Scaling of Morphology, Bite Force and Feeding Kinematics in an Iguanian and a Scleroglossan Lizard

Jay J. Meyers [1*], Anthony Herrel [2] & James Birch [3]

[1] Department of Biological Sciences, Northern Arizona University, USA
[2] Department of Biology, University of Antwerp, Belgium
[3] Department of Integrative Biology, University of California, Berkeley, USA

Abstract

Although scaling studies have become increasingly common in the literature, relatively few studies have examined the feeding behavior in terrestrial vertebrates. This is an important point as most of the previous studies examining the scaling of feeding events were performed on aquatic organisms and, in general, have failed to support the geometric similarity model of A.V. Hill.   In contrast, the results of terrestrial feeding in toads, do seem to support the Hill model. Therefore, we decided to examine the effects of size on the morphology and functioning of the feeding system in two species of lizards. To investigate ontogenetic changes in the feeding system we measured changes in skull shape, in-vivo bite forces and feeding kinematics. Scaling relationships of the head morphology generally support the Hill model, yet some variables show a tendency to being relatively smaller in adult animals. Interestingly, the in-vivo bite forces of both species scaled significantly higher than predicted, with larger animals generating much higher bite forces than juveniles. Most of the timing, displacement and velocity variables measured were significantly different than would be predicted by the Hill model and tended to support an alternative model proposed by Richard and Wainwright. Although these scaling models provide testable hypotheses, it seems that in general the predictive power across taxa (and behaviors) may be limited.

Key words: scaling, feeding, lizard, bite force.

Introduction

That animal size affects the movements and physiology of animals has long been known, and many studies have addressed scaling patterns of physiological and kinesiological variables in a wide range of animals (e.g. Hill, 1950; Schmidt-Nielsen, 1984). Despite its interest from a functional point of view, the study of scaling also has important implications for ecological and behavioral studies of animals (e.g. Carrier, 1996; Herrel et al., 1999a; Hernandez, 2000). As animals grow, they will have to face the mechanical consequences of getting bigger. As length increases, surface area (and muscle force) increases to the second power, but masses will increase even more rapidly (third power). As this may constrain movements and ultimately the performance of the animal, behavioral changes, for example in foraging mode or escape behavior, will be required if animals are to occupy similar niches throughout ontogeny (Durtsche, 2000; Irschick, 2000). Alternatively, the utilization of ecological niches may change as animals get bigger (Durtsche et al. 1997; Nilsson and Bronmark, 2000) or animals may show allometric growth patterns allowing them to occupy the

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same niche throughout ontogeny without needing radical changes in behaviour. Given that size effects influence performance throughout ontogeny and that selective pressures are typically high on juvenile stages, studies of scaling effects on locomotion and feeding are ecologically relevant (Carrier 1996; Hernandez, 2000). Scaling studies are also important for comparative studies where the animals of interest may vary widely in size (Richard and Wainwright, 1995; Wainwright and Shaw, 1999). Additionally, size is an important variable for community-level analysis as biological communities are often complex and composed of animals of different sizes (Losos, 1994). Given that size affects the performance of organisms, it in itself may play an important role in the partitioning of resources within the community (Magnusson and Da Silva, 1993; Aguirre et al., 2002). Understanding how size affects the performance of organisms is thus crucial in our understanding of animal behavior.

Whereas the effects of size often can be taken into account statistically (e.g. using analyses of covariance), sometimes this is not possible due to low sample sizes, non-overlapping size ranges or differences in the scaling relationships between groups (e.g. slopes are not parallel). To overcome this, different theoretical models have been established to predict effects of size on movement. In his ground-breaking paper, Hill (1950) predicted how muscle forces and movements would scale with body size based on the premise that animals grow isometrically and that maximal muscle shortening velocity does not change with size. In an alternative model, Richard and Wainwright (1995) predicted the effects of size on movements based on the premise that muscle shortening velocity increases with animal size. Empirical data on the effects of size on the kinesiology of locomotor and feeding systems in a variety of organisms have been used to test these models (Katz and Gosline, 1993; Nauen and Shadwick, 1999, 2001; Quillin, 1999, 2000; Wilson et al. 2000). Often, deviations from both the Hill model and the Richard and Wainwright model have been observed and no general consensus exists concerning the generality of these models. One of the few studies to support the Hill (1950) model looked at the scaling of feeding movements in terrestrial organisms (O'Reilly et al., 1993). In contrast, most studies on the scaling of feeding behavior in aquatic organisms do not support the Hill model (Richard and Wainwright, 1995; Wainwright and Shaw, 1999; Hernandez, 2000). Studies of scaling effects on feeding behavior are especially interesting as this is an ecologically relevant behavior. Moreover, feeding systems involve fairly simple lever systems which allows for specific predictions of the effect of size on movements (Hernandez, 2000).

As many ectotherms grow up to three orders of magnitude or more in the span of their life, these are ideal study subjects for scaling studies. Given the ecological relevance, but lack of data for scaling effects in terrestrial systems, we studied morphological and functional scaling of the jaw system in lizards. As ectotherms typically grow geometrically throughout their life, we predicted that bite forces and feeding movements would scale according to the Hill (1950) model.

