

The relationship between skull morphology, biting performance and foraging mode in Kalahari lacertid lizards

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Received November 2002; accepted for publication October 2003

Lizards are a diverse clade in which one radiation consists entirely of sit-and-wait foragers and another consists of wide foragers. Lizards utilizing these two foraging modes are known to differ in diet, but little is known about how feeding morphology relates to diet and/or foraging mode. This study tested the hypothesis that skull morphology and biting performance are related to diet preference, and consequently, coevolve with foraging mode. Four species of lacertid lizard were studied because they vary in foraging mode, their phylogenetic relationships are known and they are well studied ecologically. Using an 'ecomorphological' approach, skull morphology and biting performance were quantified and mapped on to the phylogeny for the species. The results indicate that sit-and-wait species have shorter, wider skulls than the wide foraging species, and that all are significantly different in overall head shape. The sit-and-wait species had similar values for biting performance; however, clear phylogenetic patterns of covariation were not present between sit-and-wait and wide foraging species for either biting performance or skull morphology. Thus, skull morphology and performance have little influence on diet and foraging mode in these species. Instead it is likely that other factors such as seasonal prey availability and/or life history strategy shape foraging mode decisions. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, 140, 403–416.

ADDITIONAL KEYWORDS: bite force – feeding – functional morphology – Lacertidae – performance – phylogenetic mapping.

INTRODUCTION

Foraging mode describes the movement patterns of organisms during the acquisition of prey (Pianka, 1966; Gerritsen & Strickler, 1977). Sit-and-wait foragers (SW) move infrequently and ambush prey as it comes within range, and thus SW predators tend to eat mobile and often fleet prey (e.g. grasshoppers). By contrast, wide foragers (WF) are active predators that move frequently through the habitat in search of sedentary, patchy prey (e.g. termites) (Eckhardt, 1979; Huey & Pianka, 1981; Magnusson *et al.*, 1985; Perry & Pianka, 1997). Foraging modes have been studied in many vertebrate taxa; however, the foraging modes of lizards have been studied extensively (e.g. Pianka,

1966; Pianka, 1986; Perry, 1999). The 'sit-and-wait/wide foraging paradigm' in lizards is based on thousands of foraging observations in the field (e.g. Schoener, 1971; Huey & Pianka, 1981; Pietruszka, 1986; McLaughlin, 1989) and is widely cited as a general descriptor of lizard ecology.

Foraging mode influences many aspects of lizard biology. Foraging mode has been correlated with lizard body and tail size (Huey & Pianka, 1981), locomotor performance (Huey *et al.*, 1984), diet (Gasnier, Magnusson & Lima, 1994), metabolic rate (Anderson & Karasov, 1981; Nagy, Huey & Bennett, 1984; Autumn, Weinstein & Full, 1994), feeding behaviour (McBrayer & Reilly, 2002), habitat use (Belluire & Carrascal, 1996), reproduction (Vitt & Price, 1982; Vitt, 1990) and learning ability (Day, Crews & Wilczynski, 1999). Thus for many aspects of lizard biology, considerable support for the SW–WF paradigm exists.

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However, foraging mode also follows phylogenetic lines. During the squamate radiation, a key behavioural shift among insectivores occurred. One large radiation, the Iguania, has retained the ancestral condition of sit-and-wait foraging (Cooper, 1995, 1997a, b), whereas virtually all of another major squamate radiation, the Autarchoglossa, evolved wide foraging (Cooper, 1994, 1995; Schwenk, 1995). The Gekkota (Scleroglossa) are thought to be primarily sit-and-wait foragers (Perry, 1999). Perry (1999) presented an extensive review of lizard movement patterns (as an indicator of foraging mode) and demonstrated that foraging patterns are highly conservative within taxonomic families. Furthermore, his analysis suggested that foraging modes are not as clearly dichotomous as has long been thought. Thus, rigorous comparative tests of the SW–WF paradigm bring into question many of the earlier correlative works that were based upon broad phylogenetic comparisons of iguanians to autarchoglossans (Perry, 1999).

