

Built to Bite: Feeding Kinematics, Bite Forces, and Head Shape of a Specialized Durophagous Lizard, *Dracaena Guianensis* (Teiidae)



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ABSTRACT

Most lizards feed on a variety of food items that may differ dramatically in their physical and behavioral characteristics. Several lizard families are known to feed upon hard-shelled prey (durophagy). Yet, specializations toward true molluscivory have been documented for only a few species. As snails are hard and brittle food items, it has been suggested that a specialized cranial morphology, high bite forces, and an adapted feeding strategy are important for such lizards. Here we compare head and skull morphology, bite forces, and feeding kinematics of a snail-crushing teiid lizard (*Dracaena guianensis*) with those in a closely related omnivorous species (*Tupinambis merianae*). Our data show that juvenile *D. guianensis* differ from *T. merianae* in having bigger heads and greater bite forces. Adults, however, do not differ in bite force. A comparison of feeding kinematics in adult *Dracaena* and *Tupinambis* revealed that *Dracaena* typically use more transport cycles, yet are more agile in manipulating snails. During transport, the tongue plays an important role in manipulating and expelling shell fragments before swallowing. Although *Dracaena* is slow, these animals are very effective in crushing and processing hard-shelled prey. *J. Exp. Zool.* 317A:371–381, 2012. © 2012 Wiley Periodicals, Inc.

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Food acquisition is very important for the daily survival and fitness of individuals and has been studied in a wide variety of animals (for vertebrates, see Schwenk, 2000 for an overview). Morphological and behavioral specializations related to prey manipulation may provide some species access to food resources that may be unavailable or unmanageable for closely related species (e.g., Aguirre et al., 2003). Indeed, there is a strong precedent for predicting a relationship between an organism's functional capacities and its potential resource use (Grant, '85; Fisher Huckins, '97; Herrel et al., 2002a, b).

In lizards, true feeding specialists are rare. Indeed, most lizards feed on a wide variety of food items that often differ in their physical and behavioral characteristics (Greene, '82;

Schaeerlaeken et al., 2007, 2008; Metzger, 2009; Montuelle et al., 2009). If prey properties impose specific mechanical demands on the feeding system of the predator, then these will likely

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influence the efficiency of prey capture and transport (Meyers and Herrel, 2005). Consequently, most lizards are capable of adjusting their feeding behavior in accordance to prey characteristics that may allow them to optimize food processing (e.g., Bels and Baltus, '88; Herrel et al., '96; Herrel and De Vree, '99; Urbani and Bels, '99; Schwenk, 2000; Ross et al., 2007; Schaerlaeken et al., 2008).

Several lizard families are known to feed upon hard-shelled prey (durophagy). Yet, for only a few species true molluscivory has been documented. As snails are hard and brittle food items, it has been suggested that lizards that eat snails should display a specialized cranial morphology with more massive cranial muscles (Dalrymple, '79; Rieppel and Labhardt, '79) and greater bite forces. Among lizards, *Chamaeleolis* lizards (Herrel and Holanova, 2008), some amphisbaenids (*Amphisbaena ridleyi*; Pregill, '84), and Nile monitors (*Varanus niloticus*; Lonnberg, '03; Rieppel and Labhardt, '79) are known to include a considerable amount of hard-shelled prey such as snails in their diet. Although relatively little is known about these animals, enlarged posterior teeth are often observed. Such blunt and rounded teeth are assumed to be important to avoid tooth breakage and to increase the contact area with the food. However, only in a few species do the blunt molariform teeth occur in juveniles (e.g., *Dracaena guianensis*; some species of the genus *Tiliqua*; Estes and Williams, '84) suggesting that in these species, juveniles may already be specialized for molluscivory.

Feeding on hard or tough prey puts demands on increased bite force. Such an increase in bite force can be achieved in multiple ways. For example, one way is to increase overall body size, or head size relative to body size. Additionally, an increase in the mass, changes in the architecture of the jaw adductors (i.e., more pennate muscles with shorter fibers), or changes in the mechanics of the lever system (i.e., increasing jaw closing in lever relative to the jaw out lever) could improve bite performance (Herrel et al., 2002a, b, 2007; Herrel and Holanova, 2008). Consequently, lizards feeding on hard prey are expected to show one or several of these specializations.

In the present study, we compare a true molluscivorous lizard, *D. guianensis*, with a closely related but omnivorous lizard, *Tupinambis merianae*. Whereas lizards from the Teiinae subfamily are typically insectivorous (Presch, '74; Vitt et al., '95, '97, 2000), Tupinambinae are characterized by a derived diet that encompasses the inclusion of vertebrates and fruits into the diet in some species (Dessem, '85; Castro et al., '91; Mercolli and Yanosky, '94; Kiefer and Sazima, 2002; Martins, 2006; see Fig. 1). Yet, only in *Dracaena* is a true durophagous diet observed. It has been suggested that the inclusion of hard-shelled prey in this species is associated with its semiaquatic lifestyle (Vanzolini, '61; Duellman, 2005). Although both *Tupinambis* and *Dracaena* are characterized by well-developed jaw adductors with complex tendinous systems, *Dracaena* stands out in having more developed pseudotemporalis profundus muscle and