Materials and Methods

To address the effects of size on morphology, bite force and feeding kinematics in lizards, we examined the feeding system in two groups of lizards: the spiny lizards (*Sceloporus*) and the whiptail lizards (*Cnemidophorus*). For each group, two species were used, which allowed us to substantially increase the size range within each group. The *Sceloporus undulatus* used for the morphometric and kinematic part of this study ranged in size from 0.45 - 7.33 g (22.34 - 65.20 mm snout-vent length, SVL; N = 19), the *Sceloporus magister* ranged from 8.30 g to 72.45g (56.5 - 119.70 mm SVL; N = 6). The *Cnemidophorus tigris* used for the morphometric analysis ranged in size from 1.15 - 21.61 g (SVL: 38.88 - 95.34 mm; N=7) and the *Cnemidophorus burti* from 34.85 - 39.75 g (SVL: 109.96-111.94 mm; N= 2). A series of external morphometric data (e.g. head width including the jaw muscle) and bite

forces were gathered for a size series of the same species (*Sceloporus undulatus*, body mass: 3.60 - 11.27 g; SVL: 46.98 - 72.70 mm; N = 38; *Sceloporus magister*, body mass: 8.35 - 72.45 g; SVL: 56.5 - 113.22 mm; N = 6; *Cnemidophorus tigris*, body mass: 6.97 - 23.11 g; SVL: 65.49 - 92.55 mm; N = 10; *Cnemidophorus burti*, body mass: 40.39 g; SVL: 108.75 mm; N = 1). For *Cnemidophorus*, these same animals were used for the kinematic part of the study.

The *Sceloporus* used for the morphological component of this study were skinned and the bones and cartilage stained following a modified procedure of Taylor (1967). The *Cnemidophorus* used for the morphometric analysis were skinned and partially dissected to expose the bones on the skull and lower jaw. This allowed us to measure 9 linear distances on the skull: (1) skull length; (2) maximum skull width; (3) interorbital width; (4) postorbital width; (5) maximum skull height; (6) lower jaw opening in-lever; (7) lower jaw closing in-lever; (8) lower jaw opening out-lever; (9) lower jaw length (Fig. 1). Additionally, we measured the maximal anatomical gape distance for the cleared and stained *Sceloporus* specimens.
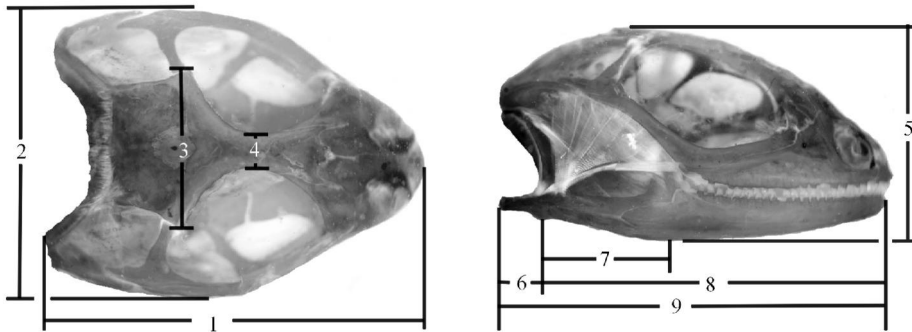
Figure 1. *Dorsal (left) and lateral (right) skull measurements taken on* Sceloporus undulatus, S. magister, Cnemidophorus tigris *and* C. burti. *The skull shown is an adult cleared and stained* S. undulatus. *1) head length; 2) head width; 3) postorbital width; 4) interorbital width; 5) head height; 6) lower jaw opening in-lever; 7) lower jaw closing in-lever; 8) lower jaw opening out-lever; 9) total jaw length.*

In vivo bite forces were measured using a Kistler force transducer (type 9203, Kistler Inc., Switzerland) mounted on a purpose-built holder (see Herrel et al., 1999a) and connected to a Kistler (model 5995) charge amplifier. Although animals were usually eager to bite, when needed they were stimulated to bite by gently tapping the sides of their jaws. Trials were separated by at least 30 minutes, during which animals were allowed to thermoregulate. This ensured that animals were biting at their preferred body temperature. For each individual, the maximum bite force measured out of 5 trials was considered to be its maximal bite capacity. After the performance trials, the following external morphometric data were determined (Tables 1, 2): head length (from the tip of the upper jaw to the back of the skull); head width at the widest point of the head; head height at the highest point of the head; and lower jaw length (from the tip of the lower jaw to the back of the retroarticular process). Note that all these measurements include soft tissues and are thus not a priori expected to scale similarly to the skull measurements (see higher).

Feeding behavior was recorded at 120 frames s-1 using a Display Integration Technologies model DIT 660 high-speed video camera with synchronized strobe. Lizards were allowed to feed unrestrained on a flat stage and prey (termites and crickets) were presented through an opening in the floor of the stage. Prey diameter was approximately 30-50% of maximum gape and increased concomitantly with lizard size. We videotaped feeding sequences from 16 of the 25 *Sceloporus* (13 *S. undulatus*, 3 *S. magister*). Three to four feeding sequences were recorded from each individual with

a total of 39 sequences for *S. undulatus*, 9 for *S. magister*. We digitized each feeding sequence using Peak Performance Technologies 2D motion analysis software (v. 5.2.1). We only digitized feeding sequences in which the lizard was perpendicular (±10°) to the plane of the camera in lateral view. For *Cnemidophorus* we were able to record and analyse only 22 sequences for six individual *C. tigris*. We computed 27 kinematic variables from the XY-coordinates obtained by digitizing seven points on the animal and prey, and one non-moving reference point. Points were located at the (1) tip of the upper jaw; (2) anterior corner of the eye; (3) jaw joint; (4) tip of the lower jaw; (5) tip of the tongue; (6) hyoid, and (7) prey item (see Fig. 1 in Meyers and Nishikawa, 2000). As the time lizards needed between mouth opening and the beginning of the lunge was highly variable, we calculated both the time until prey contact and the time until maximum tongue protraction relative to the onset of the lunge. All other timing variables were computed relative to the onset of mouth opening (t = 0) and consisted of seven durations: the time to maximum gape, measured as the time from the onset of mouth opening until maximum gape distance; the time to maximum lunge distance, measured as the time from the onset of first forward movement of the animal until its maximum displacement in the X coordinate; the duration of mouth opening, calculated as the time from the onset of mouth opening until the time of maximum gape; the duration of tongue protraction, calculated as the time from first forward movement of the tongue until the time of maximum tongue protraction; the duration of tongue retraction, calculated as the time from the onset of tongue retraction until the completion of tongue retraction; the duration of mouth closing, calculated as the time from the onset of mouth closing until the completion of mouth closing; the duration of the recovery phase, calculated as the time from the maximum displacement of the upper jaw tip, until the completion of mouth closing.