As originally described by Huey & Pianka (1981), the SW–WF paradigm hypothesized several corollaries including locomotor capacity, life history and sensory abilities (chemoreceptive or visual). Only one of these, chemoreception, has been extensively studied and corroborated in a broad and explicitly phylogenetic context. Cooper (1997a) demonstrated correlated evolution in lingual morphology, vomeronasal organ development and foraging mode across several lizard families. Several other studies argued that lingual and vomeronasal morphology have coevolved with foraging mode (Schwenk, 1993; Cooper, 1994, 1995, 1997a, b, 1999, 2000a, b; Cooper & Whiting, 1999; Cooper & Hartdegen, 2000). However, other ecological and morphological corollaries of the paradigm have yet to be studied in adequate detail.

Although improved chemoreception was surely important in the evolution of wide foraging lizards, the role of the skull in food gathering and processing was undoubtedly also important during lizard evolution (Cooper, 1997b, 2000b; Vitt *et al.*, 2003). For many vertebrate groups and foraging styles, the relationship between cranial morphology, diet and feeding performance has been explored. In fact, key biomechanical elements and regions of the skull are known to be associated with various prey types in a wide range of vertebrate taxa (e.g. mammals: Radinsky, 1981; Kiltie, 1982; fish: Lauder, 1991; birds: Zweers, Berkhoudt & Vanden Berge, 1994; Perez-Barberia & Gordon, 1999). Thus, it is surprising that the relationship(s) between the head skeleton and foraging mode has not been quantified in lizards, especially considering that dietary variation is a corollary of the SW–WF paradigm.

In terms of diet, SW and WF lizards differ in the amount of active (grasshoppers and beetles; SW) and

sedentary (termites and larvae; WF) prey included in the diet (Huey & Pianka, 1981; Pianka, 1986). Although some overlap of prey taxa exists between SW and WF (Perry *et al.*, 1990; Vitt *et al.*, 2003), the relative amounts (proportionately and volumetrically) of sedentary and active prey consistently differ statistically for each foraging mode (Huey & Pianka, 1981; Pianka, 1981). Although 'active' and 'sedentary' are broad categorizations of prey types, one might expect active prey items to be relatively hard (or tough) and sedentary prey might be relatively soft (e.g. insect pupa or larvae). In fact, arthropods such as crickets (an active prey item) and spiders (sedentary) have been shown to differ in hardness (Herrel *et al.*, 2001b).

A major pattern in vertebrate biology is the correlation of diet with feeding morphology. Data from several vertebrate groups demonstrate that certain cranial characteristics are associated with specific prey types (Kiltie, 1982; Weijs, 1994; Zweers *et al.*, 1994; Wainwright, 1996; Perez-Barberia & Gordon, 1999). Skull morphology is tightly correlated with dietary variation in fish (Lauder, 1991; Wainwright, 1996), mammals (Radinsky, 1981; Gordon & Illius, 1988) and birds (Richman & Price, 1992; Barbosa & Moreno, 1999a, b). The fact that cranial characters frequently coevolve with dietary preferences in other vertebrates and that chemoreceptive characters of the skull are known to coevolve with lizard foraging modes provides a basis to investigate not only if, but also how, cranial features might be influencing foraging mode evolution.

Given the well-established dietary differences in active and sedentary prey types for SW and WF, and the general correlation of skull design with prey type in vertebrates, one would predict that certain biomechanical and functional traits should vary with differences in preferred prey types (Radinsky, 1981; Emerson, 1985). To test if such traits coevolve with foraging mode, this study compares feeding morphology and performance in a group of lizards within the family Lacertidae. The species studied are the SW and WF species upon which the paradigm was first established, based on differences in foraging mode and diet (Huey & Pianka, 1981). In addition, Perry (1999) argued that members of the lacertid clade are a model system because they vary in movement patterns and provide close phylogenetic context for comparison. The general goal of this study is to compare feeding morphology to feeding performance from a biomechanical perspective (*sensu* Emerson, 1985; Wainwright, 1996) and to examine the relationship between morphology and performance in SW and WF lizards. Skull morphometrics and *in vivo* biting performance are compared in SW and WF species to test the hypothesis that variation in foraging mode is correlated with variation in skull design and feeding performance. To

illustrate how, or if, morphological and performance traits coevolve with foraging modes, the data are mapped on the phylogeny for the species studied to reveal character state changes during the evolution of foraging mode (e.g. Lauder, 1991; Reilly & Lauder, 1992; Losos & Miles, 1994).