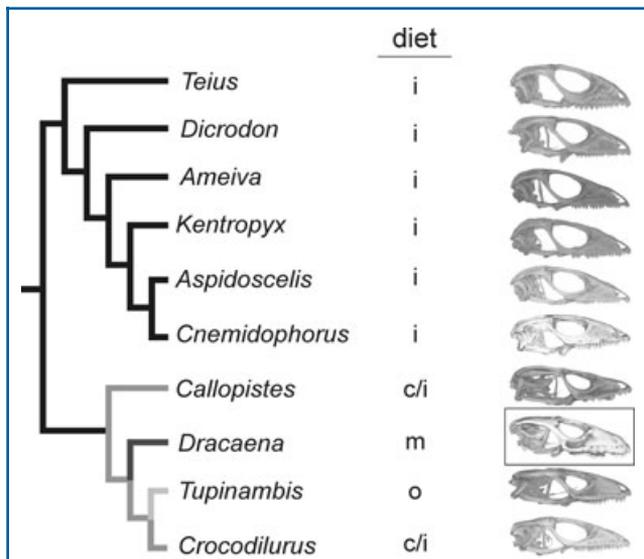


Figure 1. Phylogenetic relationships of teiid lizards (Giugliano et al., 2007). To the right, the predominant diet within the genus is indicated. Branch colors indicate the results of an ancestral state reconstruction of diet using parsimony implemented in Mesquite. Whereas the basal diet is clearly insectivory (i), the Tupinambinae are characterized by the evolution of derived diets including carnivory (c) and omnivory (o). Yet, dedicated molluscivory (m) has originated only once within the group. To the right lateral views of the skulls of representative species of each clade are shown to illustrate how divergent *Dracaena* is compared to other teiids. The skull of *Dracaena* is highlighted in the box. Images derived from CT scans.

a greater degree of muscle pennation (Dalrymple, '79; Rieppel, '80). This suggests that *Dracaena* may have greater bite forces allowing them to crush hard food items such as snails and crustaceans (Vanzolini, '61; Duellman, 2005).

Here, we focus on differences in cranial size and shape that could improve bite force in both juveniles and adults. Given their specialized teeth, we expect juvenile *D. guianensis* to have relatively bigger heads and changes in the mechanics of the lever system allowing them to generate high bite forces allowing them to crush hard prey such as snails. As adults of both *D. guianensis* and *T. merianae* reach large adult body size (over 300 mm snout-vent length), selection on bite force generation might be relaxed. We also test for differences in head shape and skull shape that could lie at the basis of a high bite force capacity. Finally, we test for behavioral differences in prey manipulation, prey transport, and swallowing in adults of both species. Given the largely aquatic lifestyle of *Dracaena*, we expect careful manipulation of food items to avoid the loss of prey when manipulating and crushing at the water's edge or in water.

MATERIAL AND METHODS

Specimens

Data for *D. guianensis* were obtained from both adults ($N = 4$; SVL: 389.0 ± 38.1 mm; mean \pm standard deviation) and juveniles ($N = 24$; 156.4 ± 10.2 mm) housed at the Prague Zoo. As these animals are extremely rare in captivity, this comprises an exceptionally large sample size. The adults were housed in a large glass vivarium on a 12 hr:12 hr light:dark cycle and were maintained on a diet of snails only. The juveniles were housed in smaller glass vivaria also on a 12 hr:12 hr light:dark cycle but were offered mostly slugs. The environmental temperature varied from 22°C during daytime to 12°C at night. An incandescent bulb provided the animals with a basking spot at a higher temperature.

For *T. merianae* bite forces from adults ($N = 35$; 375.6 ± 21.1 mm) and juveniles ($N = 25$; 163.3 ± 13.4 mm) were obtained from animals housed at the Jacarezário at the Universidade Estadual Paulista (Rio Claro, São Paulo, in south-eastern Brazil; see Herrel et al., 2009). At this laboratory, the lizards are kept in small groups (5–10 individuals) in outdoor pens and are provided with water and ground shelters, as well as shade and sunny areas for thermoregulation. In spring and summer, the animals are fed three times a week with ground beef, fruits, and/or 1-day-old chickens.

Kinematic data on feeding in *T. merianae* were obtained from two adults (383.33 ± 20.82 mm) kept at the laboratory of the University of Antwerp. These animals were housed separately in cages (120 × 80 × 80 cm) on a 12 hr:12 hr light:dark cycle and provided with snails, dog food, fruit, and mice ad libitum. The environmental temperature varied from 28°C during daytime to 22°C at night. An incandescent bulb provided the animals with a basking spot at higher temperature.

Morphometrics

Head dimensions and snout-vent length (SVL) were measured in all individuals. Head length was taken as the distance between the back of the parietal bone and the tip of the upper jaw; head width was measured at the widest part of the head; head height was measured as the highest point of the head just posterior to the orbits; lower jaw length was taken as the distance between the back of the retroarticular process and the tip of the lower jaw. Additionally, two morphological variables related to the biomechanics of the jaw system were estimated by measuring: (1) the distance from the jaw articulation to the tip of the lower jaw (i.e., the jaw outlever) and (2) the distance from the posterior edge of the jugal to the tip of the lower jaw (snout length). First, the length of the jaw-in-lever for opening was calculated by subtracting the jaw outlever from the lower jaw length. Second, by subtracting snout length from the jaw outlever, the in-lever for jaw closing was calculated. Measurements

were taken using digital callipers (Mitutoyo CD-20DC, England; precision: 0.01mm).