Other variables were calculated directly from the digitized points: maximum gape angle, defined as the maximum angle between the upper jaw tip, jaw joint, and lower jaw tip; maximal gape distance, calculated as the maximal linear distance between upper and lower jaw tips; the maximal head flexion angle, calculated as the maximum angle between the cranium and the horizontal; the tongue reach, calculated as the maximum distance from the lower jaw tip to the tongue tip; the prey distance, calculated as the rectilinear distance from the upper jaw tip to the prey at the onset of the lunge. In addition, we calculated maximum velocities and accelerations of the lunge, of tongue protraction, of tongue retraction, of the lower jaw displacement during opening, of the lower jaw displacement during closing, of angular mouth opening and of angular mouth closing. For all timing and duration events we used minimum values; for velocities, accelerations, distances and angles we used the maximum values observed for each individual. Kinematic variables were calculated using Peak Performance Technologies 2D motion analysis software. Velocities and accelerations were calculated using Peak Motus software (v 6.1). Scaled displacement data were filtered using a quintic spline routine. Next, velocities and accelerations were calculated using the smoothed data. All variables were log10 transformed before regression analysis.

Reduced major axis regressions were used to examine the scaling of our variables with animal size. Correlation coefficients, intercepts, slopes and confidence intervals on the slopes of the reduced major axis regressions were calculated using the equations in Sokal and Rohlf (1995). All variables were regressed against snout-vent length to make our results directly comparable to Richard and Wainwright's (1995) study of bass feeding. Moreover, as snout-vent length is less prone to short term fluctuations than is body mass (depending on feeding condition etc.), we considered it to be a more robust indicator of overall animal size.

Results

Morphology

Both models being tested here assume that morphological characters should increase with animal size as geometrical systems (slope of 1 for linear measures, 2 for surface areas and, 3 for volumes and masses). Slopes that are significantly greater than predicted indicate positive allometry and those slopes that are lower than predicted indicated negative allometry. Since we have two morphometric data sets for both species, one describing the skull and one describing the external anatomy, we will use the following abbreviations to help clarify which data sets are being compared: *Sceloporus* external morphometrics (Sext), *Sceloporus* skull morphometrics (Sint), *Cnemidophorus* external morphometrics (Cext) and *Cnemidophorus* skull morphometrics (Cint).

For Sext, head length and head height were the only characters that scaled isometrically. In Sint head height, interorbital width and opening in-lever scaled isometrically. All other characters showed negative allometric growth except for anatomical gape (see Table 1). In general, juvenile sceloporines have relatively larger heads than adults. In Cext, all structures exhibited isometric growth except for head length.

Morphological measurements	R	Intercept	Slope	Confidence Intervals		Hill Model	Growth
Morphometric data of *Sceloporus* (bite force)							
Body mass	0.99	-4.35	2.96	2.84	3.09	3	I
Head length	0.96	-0.46	0.89	0.81	0.97	1	A
Head width	0.95	-0.73	0.99	0.90	1.09	1	I
Head height	0.93	-1.15	1.13	1.00	1.26	1	I
Lower jaw length	0.97	-0.44	0.90	0.84	.97	1	A
Bite force	0.60	-7.73	4.60	4.00	5.19	2	A
Morphometric data of *Sceloporus* (morphometric data)							
Body mass	0.99	-4.35	2.96	2.84	3.09	3	I
Head length	0.99	-0.16	0.74	0.71	0.77	1	A
Head width	0.99	-0.50	0.90	0.87	0.94	1	A
Head height	0.98	-0.73	0.94	0.86	1.02	1	I
Interorbital width	0.94	-1.52	0.97	0.82	1.12	1	I
Postorbital width	0.98	-0.76	0.90	0.82	0.98	1	A
Anatomical gape	0.96	-2.13	2.07	1.81	2.34	1	A
Lower jaw length	0.99	-0.34	0.84	0.81	0.88	1	A
Open in lever	0.96	-1.37	0.95	0.84	1.07	1	I
Close in lever	0.95	-0.73	0.87	0.75	0.99	1	A
Out lever	0.99	-0.39	0.83	0.80	0.87	1	A

Critical values determining significant deviation from zero = 0.304 for *Sceloporus* bite force data set and 0.404 for *Sceloporus* morphometric data. Different individuals of *Sceloporus* were used for the bite force (*S. undulatus* N = 38 and *S. magister* N = 6) and morphometric analysis (*S. undulatus* N = 19 and *S. magister* N = 6). We denote whether these data support the isometric growth model of Hill (I) or show allometric growth (A)

Table 1. *Scaling relationships for morphological and in vivo bite force measurements from* Sceloporus undulatus *and* Sceloporus magister. *Statistics represent log₁₀-transformed morphological variables regressed against the log₁₀ of snout-vent length.*

In Cint, head height, interorbital width and open in-lever showed isometric growth while all other characters showed negative allometry (Table 2). Again, as in the sceloporines, juvenile *Cnemidophorus* tend to be relatively more robust than the adults. Interestingly, in both Sext and Cext head width scaled isometrically, however for Sint and Cint, head width increased negatively allometrically.

When we compare similar data sets for both species (Sext to Cext and Sint to Cint) similar growth trajectories are observed. The Sext and Cext data differ in only in head length, which grows isometrically in *Cnemidophorus* and with negative allometry in *Sceloporus*. All the characters of the Sint and Cint data sets show the same trend, with head height, interorbital width and open in-lever exhibiting isometry and all other characters negative allometry. In both species (and data sets) we found several characters scaling with negative allometry, thus failing to support the geometric similarity model of Hill.

