JOURNAL OF EXPERIMENTAL ZOOLOGY 290:101–107 (2001)

Head Shape and Bite Performance in Xenosaurid Lizards

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ABSTRACT Bite performance in lizards influences many aspects of the animal's lifestyle. During feeding, inter- and intrasexual interactions, and defensive behavior, the ability to bite hard might be advantageous. Although biomechanical considerations predict clear relations between head shape and bite performance, this has rarely been tested. Here we investigate the effect of head shape on bite performance in three closely related species of xenosaurid lizards. Our data show that in this family of lizards, bite performance is mainly determined by head height, with high headed animals biting harder than flat headed ones. Species clearly differ in head shape and bite performance and show a marked sexual dimorphism. The dimorphism in head shape also results in an intersexual difference in bite performance. As head height is the major determinant of bite performance in xenosaurid lizards, trade offs between a crevice dwelling life-style and bite performance seem to occur. The evolutionary implications of these results are discussed. *J. Exp. Zool. 290:101–107, 2001.* © 2001 Wiley-Liss, Inc.

The relation between organismal structure and function is generally assumed to be determined by the interaction of physical laws and evolutionary and developmental processes. Although this provides the opportunity to use fairly simple biomechanical models to investigate the nature of these relations, the relations between form and function (especially in seemingly highly constrained systems) are often inferred rather than tested in any explicit way (Moon '99). Yet, in the last decade or two, functional morphologists have become aware of the fact that biological systems are highly complex, and that not only physical, but also developmental (Hanken and Hall, '93), constructional (Barel, '83), and historical (Felsenstein, '85, '88) constraints act to determine the form-function relationship at the organismal level.

The relation between head shape and biting is thought to be straightforward; simple external head dimensions such as length, width, and height are assumed to be good predictors of bite strength (Carothers, '84; Molina-Borja et al., '98). Although these inferences are supported by biomechanical models (Smith and Savage, '59; Freeman, '79; Kiltie, '82; Wainwright, '87; Sinclair and Alexander, '87; Cleuren et al., '95; Herrel et al., '98a,b) actual in vivo performance has rarely been measured (Herrel et al., '99). In lizards, bite force has been determined to be important during territorial interactions (e.g., Trivers, '76; Fitch, '81; Anderson and Vitt, '90; Censky, '96; Molina-Borja et al., '98), mating (Herrel et al., '96), feeding (Preest, '94; Herrel et al., '98b; Herrel et al., '99), and defensive behaviours (Hertz et al., '82; Green, '88). If external head measurements are indeed good predictors of bite force, then these would be valuable, and easily measurable, indicators of performance.

How can head shape influence bite performance? Theoretical reasoning suggests that animals with wider heads can accommodate more jaw adductor musculature without constraining the space occupied by vital organs (i.e., brain, sensory structures). The increase in jaw adductor muscle mass is then assumed to result in a higher bite force. Also an increase in head height (i.e., the height of the skull) can theoretically increase the available space for jaw adductor muscles. By taking advantage of complexly pennate jaw muscles, an increase in head height can result in an increase in the physiological cross-section, and thus bite force. Predictions relating to total head length are less straightforward, as an increase in the to-

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Received 31 July 2000; Accepted 17 January 2001

tal head length has the potential to increase both the in- and outlevers of the jaw system. An increase in lower jaw length, on the other hand, will predominantly increase the outlever of the system, and thus reduce bite force.

Bite force is obviously not the only measure of bite performance (bite speed and endurance are two other potentially important measures) and the latter is likely not the only aspect of an animal influencing its head shape. Other functions performed by the cranial system (e.g., sensory functions) or a diversity of behaviours (reproduction, thermoregulation, anti-predation) might impose similar or conflicting demands on head shape. For example, many lizards species use crevices to hide in when escaping from predators, or even spend most of their lives in crevices (Deban et al., '94; Schlesinger and Shine, '94; Cooper et al., '99). Because an animal's escape success and/or avoidance of predators might depend on its ability to use narrow crevices, its overall body and head shape might be influenced by its habitat use (lizards with high heads cannot utilise the narrower and safer crevices; Arnold, '98; Cooper et al., '99). If the simple biomechanical predictions stated previously hold, then crevice-dwelling lizards might be highly constrained with respect to maximal bite force and this might affect their potential dietary scope and/or competitive abilities.