In addition, we measured the skulls of 70 individuals belonging to 20 species of teiids representing all known genera using digital callipers (Mitutoyo CD-20DC). Measurements were based on museum specimens located in the collections of the Museum of Comparative Zoology at Harvard, the Field Museum of Natural History in Chicago, the American Museum of Natural History, the Muséum National d'Histoire Naturelle in Paris, and one specimen of *C. tigris* from the private collection of A.H (nine *Ameiva ameiva*, two *Aspidoscelis deppei*, one *A. exsanguis*, two *A. gularis*, one *A. motaguae*, one *A. neomexicanus*, one *A. sexlineata*, four *A. tigris*, three *Callopiastes flavipunctatus*, one *C. maculatus*, two *Cnemidophorus murinus*, two *Crocodylurus lacertinus*, three *Dicrodon guttulatum*, one *Dicrodon Holmbergi*, three *D. paraguayensis*, one *D. guianensis*, five *Kentropyx calcaratus*, two *Teius teyou*, two *Tupinambis nigropunctatus*, 23 *Tupinambis teguixin*, and one *Tupinambis rufescens*). Note that *Dracaena* are rare in collections and only two intact skulls (MCZ, *D. paraguayensis* and MNHN, *D. guianensis*) were available for measurements. Data for two others were extracted from μ CT data of intact specimens (both *D. paraguayensis*). On each skull, we measured skull length from the back of the parietal to the tip of the premaxillary, the length of the skull between the posterior edge of the jugal and the tip of the premaxillary bone (muzzle length), the height of the skull at the level of the frontoparietal suture, the height of the skull at the level of the orbit, the length of the lower jaw from the symphysis to the back of the posterior most tooth, the length of the lower jaw from the symphysis to the anterior edge of the jaw articulation, the length of the lower jaw from the symphysis to the posterior edge of the jaw articulation, the length of the lower jaw from the symphysis to the back of the retroarticular process, and the length of the lower jaw from the symphysis to the tip of the coronoid bone (see also Metzger and Herrel, 2005).

Bite Forces

Isometric force transducers (Kistler, types 9203: ± 500 N and 9207: ± 5000 N) mounted on purpose-built holders and connected to a Kistler charge amplifier (type 5995A, Kistler Inc., Winterthur, Switzerland) were used to measure in vivo bite forces (see Herrel et al., '99). When placing the free end of the holder between the teeth of the animal, prolonged and repeated biting occurred. The place of application of bite forces was standardized for all animals and occurred at the tip of the jaws. Measurements were repeated five times for each animal. The maximal value recorded of the five trials was considered to be the maximal bite force for each animal. Although snails are crushed at the back of the jaws, it was impossible to obtain data on bite forces at the back of the tooth row.

Feeding Behavior and Video Analysis

Adult individuals of both species were filmed in lateral view while eating intact snails (*Cornu aspersa*). Data on feeding behavior for two adult *D. guianensis* were collected at the Prague Zoo. Data for *T. merianae* were recorded for two individuals housed at the University of Antwerp. Feeding behavior was recorded at 50 Hz using a digital camcorder (Sony DCR-HC94, Sony, Tokyo, Japan). Video recordings were reviewed using Midas Player software (Xcitex, Cambridge, MA; version 2.1.5). A total of 30 (15 and 15 for each individual) and 22 (10 and 12 for each individual) feeding sequences were recorded for *D. guianensis* and *T. merianae*, respectively. Based on these recordings, the transport and swallowing stage duration, the number of crush bites during transport, the number of transport and swallowing cycles, the average transport cycle duration, and the average swallowing cycle duration were extracted for both species. In the number of transport cycles, we included the inertial transport movements, the repeated attempts to pick up the snail, and the movements of the jaws while removing shell fragments after dropping the snail (only observed in *T. merianae*).

Data on feeding kinematics for *T. merianae* were collected at the University of Antwerp. For these animals, small lead markers were inserted at the anterior tip of the upper and lower jaw before videofluoroscopic recordings were made. Before implantation of these markers, the animals were anaesthetized using Ketamine (100 mg/kg; ketamine hydrochloride, 50 mg/mL, Parke-Davis, Brussels, Belgium). Marker placement was checked using dorsoventral and lateral radiographs. A Redlake Motion-Pro2000 digital high-speed camera attached to a Philips 14-inch image intensifier was used to record parts of the feeding event at 250 Hz. X-rays were generated using a Philips Optimus M200 X-ray generator (Philips, Eindhoven, The Netherlands). Videofluoroscopic recordings were reviewed using the Midas Player software (Redlake, San Diego, CA; version 2.1.7).

For selected transport and crush cycles where animals remained in lateral view, two externally visible landmarks (the anterior tip of the upper and lower jaws) in the case of *Dracaena*, or the two implanted markers near the tip of the jaws in the case of *Tupinambis*, were digitized frame by frame using Didge (Image Digitizing Software version 2.2.0; Alistair Cullum). Based on the X-Y coordinates of these markers, gape distance was calculated. A total of 15 cycles (10 transport and 5 crush cycles; evenly divided across individuals) were analyzed for each species. Raw displacements were smoothed using a zero-phase shift, fourth-order low-pass Butterworth filter.

Feeding events were divided into three stages: prey capture, intraoral prey transport, and swallowing. In the transport stage, we made a distinction between two cycle types, a transport cycle without crushing and a crush bite. In accordance with Bramble and Wake ('85), we divide transport and crush cycles into four phases based on the changes in velocity of the jaws: slow open (SO), fast open (FO), fast close (FC), and slow close (SC).

All procedures were approved by the animal ethics committee at the University of Antwerp (*Tupinambis*) and the Prague Zoo (*Dracaena*).

Statistical Analysis

To meet the assumptions of homoscedasticity and normality for parametric analyses (Sokal and Rohlf, '81; Kachigan, '91), all morphometric and kinematic data were \log_{10} -transformed prior to analysis.