Bite Force

In-vivo bite forces measurements in both species of lizards scaled with much higher slopes than predicted (Tables 1 and 2). Force was predicted to scale in proportion to the cross-sectional area of the muscle, and should thus scale with a slope of 2. However, *Sceloporus* bite forces scaled with a significantly larger slope of 4.6 (Fig 4b). In *Cnemidophorus*, we also observed a significant deviation from the predicted slope of 2 (slope of 3.83, Fig 5b). Both species show significant positive allometry, with larger animals biting relatively harder for their size than juveniles.

Morphological measurements	R	Intercept	Slope	Confidence Intervals		Hill Model	Growth
Morphometric data of *Cnemidophorus* (bite force)							
Head length	0.99	-0.39	0.88	0.80	0.97	1	A
Head width	0.98	-0.97	1.05	0.91	1.20	1	I
Head height	0.96	-1.23	1.16	0.91	1.42	1	I
Lower jaw length	0.98	-0.46	0.94	0.80	1.08	1	I
Bite force	0.98	-6.44	3.83	3.25	4.42	2	A
Morphometric data of *Cnemidophorus* (morphometric data)							
Body mass	0.99	-4.35	2.96	2.84	3.09	3	I
Head length	0.99	-0.16	0.74	0.71	0.77	1	A
Head width	0.95	-0.50	0.90	0.87	0.94	1	A
Head height	0.97	-0.73	0.94	0.86	1.02	1	I
Interorbital width	0.96	-1.52	0.97	0.82	1.12	1	I
Postorbital width	0.97	-0.76	0.90	0.82	0.98	1	A
Lower jaw length	0.98	-0.34	0.84	0.81	0.88	1	A
Open in lever	0.93	-1.37	0.95	0.84	1.07	1	I
Close in lever	0.71	-0.73	0.87	0.75	0.99	1	A
Out lever	0.98	-0.39	0.83	0.80	0.87	1	A

Critical values determining significant deviation from zero = 0.602 for *Cnemidophorus* bite force animals, 0.666 for *Cnemidophorus* morphometric data. Different indivdiuals of *Cnemidophorus* were used for the bite force (*C. tigris* N = 10 and *C. burti* N = 1) and morphometric analysis (*C. tigris* N = 7 and *C. burti* N = 2). We denote whether these data support the isometric growth model of Hill (I) or allometric growth (A)

Table 2. *Scaling relationship for morphological and in vivo bite force measurements from* Cnemidophorus tigris *and* Cnemidophorus burti. *Statistics represent* log_{10}-*transformed morphological variables regressed against the* log_{10} *of snout-vent length.*
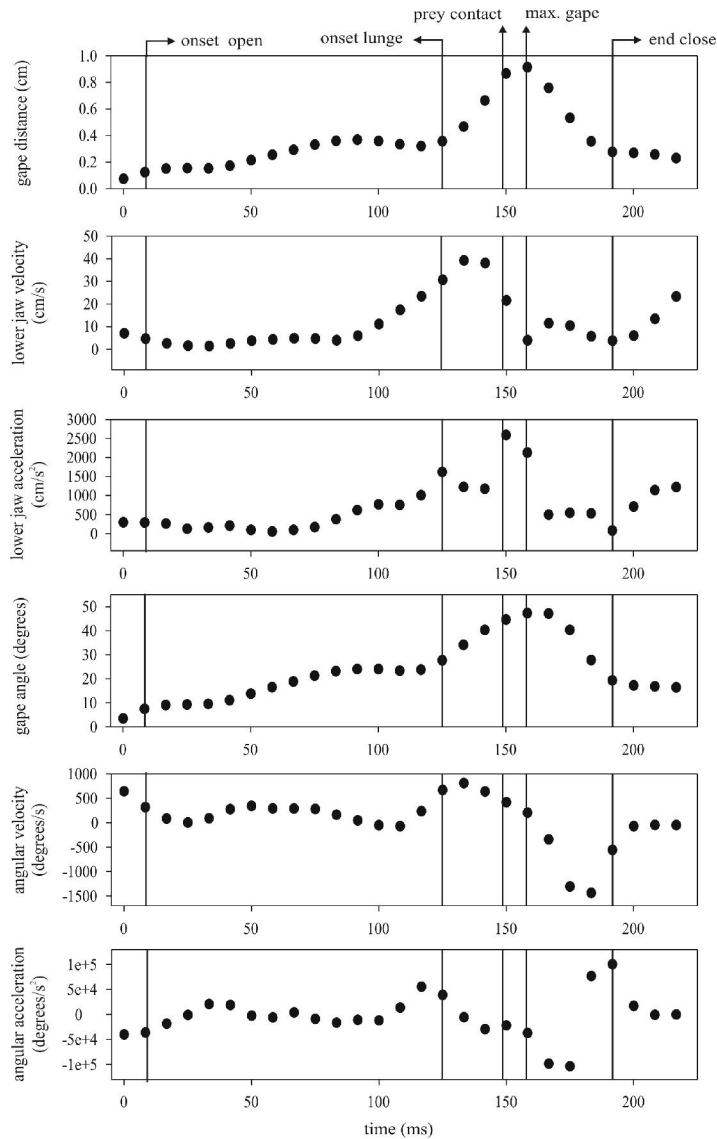
Kinematics