MATERIAL AND METHODS

Because of the phylogenetic dichotomy of foraging mode in lizards, comparative tests of foraging mode evolution are often too broad to be meaningful (Perry, 1999). Ideally, one would want to examine cranial form and foraging mode within a single, well-supported lineage that showed variation, or even reversals, in one or both of these variables. Three families of lizards (Cordylidae, Lacertidae and Scincidae) contain species that have secondarily derived the SW mode (Cordylidae: Cooper, Whiting & Van Wyk, 1997; Mouton, Geertsema & Visagie, 2000; Lacertidae: Huey & Pianka, 1981; Cooper & Whiting, 1999; Scincidae: Castanzo & Bauer, 1993; Cooper & Whiting, 2000; Cooper, 2000a). The lacertid lizards of southern Africa were chosen as the model system for this study for several reasons. Four closely related species (WF = *Heliobolus lugubris*, *Pedioplanis namaquensis*; SW = *Pedioplanis lineoocellata*, *Meroles suborbitalis*) are widely cited as varying in foraging mode and, in fact, are the original models for the SW–WF paradigm (Pianka, Huey & Lawlor, 1979; Huey & Pianka, 1981; Perry & Pianka, 1997; Cooper & Whiting, 1999). These species are broadly sympatric, similar in body size (Huey & Pianka, 1981; Pianka, 1986) and their phylogenetic relationships are known (Fig. 1). This group is also very well studied ecologically (Pianka & Huey, 1971; Pianka *et al.*, 1979; Huey & Pianka, 1981; Pianka, 1981, 1986; Bennett, Huey & John-Alder, 1984; Huey *et al.*, 1984). Finally, large series of preserved specimens are available in museum collections, which not only provide large samples for morphometric analyses but also are the voucher specimens for earlier studies of their foraging mode and diet (Pianka, 1986).

MORPHOLOGY

To quantify morphological differences among the study species, alcohol-preserved specimens were obtained from the Los Angeles County Museum of Natural History (*H. lugubris*, *N* = 69; *Meroles suborbitalis*, *N* = 51; *Pedioplanis namaquensis*, *N* = 69; *Pedioplanis lineoocellata*, *N* = 62) (LAMNH specimen numbers in the Appendix). The following external measurements were taken from each specimen: snout-vent-length (SVL), mass (g) and depth of the skull (cranial skeleton including the mandible) at the quad-