To investigate the differences in head shape and bite forces between *T. merianae* and *D. guianensis*, we first tested whether adult and juvenile individuals of both species differed in overall body size (snout-vent length, SVL) using an ANOVA. Next, we tested for differences in head dimensions for both age classes using a MANCOVA with SVL as covariate. As the species by age class interaction effect was highly significant, morphometric data were further analyzed for juveniles and adults separately using MANCOVAs. Finally, we tested for differences in bite force between species and age classes using an ANCOVA. As interaction effects were significant, we subsequently tested for differences in bite force for both age classes separately.

To explore differences in skull shape between representatives of the different teiid genera, we performed a factor analysis with varimax rotation on the skull data. First, we regressed all \log_{10} -transformed skull dimensions against the geometric mean of all the skull measures and extracted unstandardized residuals. Next, we used residual data in a factor analysis with varimax rotation and extracted factors with eigenvalues greater than one and plotted the position of *D. guianensis* relative to other individuals. Next, we ran a multivariate analysis of variance (MANOVA) testing for differences between diet groups coupled to univariate ANOVA's and Bonferroni post-hoc tests on the factor scores to test whether the molluscivorous *Dracaena* were different from other diet groups.

Kinematic data were used to test for differences between species and cycle type (transport or crush bite). A MANOVA was performed to test for species, cycle type, and interaction effects with individual entered as a random factor in the analyses. As the interaction effects were highly significant, species effects were analyzed separately for transport and crush cycles using MANOVA's. Finally, differences in overall feeding behavior (number of cycles of each type used and overall duration of feeding event) were tested using a MANOVA.

RESULTS

Morphometrics and Bite Forces

An analysis of variance indicated no differences between species in body size ($F_{1,84} = 0.04$; $P = 0.84$) or in the interaction between body size and age ($F_{1,84} = 3.3$; $P = 0.08$). Differences between age classes were, however, significant ($F_{1,84} = 1782.6$; $P < 0.001$).

Table 1. Summary table representing means and standard deviations of the morphological and bite force data in juvenile and adult *T. merianae* and *D. guianensis*.

	Adults		Juveniles	
	<i>T. merianae</i> (N = 35)	<i>D. guianensis</i> (N = 4)	<i>T. merianae</i> (N = 25)	<i>D. guianensis</i> (N = 24)
SVL (mm)	375.6 ± 21.1	389.0 ± 38.1	163.3 ± 13.4	156.4 ± 10.2
HL (mm)	78.0 ± 7.2	81.2 ± 6.6	37.3 ± 2.6	40.6 ± 2.2
HW (mm)	53.7 ± 6.1	69.9 ± 8.2	23.4 ± 2.1	28.6 ± 1.8
HH (mm)	45.6 ± 5.4	55.5 ± 6.0	18.5 ± 1.4	25.2 ± 1.5
LJL (mm)	96.6 ± 9.8	100.0 ± 8.5	42.0 ± 3.2	47.1 ± 3.8
Snout (mm)	61.4 ± 5.4	70.5 ± 4.2	28.1 ± 1.9	34.8 ± 2.1
Open in (mm)	7.6 ± 2.4	14.7 ± 3.6	3.3 ± 1.1	6.9 ± 2.0
Close in (mm)	27.6 ± 4.8	14.8 ± 5.9	10.6 ± 1.0	5.4 ± 0.8
Outlever (mm)	89.1 ± 8.7	85.3 ± 10.1	38.7 ± 2.6	40.2 ± 2.6
Bite force (N)	334.8 ± 99.6	383.3 ± 88.2	35.5 ± 10.1	56.0 ± 10.2
Close/out	0.45 ± 0.07	0.21 ± 0.07	0.38 ± 0.03	0.15 ± 0.02

SVL, snout-vent-length; HL, head length; HW, head width; HH, head height; LJL, lower jaw length; snout, distance from the back of the jugal to the tip of the jaw; open in, jaw in lever for opening; close in, jaw in lever for closing; outlever, distance from the quadrate to the snout tip; close in/out, jaw in lever for closing relative to jaw out lever.

A MANCOVA testing for differences in head shape indicated significant species (Wilks' lambda = 0.078; $F_{8,76} = 112.53$; $P < 0.001$) and species by age class interaction effects (Wilks' lambda = 0.55; $F_{8,76} = 7.72$; $P < 0.001$). Differences in head shape between age classes were, however, not significant after taking into account variation in body size (Wilks' lambda = 0.94; $F_{8,76} = 0.59$; $P = 0.78$). For juveniles, a MANCOVA performed on the morphometric data indicated significant differences in head shape between species (Wilks' lambda = 0.018; $F_{8,39} = 266.54$; $P < 0.001$). Subsequent univariate ANCOVAs indicated that differences in head shape were significant for most variables with *Dracaena* having generally bigger heads. However, the in-lever for jaw closing and the lever ratio were significantly greater in *Tupinambis* (Table 1). For adults, significant differences in head shape were also present (Wilks' lambda = 0.12; $F_{8,29} = 25.64$; $P < 0.001$). However, the univariate ANCOVAs indicated that species were not different in head length, lower jaw length, and the length of the jaw outlever after Bonferroni correction (Table 1). Although adult *Dracaena* had wider and taller heads (Fig. 2), the closing inlever and the lever ratio were greater for *Tupinambis* compared to *Dracaena*.

An ANCOVA performed on the bite force data for juveniles indicated significant differences between species with *Dracaena* biting much harder for a given body size than *Tupinambis* ($F_{1,46} = 160.45$; $P < 0.01$; Fig. 3). However, adults of both species did not differ in bite force ($F_{1,36} = 0.30$; $P = 0.59$; Fig. 3).