Here we examine the relations between head shape and bite performance in three closely related highly specialised crevice dwelling lizards of the genus *Xenosaurus*. Within the three species examined, a cline with head shape can be observed from species with relatively high heads (*X. newmanorum*) to extremely flat headed species (*X. platyceps*). We specifically test the prediction that bite performance is constrained by head shape (i.e., flatness), and discuss the ecological and evolutionary implications thereof.

MATERIALS AND METHODS

Animals

Eighteen *Xenosaurus grandis* (Veracruz), 18 *Xenosaurus platyceps* (Tamaulipas), and 16 *Xenosaurus newmanorum* (San Luis Potosi) were collected in Mexico and transferred to the University of Puget Sound (Tacoma, Washington). An additional 3 *X. grandis*, 7 *X. platyceps*, and 4 *X. newmanorum*, which were born in captivity, were used in the experiments. Different species were placed in separate cages of five individuals per cage. The animals were fed crickets dusted with calcium and vitamins, and were provided with water ad libitum. Artificial crevices were created for the animals to hide in. The animals were kept on a 12L:12D light cycle with an ambient temperature varying around 25°C.

Morphometrics

After the performance trials, the following morphological measurements were taken from each animal: mass, snout-vent length (SVL), head length (HL), lower jaw length (LJL), head width (HW), and head height (HH). Head length was measured from the anterior end of the premaxillary to the posterior edge of the parietal bone. Lower jaw length was measured from the anterior end of the dentary bone to the posterior edge of the retroartricular process. Head width was measured at the widest part of the skull and included the bulging of the m. pterygoideus and external jaw adductors. Head height was measured at the highest part of the skull just posterior to the orbita.

Bite forces

We measured in vivo bite forces using an isometric Kistler force transducer (type 9203, Kistler Inc., Switzerland), mounted on a purpose-built holder (Fig. 1) and connected to a Kistler charge amplifier (type 5995, Kistler Inc., Switzerland). Biting causes the upper plate to pivot around the fulcrum, and thus pull is exerted on the transducer. All animals were tested between 22°C and 24°C (mean activity temperatures observed in the wild; see Cooper et al., '98; Lemos-Espinal et al., '98). When the lizards were taken out of their cage, they readily assumed a characteristic threat response (opening of the jaws) and tried to bite the person holding them. When the free end of the holder (= bite plates, see Fig. 1) was placed in between the jaws of the animal, usually prolonged and repeated biting resulted. The place of application of bite forces was standardised by mounting acrylic stops onto the free end of the holder (see Fig. 1). Gape angle was standardised (15 ± 5°) by moving the bite plates away from each other for larger animals. Measurements were repeated five times for each animal with an inter-trial interval of at least 15 min. The maximal value obtained during such a recording session was considered to be the maximal bite force for that animal.

Analyses

All morphological variables were logarithmically transformed (Log10) before analyses. Because the variation in shape was of special interest, all mor-

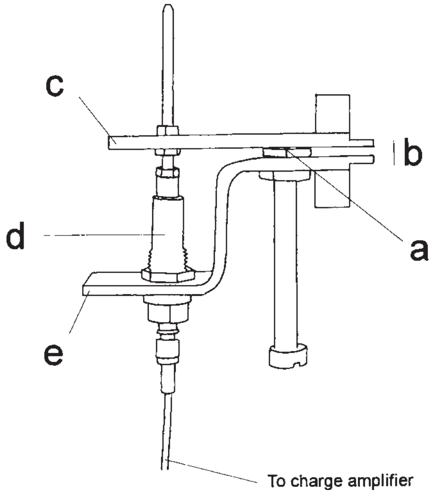

Fig. 1. Experimental set-used to register bite forces in vivo. The animals bite on the bite plates (**b**) which causes the upper plate (**c**) to rotate, thus exerting pull on the piezo-electric force transducer (**d**). The distance between bite plates is adjustable (**a**, fulcrum; **e**, holder; modified after Herrel et al., '99).

phological and performance variables were regressed against snout-vent length. Residuals were calculated and used in the subsequent analyses.