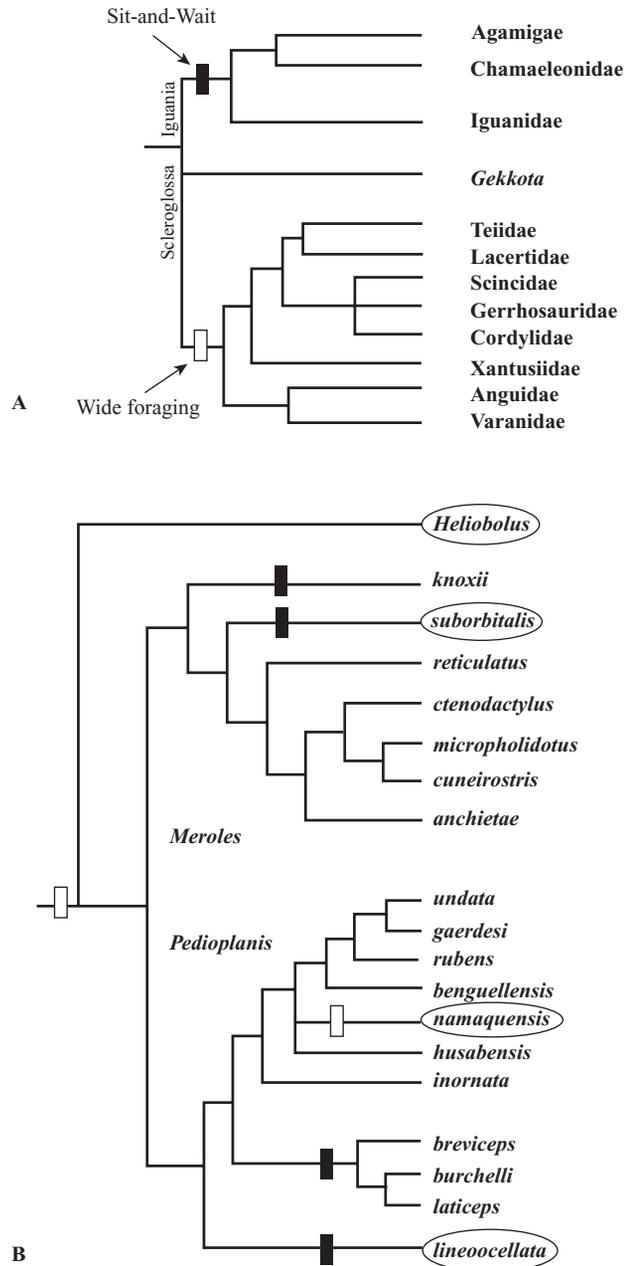


Figure 1. A, phylogenetic relationships among major lizard clades showing the evolution of foraging mode across squamates. The cladogram is based on Estes, de Queiroz & Gauthier (1988). B, phylogenetic relationships among the taxa included in this study. Sit-and-wait foraging (black bars) is presumed to be the basal condition for both *Meroles* and *Pedioplanis*. See text for details. The cladogram is based on Arnold (1991).

rate bones. Subsequently, each specimen was radiographed. Several lizards were laid flat on the film (Kodak Industrex M) and radiographed (Hewlett Packard Faxitron Series model 43805N; 30 kVp, 3 mA

for 90 s) in dorsal view. Rubber bands were placed across the heads of the lizards and around the cardboard backing of the film to hold the mandible firmly against the film to ensure a direct dorsal/ventral orientation of the skull. After exposure and developing, digital images of each lizard radiograph were downloaded to PC using a Dazzle video capture board.

Skeletal variables were measured from each radiograph using Measurement TV software (Updegraff, 1990). The following linear measurements were taken from each skeletal image: quadrate to posterior tip of retroarticular process (RAP), quadrate to tip of the coronoid process (QC), tip of coronoid process to tip of the mandible (CT), anterior tip of the lower jaw to posterior tip of the retroarticular process (i.e. jaw length, JL), width of the jaw at the coronoid process (JW), width between the lateral margins of the quadrate bones (i.e. head width, HW), tip of the snout to the skull–vertebral column articulation (i.e. head length, HL) and width of the quadrate (QW). The length of the jaw out lever (OL) was calculated by adding the values for QC and CT. This value, OL, also provided a measure of the total clearance between the upper and lower jaws (i.e. absolute gape) (Emerson, 1985), whereas differences in relative gape among taxa were determined as $HW - (2 * QW)$ (Emerson, 1985). These lacertid species have relatively flat heads anteriorly. Thus the error in the linear distances due to differences in head depth is believed to be minimal.

The linear measurements above were chosen because they are biomechanically informative and most correspond to aspects of the lever mechanics of the jaws. In the past, many of these measurements have been combined into ratios to represent the mechanical advantage of the lower jaw (e.g. QC/OL) (Radinsky, 1981; Emerson, 1985). However, ratios are often difficult to interpret in statistical tests (Packard & Boardman, 1987). Therefore, I analysed 11 morphological measures as linear distances alone. Although some biomechanical information may be lost, the statistical tests and interpretations are more straightforward.