As our size range for feeding kinematics in *Cnemidophorus* was too small to determine scaling relationships, in the next sections only data for *Sceloporus* will be presented. In *Sceloporus*, a typical feeding sequence begins with the animal spotting the prey and orienting the head towards it. Often, the mouth opens slowly and the tongue is protracted slowly to the jaw margin (note that this stage is highly variable, Fig. 3a). Once the animal initiates prey capture, it rotates forward on the forelimbs, opens the jaws wider and protrudes the tongue faster. At prey contact, the jaws are opened maximally, and the tongue is retracted with adhering prey. Fast mouth closing occurs after maximum gape and ends when the jaws impact on the prey (Fig. 3a-f).
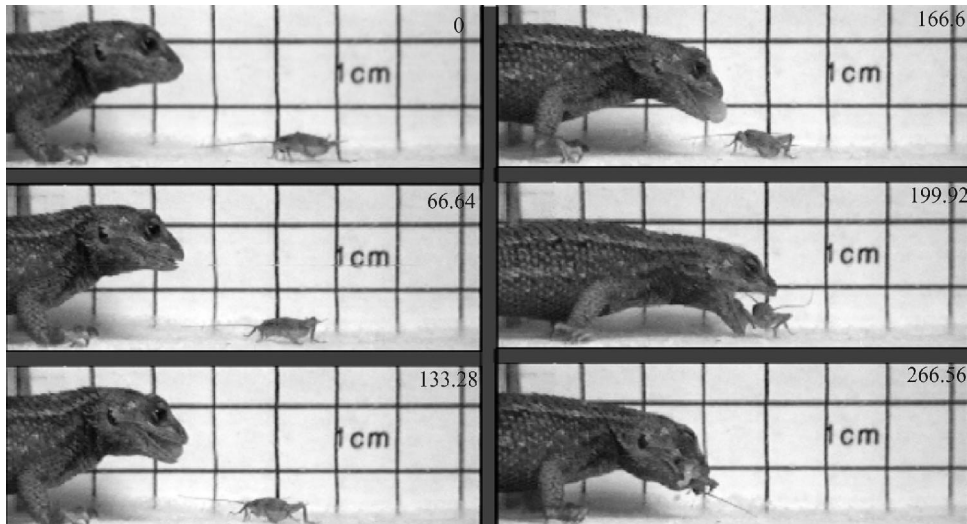
Figure 2. *Representative feeding sequence of a typical iguanian lizard. In* Sceloporus undulatus *(and iguanians in general) prey capture is always accompanied by simultaneous mouth opening and tongue protraction. The tongue contacts the prey, pulling it into the mouth and then the jaws close around the prey item. The slow mouth opening phase prior to onset of lunge can be highly variable, whereas movements after the onset of lunge are more "stereotyped". Time in milliseconds is given in the top right of each frame.*

Angular and linear displacements

Scaling effects were measured for two angular displacements: gape angle (Fig. 3d) and head angle (amount of ventro-flexion of the head relative to the horizon, note head position in fig. 2). Whereas gape angle exhibited no ontogenetic change in magnitude, head angle showed significant positive allometry. This is unexpected since the models assume that angular displacements do not change with increasing size. Linear excursions, such as gape (Fig. 3a) and prey distance also increased with positive allometry, while tongue reach increased isometrically (Table 3). Contrary to predictions, but in accordance with the morphometric data, larger animals open their mouths wider than juveniles. Although the results for the angular and linear displacements seem conflicting (e.g. angular displacements scaling differently), these may reflect behavioral rather than morphological differences (see discussion).

Figure 3. *Kinematic variables plotted against time during a normal prey capture event in* Sceloporus magister. *Vertical lines denote distinct kinematic events (onset of mouth opening, onset of lunge, prey contact, maximum gape and mouth closing) during the feeding cycle. The duration between mouth opening and onset of lunge is variable between trials and individuals, making some timing events rather variable (see text).*

Kinematic Variables	R	Intercept	Slope	Confidence Intervals		Hill Model	RW Model	Model Supported
Timing variables								
Duration mouth opening	-0.49	1.73	0.72	0.36	1.08	1	0	RW
Duration mouth closing	-0.03	1.11	0.49	0.21	0.76	1	0	RW
Duration tongue protraction	-0.13	1.29	0.81	0.35	1.27	1	0	RW
Duration tongue retraction	-0.03	0.03	4.28	1.83	6.74	1	0	RW
Time to maximum gape	-0.50	1.72	0.73	0.37	1.10	1	0	H
Time to maximum lunge distance	-0.38	1.70	0.75	0.35	1.15	1	0	RW
Time to prey contact	-0.45	1.60	0.82	0.40	1.24	1	0	RW
Time to maximum tongue protraction	-0.51	1.56	0.85	0.43	1.26	1	0	H
Displacements								
Maximum gape angle	0.49	1.41	0.44	0.22	0.66	0	0	H, RW
Maximum gape distance	0.96	-0.99	1.20	1.01	1.39	1	1	N
Maximum head angle	0.52	1.03	0.69	0.35	1.03	0	0	N
Maximum prey distance	0.85	-0.89	1.55	1.08	2.02	1	1	N
Maximum tongue reach	0.97	-1.27	1.08	0.93	1.22	1	1	H, RW
Velocities and Accelerations								
Maximum angular velocity of mouth opening	0.07	2.17	1.26	0.54	1.98	-1	0	RW
Maximum angular acceleration of mouth opening	-0.02	3.83	1.76	0.75	2.78	-1	0	RW
Maximum angular velocity of mouth closing	0.44	2.88	0.53	0.26	0.80	-1	0	RW
Maximum angular acceleration of mouth closing	0.15	4.28	1.60	0.69	2.50	-1	0	RW
Maximum mouth opening velocity	0.76	0.37	1.55	0.98	2.12	0	1	RW
Maximum mouth opening acceleration	0.58	2.03	1.83	0.98	2.67	-1	1	RW
Maximum mouth closing velocity	0.78	0.55	1.11	0.71	1.51	0	1	RW
Maximum mouth closing acceleration	0.50	1.79	2.10	1.06	3.14	-1	1	N
Maximum tongue protraction velocity	0.86	0.54	1.38	0.97	1.78	0	1	RW
Maximum tongue protraction acceleration	0.71	1.89	1.85	1.11	2.59	-1	1	N
Maximum tongue retraction velocity	0.69	0.48	1.33	0.78	1.89	0	1	RW
Maximum tongue retraction acceleration	0.85	2.20	1.81	1.26	2.37	-1	1	N
Maximum lunge velocity	0.80	0.44	1.46	0.96	1.97	0	1	RW
Maximum lunge acceleration	0.69	1.71	2.12	1.24	3.00	-1	1	N

Critical value determining significant deviation from zero = 0.4975. Values represent minima for timing variables and maxima for distances, angles, velocities and accelerations. We denote the model supported by this data as H = Hill model, RW = Richard and Wainwright Model or N = neither model supported.