To investigate the effect of head shape on bite performance, a multiple regression was performed with bite performance as the dependent variable, and the residual morphological traits, species and sex, as independent variables. Next, head shape and bite force data were analysed using a multivariate analysis of variance (MANOVA) with species and sex as factors in the model. Univariate analyses of variance were performed to investigate which measures were significantly different between species.

RESULTS

Effect of head shape on bite performance

Regression analysis of the head measures and bite force against snout-vent length revealed highly significant correlations (Table 1). Because both head size and bite force are highly correlated with body size, residual data were calculated and used in further analyses.

A multiple regression analysis (stepwise) of the data for all species resulted in a significant model which included residual head height only ($r = 0.55$, $F_{1,64} = 28.33$, $P < 0.0001$). Residual head width, head length and lower jaw length were not retained in the model (partial correlations: all $P > 0.12$). This means that lizards with relatively higher heads bite significantly harder than lizards with relatively flatter heads.

TABLE 1. Regression summary

Variables	r	Intercept	Slope	F1,64	P
SVL~HL	0.97	–0.41	0.90	926	<0.001
SVL~HW	0.96	–0.59	0.94	754	<0.001
SVL~HH	0.87	–0.66	0.86	447	<0.001
SVL~LJL	0.97	–0.48	0.95	1190	<0.001
SVL~BF	0.86	–2.30	1.73	185	<0.001
HL~BF	0.89	–1.50	1.91	238	<0.001
HW~BF	0.85	–1.10	1.74	169	<0.001
HH~BF	0.91	–0.96	1.98	314	<0.001
LJL~BF	0.87	–1.39	1.79	202	<0.001

All data were LOG_{10} transformed before regression. BF, bite force; HH, head height; HL, head length; HW, head width; LJL, lower jaw length; SVL, snout-vent length.

Species and sex effects

The results of a MANOVA on the residual morphological and performance data indicated significant species (Rao's $R = 10.95$; d.f. = 10,112; $P < 0.0001$) and sex (Rao's $R = 8.11$; d.f. = 5,56; $P < 0.0001$) effects. Interaction effects were not significant (Rao's $r = 1.14$; d.f. = 10,112; $P = 0.34$). Subsequent univariate F-tests showed that species differed significantly in residual head length ($F_{2,60} = 13.68$; $P < 0.001$), residual head height ($F_{2,60} = 20.97$; $P < 0.001$), residual lower jaw length ($F_{2,60} = 11.12$; $P < 0.001$) and residual bite force ($F_{2,60} = 8.42$; $P < 0.001$), but not in residual head width ($F_{2,60} = 2.52$; $P = 0.09$). Post-hoc tests (Duncan multiple range test) showed that *Xenosaurus newmanorum* have a significantly longer head and longer lower jaws than *X. grandis* and *X. platyceps* (Table 2, Fig. 3). *Xenosaurus platyceps* on the other hand have a significantly flatter head and bite less hard than the other two species tested (Table 2, Figs. 2 and 3).

Sexes of the three species differed in all variables tested (all $P < 0.001$), with males having larger heads and bite forces than females. Multiple regressions performed on the residual data for both sexes separately showed that head shape influences bite performance differently in male and female lizards. The multiple regression analysis for male lizards did not result in a significant model ($r = 0.42$; $F_{4,27} = 1.20$; $P = 0.34$) indicating that none of the head shape variables explained the observed differences in bite performance. Consequently, size rather than shape determines bite performance in male xenosaurid lizards. Yet, for female lizards a model with residual head height as a significant variable was retained ($r = 0.62$; $F_{1,37} = 22.43$; $P < 0.001$), indicating that females with relatively higher heads bite harder than ones with relatively flat heads. Backward and forward analyses gave the same results.