The SW lacertids (*P. lineoocellata*, *M. suborbitalis*) are predicted to have deeper and/or wider heads in relation to WF lacertids (*P. namaquensis*, *H. lugubris*). If the other skeletal elements are equal in size and proportion, having a deeper and/or wider head allows for increased packing of jaw adductor musculature and thereby increases the force production required to capture large, active prey items. However, a deeper and/or wider head will also increase relative gape. In addition, the SW species are predicted to have a longer quadrate–coronoid (QC) distance relative to out lever distance (OL) than the WF. The QC and OL variables represent the jaw closing force in and out levers, respectively. Having a longer

QC distance relative to OL distance will increase the mechanical advantage of jaws, and thus the bite force that is needed to subdue large active prey. This hypothesis would be rejected if the SW species do not covary or if they have lower values than the WF species. Wide foragers should minimize gape cycle times (prey handling) given that their prey is patchily distributed (Emerson, 1985). Thus, wide foragers are predicted to have longer, narrower heads and smaller relative gapes than SW species. Having a longer head would increase the opening and closing velocity potential of the jaws, thereby serving to minimize gape cycle times (Emerson, 1985). This hypothesis would be rejected if cranial characteristics (HL, HW, GAPE) did not covary between the WF species or if these values were smaller for wide foragers than for sit-and-wait foragers.

FIELD MEASUREMENT OF BITING PERFORMANCE

Bite force is a performance measure that could be crucial in determining the prey spectrum available to lizards (Herrel, De Grauw & Lemos-Espinal, 2001a). Biting performance was quantified by measuring maximal compressive bite force. Using foil strain gages arranged in a wheatstone bridge circuit, a double cantilever bite force transducer measured the change in resistance produced as the cantilever beams were displaced towards each other when the lizard bit down upon it (R. A. Anderson & L. D. McBrayer, unpubl. data; Sinclair, 1983). This change in resistance was generated as a voltage change, digitized (ComputerBoards, PCMCIA DAS-08) and stored in Microsoft Excel (ComputerBoards DAS Wizard software). The transducer was calibrated by placing known masses at a specific location (2 mm from the end of bite bars). All lizards bit the transducer at this location so that actual force values were obtained by scaling the millivolt output to Newtons after the calibration with known weights.

To obtain bite forces, lizards were collected via noosing in December 2001 in the Kalahari of South Africa and Namibia (Permit nos.: South Africa N 031/2001; Namibia 437/2001). Field captured lizards were measured for mass (g) and SVL (mm). Each individual was then induced to bite the transducer a minimum of three times to achieve a maximal bite from each individual (R. A. Anderson & L. D. McBrayer, unpubl. data). The largest force value from these trials was used for further analysis. Following all data collection, lizards were released at the point of capture. The maximum voluntary bite forces were measured for each of the four species (*Heliobolus lugubris*, $N = 26$; *Meroles suborbitalis*, $N = 16$; *Pedioplanis lineoocellata*, $N = 34$; *Pedioplanis namaquensis*, $N = 21$) at their preferred body temperature (35–39°C; Huey, Pianka & Hoffman,

1977). In terms of feeding performance, I predicted maximum bite force would be greater in SW species owing to their ability to capture large, active prey items and the above prediction that SW species have relatively higher QC distances relative to OL distances (Emerson, 1985).

STATISTICAL ANALYSES

Univariate analysis of variance (GLM ANOVA) and Scheffe's multiple comparison post hoc tests were used to test the specific predictions regarding head design (i.e. differences in HD, HW, HL, GAPE, OL). Because one of the species was significantly smaller than the other three, these tests were run both before and after a size correction. The variation in body size was corrected for all morphological variables via the technique of Mosimann & James (1979). The 11 raw morphological measures of each individual were \log_{10} transformed, summed and divided by the total number of measurements. This quotient represents the log-size component. Each measurement of each individual was divided by its log-size value to yield a size-free estimate of that measurement. Following size-removal, the data were centred by adding a value of two to each observation. Each log-transformed, size-removed, centred variable for each species was scanned for outliers and checked to ensure that it conformed to a normal distribution. Finally, the data were tested for sexual dimorphism; no significant differences were observed.