Skull Shape

A factor analysis performed on the size-free skull and lower jaw dimensions retained three factors jointly explaining 73.14% of

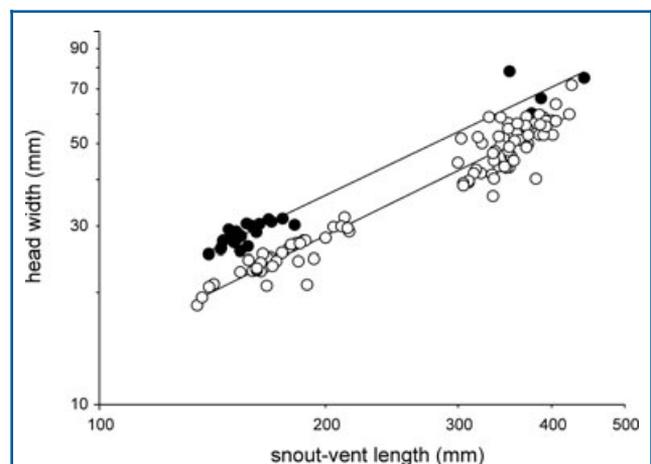


Figure 2. Plot of head width against snout-vent length for juvenile and adult *D. guianensis* (filled circles) and *T. merianae* (open circles) showing that *D. guianensis* has a wider head for its body size compared to *T. merianae*. Note the log scale on both X- and Y-axes.

the total variance in the dataset. Whereas the first factor was strongly correlated with relative jaw length and the distance between the symphysis and the jaw articulation, the second one was strongly positively correlated with muzzle length and negatively with frontoparietal skull height. The third axis was correlated with the distance from the symphysis to the most posterior tooth and to the coronoid (Table 2). A MANOVA detected

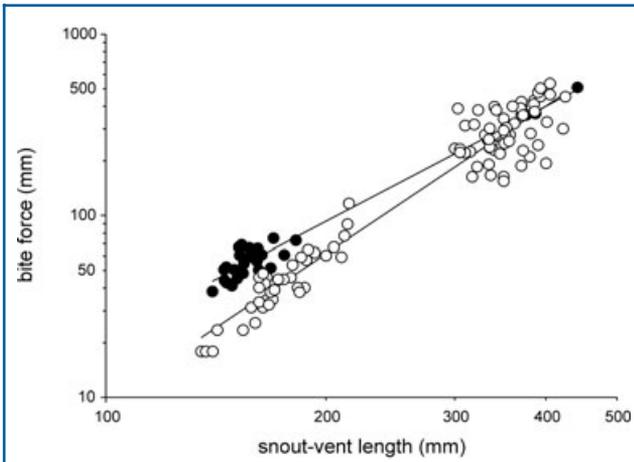


Figure 3. Plot of bite force against snout-vent length for juvenile and adult *D. guianensis* (full circles) and *T. meriana* (open circles). Whereas juveniles *D. guianensis* bite harder than juvenile *T. meriana*, this is not the case for adults. Note the log scale on X- and Y-axes.

Table 2. Results of a factor analysis with varimax rotation performed on the size free morphometric data of the skull and mandible in Teiid lizards (see Material and Methods for details about sample).

	Factor 1	Factor 2
Eigenvalue	2.65	2.98
Percentage variance explained	29.43	22.00
Residual distance symphysis – posterior tooth (mm)	–0.327	0.201
Residual distance symphysis – anterior articulation (mm)	0.856	–0.075
Residual distance symphysis – posterior articulation (mm)	0.869	0.184
Residual distance symphysis to back retroarticular process (mm)	0.745	0.164
Residual distance symphysis to tip of coronoid process (mm)	0.138	0.007
Residual skull length (mm)	0.248	0.630
Residual muzzle length (mm)	–0.307	0.780
Residual frontoparietal skull height (mm)	–0.197	–0.775
Residual mid-orbital skull height (mm)	–0.532	–0.517

Bolded values represent loadings greater than 0.7.

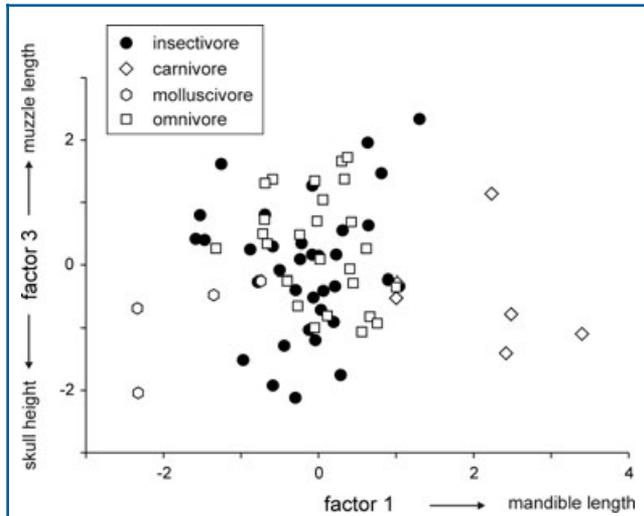


Figure 4. Scatter plot illustrating the results of a principal component analysis performed on linear dimensions describing skull shape in a wide range of teiid lizards encompassing all genera represented in Figure 1. *Dracaena* is characterized by a tall skull with a relatively short mandible and muzzle relative to other teiids. Open symbols represent individuals belonging to the Tupinambinae; dietary groups (see Fig. 1) are indicated by different symbols. Note that whereas the two clades do not differ from one another in skull shape, dietary groups do.