TABLE 2. Summary of morphometric and bite force data

Species	Sex	*N*	SVL (mm)	HL (mm)	HW (mm)	HH (mm)	LJL (mm)	BF (N)
Xenosaurus	♂	10	89.37 ± 16.51	22.35 ± 4.25	18.99 ± 4.83	10.37 ± 2.06	24.21 ± 5.28	12.43 ± 4.36
platyceps	♀	15	98.54 ± 20.71	23.11 ± 4.39	19.62 ± 4.11	10.66 ± 1.91	25.32 ± 5.15	11.34 ± 3.61
Xenosaurus	♂	11	109.78 ± 7.51	26.45 ± 2.32	21.63 ± 1.64	13.18 ± 0.58	28.79 ± 1.96	18.94 ± 5.12
grandis	♀	10	112.49 ± 8.10	26.95 ± 2.33	21.84 ± 1.83	13.16 ± 1.08	28.46 ± 2.09	18.30 ± 4.93
Xenosaurus	♂	7	106.42 ± 6.13	28.06 ± 1.61	21.65 ± 0.93	13.31 ± 0.72	30.07 ± 1.80	20.38 ± 5.29
newmanorum	♀	13	90.09 ± 28.09	22.39 ± 6.16	17.72 ± 4.75	10.89 ± 2.69	23.87 ± 6.85	13.36 ± 7.55

Table entries are averages ± standard deviations. BF, bite force; HH, head height; HL, head length; HW, head width; LJL, lower jaw length; N, number of observations; SVL, snout-vent length.

DISCUSSION

The results gathered here for three species of *Xenosaurus* indicate that in lizards, body and head size are indeed good predictors of bite performance (Table 1). Moreover, not only head size, but also head shape (mainly head height) is a good indicator of bite performance in these lizards. Simple external head measurements are thus indeed informative with respect to bite capacity, and are valid indicators of performance. However, a multiple regression performed on bite force data for a lacertid lizard (*Gallotia galloti*, see Herrel et al., '99) indicates that although head size is important, head length and head width are the most important shape variables predicting bite force ($r = 0.42$; $F_{2,100} = 10.69$; $P < 0.001$). The differences among these groups of lizards in the relations between head shape and bite performance are most likely related to the structure of the jaw adductor musculature. Whereas in xenosaurid lizards the jaw adductors have lost most of their internal tendinous skeleton (Haas, '60; Rieppel, '80), in lacertid lizards the jaw adductors are characterised by a well-developed tendon system (Haas, '73; Herrel et al., '99). Without a well-developed tendon system, head height might indeed constrain bite performance as the orientation of the jaw adductors will become less favourable. Despite these differences, the results for both groups indicate that head shape is an important factor and should be taken into account in studies trying to explain patterns of sexual dimorphism or food resource utilisation in lizards. Clearly, data for more groups of lizards are needed to evaluate the effects of head shape on bite performance.

Within the xenosaurid lizards examined here, clear differences in head shape, associated with differences in bite performance, are observed. Whereas the species with the flattest head (*X. platyceps*) has the poorest performance, the species with the highest head (*X. newmanorum*) bites hardest. Head shape thus seems to constrain maximal bite force in this group of lizards. At present, one can only speculate on the reason why one species has a much flatter head than the other, as very little is known about the biology of these lizards. Although all species of the genus are crevice dwellers (Ballinger et al., '95; Lemos-Espinal et al., '98), possibly, *X. platyceps* lives in areas where the available crevices are narrower, and/or where predation pressures are high. It is known, however, that *X. newmanorum*, the species with the highest head, lives in areas with relatively dense second growth forest, and occupies crevices with a mean width of about 18 mm (Lemos-Espinal et al., '98). Apparently, head