Quantitative variation in the size-corrected skeletal measurements was assessed via canonical variates analysis (CVA) (PROC CANDISC; SAS, 2001). This analysis produces an uncorrelated set of linear combinations of the original variables called canonical variates. These variates define the morphological space encompassed by each species. The species were entered as the discriminating independent variable and the 11 skeletal measures were used as independent variables. I determined which variables characterized each canonical axis by examining the direction and magnitude of the correlations between the canonical variates and the original variables. In addition, Mahalanobis' D^2 values were computed among the centroids of the species (and the associated critical values) to reveal the degree of morphological differentiation. For significance tests among the species, all possible pairwise comparisons were computed and, consequently, the significance levels were adjusted using the Bonferroni correction.

Prior to analysis of the bite force data, diagnostic tests for outliers and normal distribution were performed. The raw data were normally distributed and used in subsequent analyses. To control for differences in body size among species, the data were regressed on

head length and the residuals collected. Univariate analysis of variance and Scheffe's multiple comparison post hoc tests were used to test for differences in mean bite force among species using both raw and size-corrected data sets.

Finally, patterns of covariation in morphology and bite force among the SW and WF lacertids were explored. Traits were mapped on to the phylogenetic relationships of the four species to test the prediction that morphology and performance would change in tandem with foraging mode. The morphological differences mapped were taken from the results of the raw and size corrected ANOVAs and the canonical variates analysis. The performance differences mapped were taken from the results of the raw and size-corrected ANOVAs of bite force.

Ideally, several more species of *Meroles* and *Pedioplanis* would have been included in this study. However, the foraging modes of most other species in these genera are not well established. Furthermore many of these additional species have isolated or restricted distributions, thereby making field studies and statistically meaningful samples extremely difficult to obtain. Therefore, only the four species originally used to describe the SW and WF paradigm were included. However, because of this, two equally parsimonious possibilities exist to describe the sequence of foraging mode evolution in the four study taxa. The SW foraging mode either evolved twice, once in *Meroles* and once in *Pedioplanis*, or the SW mode evolved once in *Meroles* and remained unchanged until the ancestral WF mode reappeared in *P. namaquensis*. For this study, I assumed that the SW mode and any associated characters evolved once at the *Meroles-Pedioplanis* node and that *P. namaquensis* has secondarily derived WF. The justification for this assumption was that (1) there is good support for the sister relationship between *Meroles* and *Pedioplanis* (Arnold, 1991); (2) *Meroles suborbitalis* is a basal member of its genus (Arnold, 1991) and several descendant species of *Meroles* are cited as being SW (Cooper & Whiting, 1999); and (3) *P. lineocellata* is probably the basal member of its genus (Arnold, 1991). Thus, it is probable that the SW mode arose at the *Meroles-Pedioplanis* node and was subsequently lost in descendant taxa such as *P. namaquensis*.

RESULTS

MORPHOLOGY

Morphological variation is summarized in Table 1. The analysis of the raw, non-size-corrected morphological data showed mixed support for the specific predictions made regarding head design. The SW species

Table 1. Variation in head morphology and maximum bite force in sit-and-wait (*Meroles suborbitalis*, *Pedioplanis lineocellata*) and wide foraging (*Heliobolus lugubris*, *Pedioplanis namaquensis*) lizards. The means (\pm 1SE) for each species are based on sample size (morphology/bite force) indicated in the bottom row. Values in parentheses below the raw data are the size-corrected means (\pm 1SE). Five variables (head depth, head width, head length, gape, out lever) were used to test specific predictions of variation in head morphology between SW and WF species. Underlining indicates the raw species means of these variables are not significantly different based on Scheffe's multiple comparison post hoc test. Shared letters indicate no significant difference between size-corrected species means. *Abbreviations:* SVL = snout vent length; HD = head depth; RAP = retroarticular process; QC = quadrate–coronoid distance; CT = coronoid tip distance; JL = jaw length; JW = jaw width; HW = head width; HL = head length; QW = quadrate width; GAPE = gape; OL = jaw closing out lever

