Weerd, and F.A. Sibbing. 2003. Functional link between foraging performance, functional morphology and diet shift in roach (*Rutilus rutilus*). Can J Fish Aquat Sci 60:700–709.

Hoyle J.A. and A. Keast. 1987. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). Can J Zool 65:1972–1977.

Irschick D.J. 2000. Effects of behaviour and ontogeny on the locomotor performance of a West Indian lizard, *Anolis lineatopus*. Funct Ecol 14:438–444.

Irschick D.J., T.E. Macrini, S. Koruba, and J. Forman. 2000. Ontogenetic differences in morphology, habitat use, behavior and sprinting capacity in two west Indian *Anolis* lizards. J Herpetol 34:444–451.

Jayne B.C. and A.F. Bennett. 1990. Scaling of speed and endurance in garter snakes: a comparison of cross-sectional and longitudinal allometries. J Zool (Lond) 220:257–277.

Katz S.L. and J.M. Gosline. 1993. Ontogenetic scaling of jump performance in the African desert locust (*Schistocerca gregaria*). J Exp Biol 177:81–111.

La Barbera M. 1989. Analyzing body size as a factor in ecology and evolution. Annu Rev Ecol Syst 20:97–117.

Lindeman P.V. 2000. Evolution of the relative width of the head and alveolar surfaces in map turtles (Testudines: Emydidae: *Graptemys*). Biol J Linn Soc 69:549–576.

Meyers J.J., A. Herrel, and J. Birch. 2002. Scaling of morphology, bite force and feeding kinematics in an iguanian and a scleroglossan lizard. Pp. 47–62 in P. Aerts, K. D'Aout, A. Herrel, and R. Van Damme, eds. Topics in Functional and Ecological Vertebrate Morphology. Shaker, Maastricht.

Nauen J.C. and R.E. Shadwick. 1999. The scaling of acceleratory aquatic locomotion: body size and tail-flip performance of the California spiny lobster *Panulirus interruptus*. J Exp Biol 202:3181–3193.

O'Reilly J.C., S.L. Lindstedt, and K.C. Nishikawa. 1993. The scaling of feeding kinematics in toads (Anura: Bufonidae). Am Zool 33:147A.

Osenberg C.W. and G.G. Mittelbach. 1989. Effects of body size on the predator-prey interaction between pumpkinseed sunfish and gastropods. Ecol Monogr 59:405–432.

Paulissen M.A. 1987. Optimal foraging and intraspecific diet differences in the lizard *Cnemidophorus sexlineatus*. Oecologia 71:439–446.

Pough H.F., M.R. Preest, and M.H. Fusari. 1997. Prey-handling and the evolutionary ecology of sand swimming lizards (*Lerista*: Scincidae). Oecologia 112:351–361.

Preest M.R. 1991. Energetic costs of prey ingestion in a scincid lizard, *Scincella lateralis*. J Comp Physiol B 161:327–332.

———. 1994. Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: why do females take smaller prey than males? J Herpetol 28:292–298.

Pritchard P.C.H. 1979. Encyclopedia of Turtles. TFH, Neptune, NJ.

Quillin K.J. 2000. Ontogenetic scaling of burrowing forces in the earthworm *Lumbricus terrestris*. J Exp Biol 203:2757–2770.

Richard B.A. and P.C. Wainwright. 1995. Scaling of the feeding mechanism of large mouth bass (*Micropterus salmoides*): kinematics of prey capture. J Exp Biol 198:419–433.

Robinson M.P. and P.J. Motta. 2002. Patterns of growth and the effects of scale on the feeding kinematics of the nurse shark (*Ginglymostoma cirratum*). J Zool (Lond) 256:449–462.

Schmidt-Nielsen K. 1984. Scaling: Why Is Animal Size So Important? Cambridge University Press, Cambridge.

Toro E., A. Herrel, B. Vanhooydonck, and D.J. Irschick. 2003. A biomechanical analysis of intra- and interspecific scaling of jumping and morphology in Caribbean *Anolis* lizards. J Exp Biol 206:2641–2652.

Trillmich F., M. Bieneck, E. Geissler, and H.-J. Bischof. 2003. Ontogeny of running performance in the wild guinea pig (*Cavia aperea*). Mamm Biol 68:214–223.

Verwaijen D., R. Van Damme, and A. Herrel. 2002. Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. Funct Ecol 16:842–850.

Wilson R.S., C.E. Franklin, and R.S. James. 2000. Allometric scaling relationships of jumping performance in the striped marsh frog *Limnodynastes peronii*. J Exp Biol 203:1937–1946.