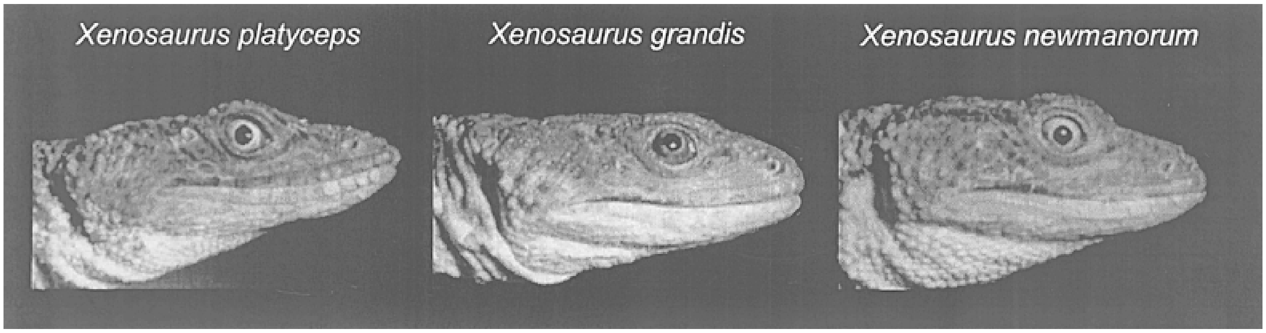

Fig. 2. Photographs of the heads of the species in lateral view to illustrate differences in head shape. All pictures were salced to the same head length. Left, *Xenosaurus platyceps*; middle, *Xenosaurus grandis*; right, *Xenosaurus newmanorum*.