significant differences in skull shape between diet groups (Wilks' Lambda = 0.369; $F_{9, 155,91} = 8.78$; $P < 0.001$). Subsequent univariate F -tests indicated that effects of diet were significant on factor one ($F_{3,66} = 28.93$; $P < 0.001$) and approached significance on factor two ($F_{3,66} = 2.25$; $P = 0.09$). Differences between dietary groups were nonsignificant on factor 3 ($F_{3,66} = 1.28$; $P = 0.29$). Bonferroni post-hoc tests indicated that insectivores and omnivores were not different from one another ($P > 0.05$). Yet, all other dietary groups, including the molluscivorous *Dracaena* were different from one another (all $P < 0.001$). An examination of the plot of factor one against factor two shows that *Dracaena* is characterized by having a short mandible, a short muzzle, and a tall skull compared to other teiids (Fig. 4).

Feeding Behavior

Dracaena guianensis approached snails immediately when offered and picked them up with their jaws. Next, the head was rotated dorsally and the jaws opened slightly causing the snail to roll toward the back of the tooth rows. Snails were repositioned in the oral cavity using the tongue before being crushed. Multiple bites were used to crush snails and repositioning took

place in between crushing. Shell fragments were expelled from the mouth by the tongue before swallowing (Dalrymple, '79) as has been observed in other snail-eating lizards (Herrel and Holanova, 2008). During the manipulation, snails were never dropped.

In contrast, although *T. merianae* also used the jaws to grab the snails, it used kinetic inertial food transport. During inertial transport, the jaws are opened rapidly and simultaneously the head-neck system is drawn back, initiating the backward displacement of the prey after release from the jaws. At maximal gape, the entire head and body move forward and the jaws are closed (Gans, '69; Smith, '82; Schwenk, 2000; Montuelle et al., 2009). *Tupinambis merianae* used mostly inertial movements to reposition the snails for crushing in contrast to the tongue-based repositioning observed in *Dracaena*. *Tupinambis* lizards often needed several attempts and snails were dropped repeatedly. After crushing, shell fragments were removed by the tongue, by shaking the head, but also by dropping the snail followed by wiping movements of the jaws on the bottom of the cage resulting in the removal of shell fragments.

Video Analysis

A MANOVA performed on the kinematic dataset of transport cycles and crush bites revealed significant species (Wilks' lambda = 0.13; $F_{6,21} = 23.81$, $P < 0.001$) and cycle type effects (transport/crush cycle; Wilks' lambda = 0.061; $F_{6,21} = 54.26$, $P < 0.001$). Interaction effects were also significant (Wilks' lambda = 0.34; $F_{6,21} = 6.93$, $P < 0.001$) suggesting that the changes in kinematics with cycle type are species dependent. Owing to the significance of the interaction effects, transport and crush cycles were analyzed separately for *T. merianae* and *D. guianensis*.

For pure transport cycles significant species effects were observed (Wilks' lambda = 0.10; $F_{6,13} = 19.07$, $P < 0.001$) with differences in gape distance ($F = 5.04$, $P = 0.038$), the duration of the slow open phase (dSO; $F = 6.8$, $P = 0.02$), the duration of the fast open phase (dFO; $F = 39.09$, $P < 0.001$) and the duration of fast close phase (dFC; $F = 25.49$, $P < 0.001$) being significant. Transport of snails in *D. guianensis* is associated with greater gape distances and shorter slow open phases than in *T. merianae* (Fig. 5). The duration of the fast open and fast close phases is, however, longer in *D. guianensis* (Table 3). These kinematic differences reflect the difference in feeding strategy contrasting tongue based with inertial transport and repositioning.

For crush bites, we also detected a significant species effect (Wilks' lambda = 0.035; $F_{6,3} = 13.65$, $P = 0.028$) with significant differences in the duration of the slow open phase ($F_{1,8} = 9.36$, $P = 0.02$), the duration of the fast open phase ($F_{1,8} = 49.81$, $P < 0.001$), the duration of the slow close phase ($F_{1,8} = 19.84$, $P = 0.002$), and the total duration of a crush cycle ($F_{1,8} = 16.59$, $P = 0.004$). Crushing of snails in *D. guianensis* is associated with shorter slow open phases, longer fast open phases, longer slow close phases, and a greater total crush cycle duration compared

to *T. merianae* reflecting a careful handling and pronounced crushing of snails (Fig. 5; Table 3).

An analysis performed on variables related to the entire feeding event revealed a significant species effect (Wilks' lambda = 0.38; $F_{7,44} = 10.08$, $P < 0.001$) with significant differences in the total number of transport cycles ($F_{1,50} = 61.11$, $P < 0.001$), the total number of crush bites ($F_{1,50} = 34.28$, $P < 0.001$), the total duration of transport ($F_{1,50} = 40.58$, $P < 0.001$), and the total number of swallowing cycles ($F_{1,50} = 12.97$, $P = 0.001$). The total number of transport and swallowing cycles, the number of crush bites, and the total transport duration are greater in *D. guianensis* (Table 4; Fig. 5). The duration of the swallowing stage is, however, not different between species ($F_{1,50} = 1.49$, $P = 0.23$) suggesting a more careful handling of snails during intraoral transport rather than an intrinsic limitation on the speed of jaw movement.

DISCUSSION

Although both species include snails in their diet, *D. guianensis* is a true molluscivorous lizard. *Tupinambis merianae* is omnivorous and eats a wide variety of foods including fruits, vertebrates, insects, and molluscs (Dessem '85; Castro et al., '91; Mercoli and Yanosky, '94; Kiefer and Sazima, 2002; Martins, 2006). Our data demonstrate that *D. guianensis* is morphologically and behaviorally different from *T. merianae* and that these differences appear related to their specialized diet.