Table 3. *Kinematic relationships for 27 kinematic variables measured from feeding sequences of* Sceloporus undulatus *(N = 13) and* Sceloporus magister *(N = 3). Statistics represent $\log_{10}$-transformed kinematic variables regressed against the $\log_{10}$ of snout-vent length.*

Timing Variables
Most of the timing events measured here showed no changes with animal size (slope not significantly different from 0, Table 3). These include duration of mouth opening, the duration of mouth closing, the duration of tongue protraction, of tongue retraction, the time to maximal lunge and the time to prey contact. These findings are in accordance with the Richard and Wainwright (1995) model, which predicted that timing events should not change with body size. However, some events such as time to maximum gape and time to maximum tongue protraction scaled isometrically (as predicted by Hill, 1950). This implies that as animals get bigger, the overall duration of mouth opening is similar, yet in larger animals it takes longer to reach maximal gape and to protrude the tongue maximally.

Velocities and Accelerations
Despite the relatively slow recording speed (120 frames/second), velocity and acceleration profiles were fairly clean (Fig. 3). As predicted by the Richard and Wainwright model (1995) angular velocities and accelerations did not scale with increasing animal length (Table 3; Fig. 4). However, all linear velocities and some accelerations (mouth opening acceleration) scaled with slopes not significantly different from one. The speed of the movements of jaws and tongue during the prey capture thus increase proportionally to body size. Interestingly, the linear accelerations scaled with slopes close to 2 (note however, that these were not significantly different from 1 due to the large variation in the data). Larger animals thus seem to generate larger accelerations of the jaws and tongue than were predicted by either model

Discussion

<u>Scaling analysis</u>
The goal of our study was to test the validity of two different models predicting effects of size on the morphology and function of the feeding system in lizards. Although the Hill (1950) and Richard and Wainwright (1995) models have been tested in the past (e.g. Wainwright and Shaw, 1999; Nauen and Shadwick 1999; Hernandez, 2000), intraspecific scaling data for terrestrial systems are rare (but see O'Reilly et al. 1993). Yet, as mentioned in the introduction, this type of data is crucial for the interpretation of comparative, community level and ontogenetic studies. One of the basic, yet often ignored, assumptions of both models is that the organism grows geometrically throughout ontogeny. If this basic assumption is not met, then deviations from the predicted slopes should not be unexpected (Hernandez, 2000). For the species studied here, some deviations from this basic assumption were indeed observed. Whereas external width, height, and lower jaw length typically grow as predicted, head length scales with negative allometry to body length in both species. This implies that as these lizards grow, their heads become relatively shorter, which may have important effects on the performance of the jaw system. More detailed measurements of the skulls of both species indicated further deviations from geometric similarity. Many of the linear skull measurements in *Sceloporus* showed significant negative allometries. Remarkably, the anatomical gape distance (i.e. the maximal linear distance the jaws can be opened) scaled with strong positive allometry (slope = 2). Whereas the negative allometries of the skulls remain hard to explain, the strong positive deviation of anatomical gape likely has a strong functional advantage (see below). The discrepancy between the scaling relationships of the external measurements and the actual skull measurements indicates that during ontogeny the bulk of the jaw muscle likely grows disproportionately (see also Birch, 1999). Unfortunately, no data are available on the scaling of jaw muscle mass in these animals.
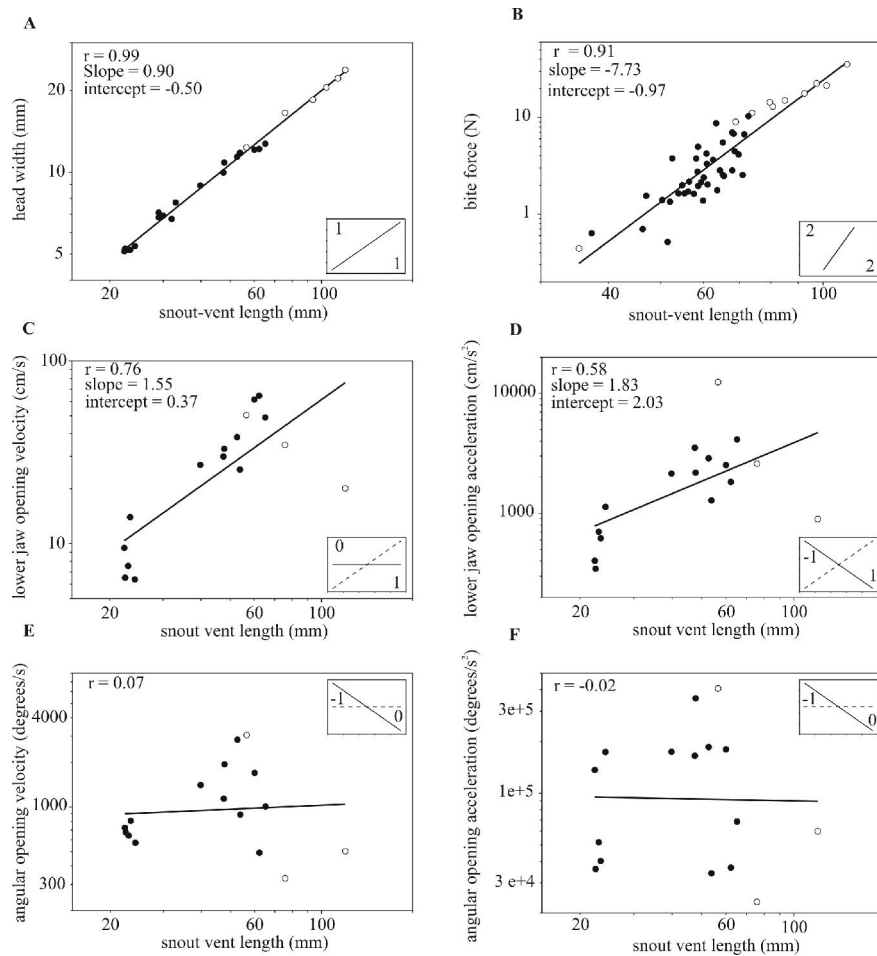
Figure 4. *Selected morphological and kinematic variables regressed against snout-vent length for* Sceloporus undulatus *and* Sceloporus magister. *Predicted slopes for each variable are presented in the right hand corner of each graph (Hill prediction numerically upper left (solid line), Richard and Wainwright prediction lower right (dashed line)).*