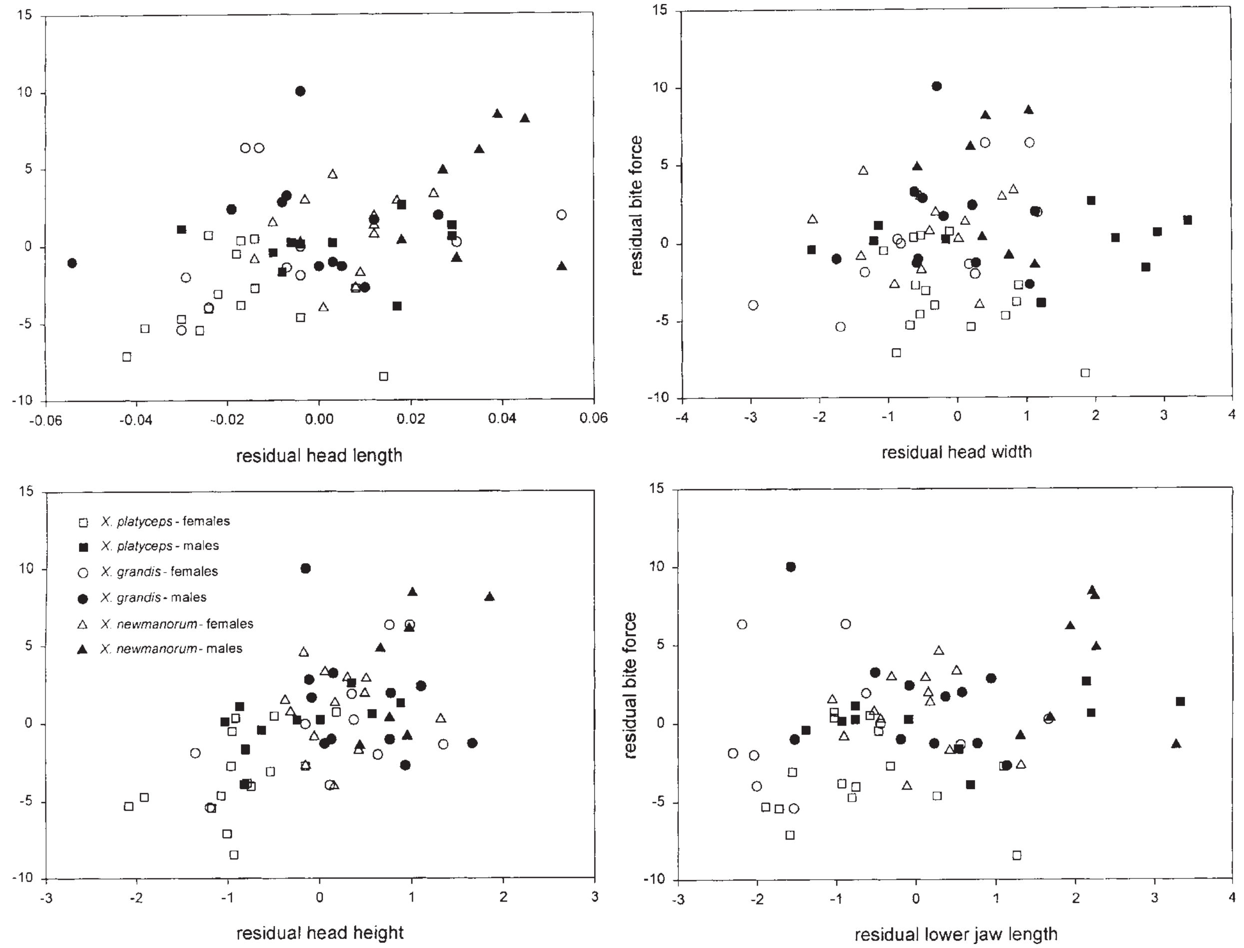

Fig. 3. Relations of head shape with bite force in *Xenosaurus*. Plotted are residual head length, residual head width, residual head height and residual lower jaw length versus residual bite force. Squares represent *X. platyceps,* circles *X. grandis*, triangles *X. newmanorum*. Filled symbols indicate males, open symbols females.

height is fairly tightly linked to the height of the crevices occupied by the animals (compare with head height data in Table 2). Still, data on habitat use of other species of xenosaurids are essential to gain insights into the proximate causes for the observed difference in head shape.

Is there any indication that the crevice dwelling lifestyle constrains bite performance in xenosaurids? Given that head height strongly influences bite performance, and that crevice dwelling lizards such as xenosaurids have relatively flat heads, there does seem to be a constraint on bite performance (male *G. galloti* bite 108 N on average, Herrel et al., '99; compare to data in Table 2). The question remains, however, if the observed reduction in bite performance is relevant to the ecology of the animal. To be ecologically relevant, the reduction in bite capacity should result in a reduced dietary scope, a smaller territory and/or a decreased mating success, or a reduced defensive potential. As information on the diet of only one of the species studied is available (Ballinger et al., '95), the first hypothesis is hard to test. These data suggest that xenosaurids are opportunistic insectivores (with the exception of two lizards that have been found in the gut of *X. grandis*; Presch, '81; Ballinger et al., '95) that will eat anything that comes into the crack in which they live (Ballinger et al., '95; Smith et al., '97). Based on the literature on forces needed to crush insect prey (Andrews and Bertram, '97; Herrel et al., '96, '99), we suggest that xenosaurids are presumably generally not constrained in their prey spectrum (average forces needed to crush most insects are less than 8 N; compared to average bite forces in Table 2). Similarly, as xenosaurids rely heavily on their crevice dwelling lifestyle and head wedging behaviour (personal observation) as an anti-predatory tactic and hardly ever leave their cracks, we do not think that the reduced bite performance in these lizards will constrain their survival because of increased predation.

However, bite performance is most likely ecologically relevant in intra-specific interactions. The xenosaurids examined here are dimorphic in head size with males having larger heads than females (see also Smith et al., '97). Because of their larger heads, males bite harder than their female conspecifics (Table 2). Because primarily male xenosaurids are assumed to engage in aggressive interactions (Ballinger et al., '95; Smith et al., '97), higher bite forces are likely important and presumably determine the outcome of male–male contests. Also, during inter-sexual interactions (i.e., copulations), males may benefit from increased bite performance, because females can actively resist copulation. If females do resist, only males with large bite forces will be able to successfully copulate with a female. Remarkably, when the bite force data are analysed for males separately, head height no longer seems to be limiting bite performance. This indicates that males somehow partially escape the constraint imposed by their crevice dwelling way of life. Possibly, in male xenosaurids the morphology of the jaw adductors has undergone changes (changed orientation, degree of pennation), allowing them to bite hard independent of their head height. This becomes especially apparent for the extremely flat headed *X. platyceps* (see Table 2). Clearly, morphological (muscle masses, orientation of muscles, degree of pennation) and physiological data (twitch characteristics, histochemistry) on the jaw muscle complex of male and female xenosaurids are required to be able to test this hypothesis.