Our data on head morphometrics in *D. guianensis* and *T. merianae* show that juvenile *D. guianensis* have longer, wider, and taller heads allowing for bigger jaw muscles and resulting in a greater bite force. Unexpectedly, the in-lever for closing is smaller in *D. guianensis* compared to *T. merianae* in both juveniles and adults. Yet, juvenile *D. guianensis* do bite harder than juvenile *T. merianae* which may be due to their relatively bigger heads. Our data on skull morphology show that the mandible of *Dracaena* is relatively short, yet the skull is tall and the muzzle short. Although one would expect this to result in a greater bite performance, this is not the case. Consequently, the relative decrease in bite force in adult relative to juvenile *D. guianensis* in comparison to *T. merianae* suggests growth-related differences in the jaw adductor musculature, yet this remains to be tested explicitly.

The size-dependent decrease in bite force suggests that selection on bite-force capacity may be stronger in juvenile *D. guianensis* or, alternatively, that selection on relative bite force capacity is high in adult *T. merianae*. As adults of both *D. guianensis* and *T. merianae* have large bite forces in absolute terms because of their large body and head size, hard-shelled prey become potential dietary items. Juvenile lizards have smaller heads resulting in lower absolute bite forces thus preventing them from crushing hard or tough prey items. The enlarged heads of juvenile *D. guianensis* may, however, allow them to exploit this food resource as has been suggested for other specialized

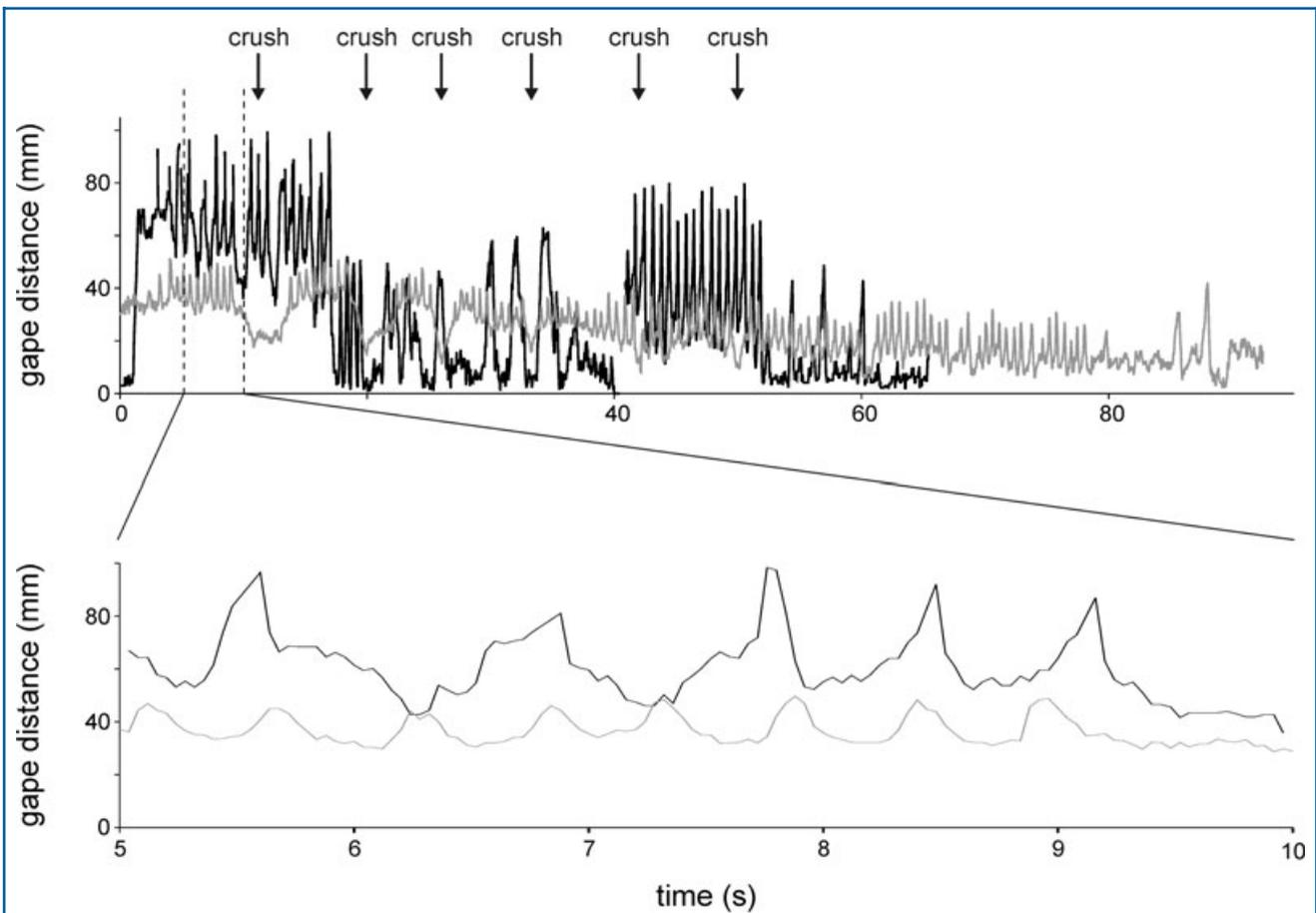


Figure 5. Top: plot of gape distance against time for a total feeding event in *D. guianensis* (gray line) and *T. merianae* (black line). Bottom: blow-up of 5 sec of the sequence to illustrate individual gape cycles in both species. Selected crushing events for *D. guianensis* are indicated by arrows.

molluscivores such as *Chamaeleolis* (Herrel and Holanova, 2008). Unfortunately, no quantitative data on the diet of juvenile *D. guianensis* are available, and we can only speculate about the relative importance of snails in the diet of the juveniles. However, one argument for the importance of snails in the diet of juveniles is that, unlike in *Tupinambis* and many other lizards, molariform teeth are present in juveniles.