Bite force is a measure of the performance of the jaw apparatus that is directly relevant to the ecology of the animals. As forces are assumed to be proportional to the physiological cross sectional area of a muscle, the prediction from both the Hill (1950) and Richard and Wainwright (1995) models is that force increases with length squared. Our data for both species show substantial deviations from this prediction, as bite forces scale with a slope of nearly 5 and 4 for *Sceloporus* and *Cnemidophorus*, respectively. Moreover, this difference cannot be explained by changes in lever arms as indicated by the morphometric data. Although skull length and the out lever scale with negative allometry (i.e. increasing bite force in larger animals), the in-lever of the jaw adductors scale isometrically. Whereas the forces during take-off in jumping frogs (Wilson et al. 2000) scale isometrically with size, data for forces generated during lobster escape responses (Nauen and Shadwick, 2001) and bite forces in another lizard species (Herrel et al., 1999a) also show strong positive allometries. Why do forces not scale as predicted by the models? Nauen and Shadwick

(2001) suggested that in the lobster, complex changes in muscle geometry or changes in the muscle physiology during ontogeny might lie at the basis of the observed scaling patterns. In the lizard jaw system, changes in geometry likely involve complex packing of the jaw muscle and increase in the pennation of the jaw adductors. The jaw adductors in adult lizards are characterized by highly pennate muscle and complex geometries (Gans and De Vree, 1985, 1987). However, the discrepancy between the scaling of head width (including bulging of the jaw muscles) and skull width indicates that the adductor muscles do grow disproportionately during ontogeny in both species. This disproportionate growth may at least partially explain the much higher forces in larger animals. Given the potential ecological and selective advantage for high bite forces in early ontogenetic stages (Carrier, 1996) these results are rather surprising. One possible functional explanation might be that force generation in juvenile lizards is constrained by their relatively weak skulls. The smallest individuals examined in both species showed largely unossified skulls, and poorly developed interdigitations between skeletal elements (see Fig. 1). If large forces were to be exerted by the jaws, the joint reaction forces, which are typically higher than the bite forces (Herrel et al., 1999a,b), might result in dislodging of the lower jaw or even failure of the jaw suspension. However, also ecological factors (i.e. prey availability) might lie at the basis of this unexpected result (see further).

Overall, the scaling the feeding system in *Sceloporus* tended to support the Richard and Wainwright (1995) model. However, duration and timing variables did not increase with lizard body length and the time to maximal gape and the duration of tongue protraction, scaled as assumed by the Hill model (slope not significantly different from 1). It should be noted though, that the latter variables are largely determined by the slow initial tongue protraction during prey capture, which can be extremely variable even within individuals. Unexpectedly, few of the predictions regarding the scaling of displacements and angles (note that predictions are the same for both models) were supported by our data. Both maximal prey distance at the onset of lunge and the maximal gape distance scaled with positive allometry (Table 3). Also maximum head angle scaled with positive allometry, indicating that larger animals start lunging with their heads at a greater angle than smaller animals. This is not totally unexpected and might be governed by behavioral differences rather than mechanical constraints. As larger animals are positioned higher above the substrate, the head will have to be bent down more to align the head and tongue with the prey.

Most of the results for the velocities and accelerations were again largely in accordance with the predictions of the Richard and Wainwright (1995) model. Angular velocities and accelerations remained constant as animals grow, and linear velocities increased proportionately to animal length. Preliminary data for *Cnemidophorus* show this pattern as well (Fig 5). Although not significant due to the low sample size, a plot of linear velocities on body length indicates that velocities do indeed increase with body length (Fig. 5). Thus our data for lizard feeding kinematics support the idea that speed increases with length. The assumption that linear velocities increase linearly to length seem logical as larger animals/muscles will have more sarcomeres in series, which will result in a greater shortening in the same time interval (i.e. increased velocity). The scaling of linear accelerations (slope = 2), on the other hand, strongly deviated from the predictions of either model (slopes of -1 and 1 for Hill, 1950 and Richard and Wainwright, 1995 models respectively). However if one adopts the reasoning put forward by Nauen and Shadwick (2001) and considers Newton's second law (force equals mass times acceleration) then accelerations can be predicted from the scaling of muscle forces. Indeed, given that our in vivo data indicate that for *Sceloporus* force scales as length to the fifth and mass as length cubed, then accelerations should be scaling with a slope of two. In *Sceloporus* accelerations scale with slopes varying between 1.79 and 2.12 indicating that this reasoning seems valid here too. Along this line, we would thus predict that in *Cnemidophorus*, where forces scale with a slope of 3, accelerations should scale proportionally to body length. Unfortunately our

small sample size, and size range for this species does not allow us to test the validity of this prediction.