In summary, we have shown how bite performance is related to (1) body and head size and (2) head shape (head height of females) in three species of *Xenosaurus*. Moreover, the bite performance of these animals seems to be limited by their crevice dwelling lifestyle imposing a flat head shape. However, the reduced bite performance is likely only relevant in intraspecific interactions. Yet male xenosaurids seem to have found a way to escape the imposed constraint. These data might have implications for other species where demands on head shape are imposed as a result of other aspects of animals' ecology (e.g., climbing lizards tend to be flatter than ground dwelling ones; see Vanhooydonck and Van Damme, '99), but data on a wider array of species and genera are clearly required to test the generalisability of these results.

ACKNOWLEDGMENTS

The authors wish to thank an anonymous referee for helpful comments on the manuscript; B. Vanhooydonck and R. Van Damme for help with the statistical analyses and B. Moon for taking the pictures used in Figure 2. All necessary permits and permissions were obtained from the Mexican government by J.A.L. A.H. is a postdoctoral fellow of the Fund for Scientific Research, Flanders, Belgium.

LITERATURE CITED

Anderson RA, Vitt RJ. 1990. Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. Oecologia 84:145–157.

Andrews C, Bertram JEA. 1997. Mechanical work as a determinant of prey-handling behavior in the Tokay gecko (*Gekko gecko*). Physiol Zool 70(2):193–201.

Arnold EN. 1998. Cranial kinesis in lizards, variations uses and origins. Evol Biol 30:323–357.

Ballinger RE, Lemos-Espinal JA, Sanoja-Sarabia S, Coady NR. 1995. Ecological observations of the lizard *Xenosaurus grandis* in Cuautlapán, Veracruz, México. Biotropica 27:18–132.

Barel CDN. 1983. Towards a constructional morphology of chichlid fishes (Teleostei, Perciformes). Neth J Zool 33: 357–424.

Carothers JH. 1984. Sexual selection and sexual dimorphism in some herbivorous lizards. Am Nat 124:244–254.

Censky EJ. 1996. The evolution of sexual dimorphism in the teiid lizard *Ameiva plei*: a test of alterntive hypothesis. In: Powell R, Henderson RW, editors. Contributions to West Indian Herpetology: a tribute to Albert Schwartz. New York: SSAR. p 277–289.

Cleuren J, Aerts P, De Vree F. 1995. Bite and joint force analysis in *Caiman crocodilus*. Belg J Zool 125:79–94.

Cooper WE Jr, Lemos-Espinal JA, Smith GR. 1998. Presence and effect of defensiveness or context on detectability of prey chemical discrimination in the lizard *Xenosaurus platyceps*. Herpetologica 54(3):409–413.

Cooper WE Jr, van Wijk JH, Mouton PLeFN. 1999. Incompletely protective refuges: selection and associated defences by a lizard, *Cordylus cordylus* (Squamata: Cordylidae). Ethology 105:687–700.

Deban SM, O'Reilly JC, Theimer T. 1994. Mechanism of defensive inflation in the chuckwalla *Sauromalus obesus*. J Exp Zool 270:451–459.

Felsenstein J. 1985. Phylogenies and the comparative method. Am Nat 125:1–15.

Felsenstein J. 1988. Phylogenies and quantitative characters. Ann Rev Ecol Syst 19:445–472.

Fitch HS. 1981. Sexual size differences in reptiles. Misc Pub Mus Nat Hist, Univ Kansas 70:1–72.