Given the semiaquatic lifestyle of *D. guianensis*, we predicted a specialized mechanism for food transport allowing precise manipulation and repositioning of snails during intraoral transport. Whereas *D. guianensis* uses its tongue to reposition snails, *T. merianae* uses predominantly inertial movements to reposition and transport snails. Consequently, snails were often dropped by *T. merianae* during transport and repositioning (on average 4 ± 2 times in a single sequence). Given the aquatic lifestyle of *Dracaena*, dropping snails could involve losing them

in the water and thus an alternative transport method is used that assures accurate transport and repositioning and is dependent on the use of the tongue. Another striking difference in the manipulation of snails was associated with the use of the tongue to expel snail fragments in *Dracaena*. Whereas this has been observed in other specialized molluscivorous lizards (Herrel and Holanova, 2008), *T. merianae*, in contrast, tends to drop the snail to wipe the snail fragments from its mouth after which the snail is picked up again. Whether these differences in tongue use are reflected in tongue morphology remains unknown as data on tongue structure in *Dracaena* are not available in the literature.

During transport cycles, the gape distance in *T. merianae* is smaller than that observed in *D. guianensis*. This can be explained by the differences in feeding behavior between the two species whereby *D. guianensis* flexes the head dorsally and lets the snail roll to the back of the tooth rows while opening the

Table 3. Summary table representing the means and standard deviations of the kinematic data of transport and crush cycles in adult *T. merianae* and *D. guianensis*.

	Transport		Crushing	
	<i>T. merianae</i>	<i>D. guianensis</i>	<i>T. merianae</i>	<i>D. guianensis</i>
Gape distance (mm)	37.23 ± 8.78	43.07 ± 2.02	46.77 ± 9.32	38.86 ± 6.54
Duration slow opening (s)	0.29 ± 0.09	0.20 ± 0.08	0.29 ± 0.09	0.18 ± 0.02
Duration fast opening (s)	0.07 ± 0.02	0.13 ± 0.02	0.06 ± 0.01	0.12 ± 0.01
Duration fast closing (s)	0.12 ± 0.03	0.18 ± 0.02	0.09 ± 0.02	0.18 ± 0.11
Duration slow closing (s)	0.23 ± 0.06	0.18 ± 0.06	0.73 ± 0.23	1.64 ± 0.44
Gape cycle duration (s)	0.71 ± 0.13	0.69 ± 0.11	1.16 ± 0.30	2.12 ± 0.48

Significant differences between the species are indicated in bold.

Table 4. Summary table representing the means and standard deviations of variables describing the entire feeding event in adult *T. merianae* and *D. guianensis*.

	<i>T. merianae</i> (N = 22)	<i>D. guianensis</i> (N = 30)
Number of transport cycles	59.73 ± 17.07	99.47 ± 22.03
Number of crush cycles	4.27 ± 1.12	6.93 ± 1.96
Number of swallowing cycles	13.05 ± 4.18	18.93 ± 7.08
Duration of intraoral transport stage (s)	52.21 ± 16.84	86.03 ± 23.40
Duration of swallowing stage (s)	17.83 ± 5.33	19.58 ± 5.76

Significant differences between species are indicated in bold. *N*, number of feeding events analyzed.

jaws widely. In contrast, *T. merianae* transports the snail using inertial movements. The shorter fast opening and fast closing phase durations in *T. merianae* can also be explained by the differences in feeding behavior with rapid inertial movements being associated with short FO and FC durations (Montuelle et al., 2009).

Although we expected the SO duration to be shorter in *T. merianae* compared to *D. guianensis*, this was not the case and may be explained by the extensive positioning of the snail in *T. merianae* before initiating inertial transport and repositioning. Moreover, our data indicated a difference in the duration of the slow closing phase with *D. guianensis* having longer slow closing phase durations than *T. merianae* that may be associated with extensive crushing. In addition, a significant difference between transport and crush cycles was observed with crush cycles being associated with longer SC phases than transport cycles as

predicted (Table 3). *Dracaena guianensis* also used a larger number of transport, crush, and swallowing cycles resulting in an increase in total transport duration. Thus, the feeding behavior in *D. guianensis* seems more specialized for eating snails and is associated with a greater overall duration of food manipulation. This can be explained by the more accurate and secure handling of snails and expelling of the shell fragments by the tongue during transport and crushing (Dalrymple, '79).

In summary, our data demonstrate morphological and behavioral differences between *D. guianensis* and *T. merianae*. Although feeding upon snails takes longer in *D. guianensis*, their feeding behavior seems to be better suited to handle this hard and brittle food type while minimizing prey loss. Our results suggest, moreover, that selection may operate on juvenile life-history stages in *D. guianensis*, resulting in large heads and large bite forces. Since adults do not differ in bite force from adult *T. merianae*, but do have larger heads, this suggests that the adult phenotype may be simply the result of selection on juveniles. In contrast, adult *T. merianae* have greater jaw in-levers for closing suggesting selection on bite performance in adults which may be related to their territorial or antipredator behavior (Herrel et al., 2009).

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