In summary, we can say that although the scaling of the feeding system partially deviated from the basic assumption of geometric similarity, our results generally were in accordance with the Richard and Wainwright (1995) model. Noticeable deviations were the scaling of gape and prey distance, which both scaled with significant positive allometry. The most striking deviations, however, were the scaling of forces and accelerations. Although the scaling of accelerations can be predicted based on the experimentally determined relationship of force versus body length, this is in discrepancy with the scaling of velocities and durations. Given that our data largely supported the Richard and Wainwright model, the data for the scaling of the feeding system in toads seem unique in their support of the Hill (1950) model. As the scaling of forces was rather unexpected and varied considerably between species, our data seem to indicate that the scaling of forces (and potentially thus also of accelerations) does not occur according to a general model. Previous data for the scaling of forces indicated slopes of close to two (Wilson et al. 2000), between two and three (Nauen and Shadwick, 2001), close to three (Herrel et al. 1999a), close to four (*Cnemidophorus*, this study) and close to five (*Sceloporus*, this study). Scaling of forces with size is thus presumably more dependent on the intrinsic geometry of the system, potentially coupled to ontogenetic changes in muscle physiology. Clearly data on a wider range of taxa are essential to refine our models of scaling. Moreover, future studies examining the scaling of muscle contractile properties (force, velocity) and muscular recruitment will be essential in our understanding of scaling of kinesiological data.
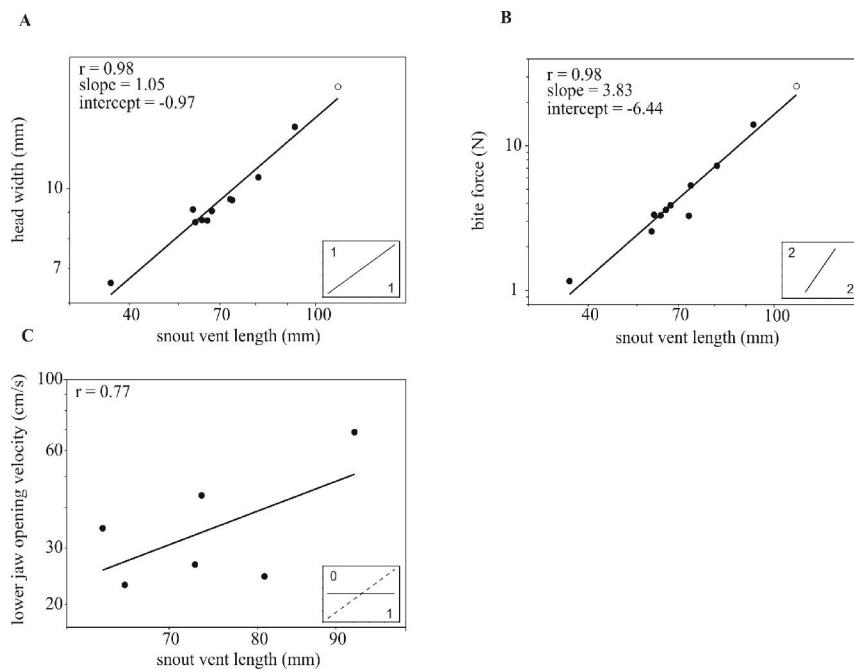
Figure 5. *Selected morphological variable, jaw velocity and bite force regressed against snout-vent length for* Cnemidophorus tigris *and* Cnemidophorus burti. *Predicted slopes for each variable are presented in the right hand corner of each graph (Hill prediction upper left, Richard and Wainwright prediction lower right).*

Ecological relevance

Because of the difference in scaling relationships between lengths, surface areas and volumes, growth may constrain the behavior of animals throughout ontogeny (Emerson and Bramble, 1993; Carrier, 1996; Svanback and Eklov, 2002). Unfortunately, this aspect of scaling analysis has received little attention in the past (but see Carrier, 1996; Herrel et al., 1999a), and data are typically restricted to morphological measurements. The scaling of ecologically relevant performance measurements is rare, but may lead to insights into ontogenetic niche shifts, or changes in behavior. Here we examined several functionally important measures of whole animal performance (anatomical gape distance, bite force and jaw velocity). Our data indicate that these characteristics scale in complex ways with animal size, such that larger lizards will be able to open and close their jaws faster, open their mouths disproportionately wider and bite disproportionately harder than juveniles. Given that prey hardness typically increases with prey size (Herrel et al. 1996, 1999b, 2001), and that larger and harder prey require longer handling times (Pough et al. 1997), harder and larger prey will become available to larger animals. Consequently, larger animals are predicted to exploit larger and harder prey (e.g. Sadzikowski and Wallace, 1976; Durtsche et al., 1997).

Published accounts of diet and prey size selection in Sceloporus indicate that adult sceloporines typically include more plant material and large arthropods into their diets (Simon, 1976; Ballinger et al. 1977). As plant material is tough and requires large forces to reduce or crop (Herrel et al., 1999b), higher bite forces would be beneficial. Similarly, studies on diet in *Cnemidophorus* indicate that adults select both larger and potentially harder prey (e.g. beetles, grasshoppers) (Hardy, 1962; Paulissen, 1987a, b). Moreover, Paulissen (1987a) demonstrated that handling times for the consumption of grasshoppers are significantly greater for juveniles compared to adults. Here too, large gapes and high bite forces are of ecological relevance.

Given that selection pressures are usually highest for the earlier life-stages (Carrier, 1996), we would have predicted disproportionately higher bite forces, gape distances and jaw speed for juveniles (i.e. exactly opposite from the results in this study). This would not only allow juveniles to exploit large and energetically rich prey, but would broaden the potential niche breadth of juveniles considerably. The absence of this expected pattern seems rather puzzling at first. However, when examining prey availability data in literature (Paulissen, 1987a) it becomes apparent that small prey are disproportionately abundant in the environment. Apparently, unlike adult lizards, juveniles are not constrained by the availability of prey in the appropriate size class. As it becomes energetically less profitable to catch small prey as lizards get bigger due to increased foraging costs (Ballinger et al., 1977; Paulissen, 1987a), big lizards will select large prey from the environment. However, as these large prey are relatively scarce, larger lizards are likely to benefit from any strategy that maximizes niche breadth. High bite forces (allowing lizards to eat hard prey and plant material), large gapes (facilitating the passage of large prey to the oesophagus) and fast jaws (enabling lizards to capture elusive prey) likely allow lizards to catch a wide variety of prey and may help overcome the constraints on the abundance of large prey.

Acknowledgements

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