Freeman PW. 1979. Specialised insectivory: beetle-eating and moth-eating molossid bats. J Mammalogy 60:467–479.

Greene HW. 1988. Antipredator mechanisms in reptiles. In: Gans C, Huey RB, editors. Biology of the Reptilia. New York: Alan R. Liss. p 1–152.

Haas G. 1960. On the trigeminal muscles of the lizards *Xenosaurus grandis* and *Shinisaurus crocodilurus*. Am Mus Novitates 2017:1–54.

Haas G. 1973. Muscles of the jaws and associated structures in the Rhynchocephalia and Squamata. In: Gans C, Parsons TS, editors. Biology of the Reptilia. New York: Academic Press. p 285–490.

Hanken J, Hall BK. 1993. Mechanisms of skull diversity and evolution. In: Hanken J, Hall BK, editors. The Skull, Vol. 3. Chicago: University of Chicago Press. p 1–36.

Herrel A. Aerts P, De Vree F. 1998a. Static biting in lizards with a primitive skull: functional morphology of the temporal ligaments. J Zool, Lond 244:135–143.

Herrel A, Aerts P, De Vree F. 1998b. Ecomorphology of the lizard feeding apparatus: a modelling approach. Neth J Zool 45(1):1–25.

Herrel A, Van Damme R, De Vree F. 1996. Testing the niche divergence hypothesis by bite force analysis. Neth J Zool 46:253–262.

Herrel A, Spithoven L, Van Damme R, De Vree F. 1999. Sexual dimorphism of head size in *Gallotia galloti*; testing the niche divergence hypothesis by functional analyses. Funct Ecol 13(3):289–297.

Hertz PE, Huey RB, Nevo E. 1982. Fight versus flight: body temperature influences defensive responses of lizards. Anim Behav 30:676–679.

Kiltie RA. 1982. Bite force as a basis for niche differentiation between rain forest peccaries (*Tayassu tajacu* and *T. peccari*). Biotropica 14:183–195.

Lemos-Espinal JA, Smith GR, Ballinger RE. 1998. Thermal ecology of the crevice-dwelling lizard *Xenosaurus newmanorum*. J Herpetol 32(1):141–144.

Molina-Borja M, Padron-Fumero M, Alfonso-Martin MT. 1998. Morphological and behavioural traits affect the intensity and outcome of male contests in *Gallotia galloti* (Family Lacertidae). Ethology 104:314–322.

Moon BR. 1999. Testing an inference of function from structure: snake vertebrae do the twist. J Morphol 241: 217–225.

Preest MR. 1994. Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: who do females take smaller prey than males? J Herpetol 28(3):292–298.

Presch W. 1981. Life history notes. Sauri. *Xenosaurus grandis*. Food. Herpetol Rev 12:81.

Rieppel O. 1980. The phylogeny of anguinomorph lizards. Denkschriften der Schweizerischen Naturforschenden Gesellschaft 94:1–86.

Schlesinger CA, Shine R. 1994. Selection of diurnal retreat sites by the nocturnal gekkonid lizard *Oedura leseurii*. Herpetologica 50:156–163.

Sinclair AG, Alexander RMcN. 1987. Estimates of forces exerted by the jaw muscles of some reptiles. J Zool, Lond 213: 107–115.

Smith JM, Savage RJG. 1959. The mechanics of mammalian jaws. School Science Review 40:289–301.

Smith GR, Lemos-Espinal JA, Ballinger RE. 1997. Sexual dimorphism in two species of knob-scaled lizards (genus *Xenosaurus*) from Mexico. Herpetologica 53:200–205.

Trivers RL. 1976. Sexual selection and resource-accruing abilities in *Anolis garmani*. Evolution 30:253–269.

Vanhooydonck B, Van Damme R. 1999. Evolutionary relationships between body shape and habitat use in lacertid lizards. Evol Ecol Res 1:785–805.

Wainwright PC. 1987. Biomechanical limits to ecological performance: mollusc-crushing by the Caribbean hogfish, *Lachnolaimus maximus* (Labridae). J Zool, Lond 213: 283–297.