	<i>H. lugubris</i> WF	<i>M. suborbitalis</i> SW	<i>P. lineocellata</i> SW	<i>P. namaquensis</i> WF
SVL	56.75 \pm 0.40	58.21 \pm 0.47	57.26 \pm 0.40	49.52 \pm 0.42
HD	6.72 \pm 0.10 (0.066 \pm 0.003) ^A	6.28 \pm 0.07 (0.040 \pm 0.003) ^C	6.43 \pm 0.06 (0.052 \pm 0.003) ^B	5.01 \pm 0.05 (0.026 \pm 0.003) ^D
HW	7.78 \pm 0.06 (0.127 \pm 0.002) ^B	8.21 \pm 0.07 (0.138 \pm 0.001) ^A	7.93 \pm 0.08 (0.133 \pm 0.001) ^A	6.51 \pm 0.05 (0.122 \pm 0.001) ^B
HL	14.27 \pm 0.10 (0.366 \pm 0.002) ^A	13.99 \pm 0.12 (0.354 \pm 0.002) ^B	13.94 \pm 0.13 (0.359 \pm 0.002) ^B	12.47 \pm 0.10 (0.373 \pm 0.002) ^A
GAPE	5.18 \pm 0.06 (-0.026 \pm 0.003) ^A	5.34 \pm 0.07 (-0.023 \pm 0.004) ^A	5.16 \pm 0.09 (-0.025 \pm 0.003) ^A	4.43 \pm 0.04 (-0.018 \pm 0.003) ^A
OL	12.36 \pm 0.10 (0.307 \pm 0.001) ^A	12.22 \pm 0.12 (0.299 \pm 0.001) ^B	12.26 \pm 0.12 (0.309 \pm 0.001) ^A	10.58 \pm 0.09 (0.307 \pm 0.001) ^A
RAP	2.26 \pm 0.03	2.45 \pm 0.03	2.15 \pm 0.03	1.88 \pm 0.03
QC	4.02 \pm 0.06	3.78 \pm 0.06	4.23 \pm 0.06	3.54 \pm 0.04
CT	8.35 \pm 0.06	8.44 \pm 0.07	8.03 \pm 0.08	7.04 \pm 0.06
JL	14.48 \pm 0.10	14.41 \pm 0.11	14.16 \pm 0.13	12.28 \pm 0.10
JW	1.15 \pm 0.03	1.28 \pm 0.04	1.15 \pm 0.03	0.93 \pm 0.03
QW	1.30 \pm 0.02	1.43 \pm 0.03	1.39 \pm 0.02	1.04 \pm 0.02
Newtons	2.75 \pm 0.17 (0.5551 \pm 0.1877) ^A	2.49 \pm 0.16 (-0.0260 \pm 0.1156) ^{BC}	2.26 \pm 0.09 (-0.1483 \pm 0.0728) ^{AB}	1.06 \pm 0.05 (-0.4132 \pm 0.0719) ^C
N	69/26	51/16	69/36	62/21

were not different from each other in head depth but were different from each WF species. For head width, *M. suborbitalis* (SW) and *P. namaquensis* (WF) were significantly different from *P. lineocellata* (SW) and *H. lugubris* (WF). Morphological differences in head length, GAPE and out lever followed the same pattern observed in overall body size (SVL); *H. lugubris*, *M. suborbitalis* and *P. lineocellata* were not different from one another but all were significantly different from *P. namaquensis*. After correcting for size differences, the predicted pattern of SW species having wider and shorter heads was observed (Table 1, lettering). Size-corrected head depth was significantly different in each of the four species, whereas GAPE was not different in any of the four. The length of the jaw out lever (OL) was significantly shorter in *M. suborbitalis* than in the other three species.

The canonical variates analysis determined that significant differences existed among the four species in skull morphology (Wilks' $\Lambda = 0.2007$, $P < 0.0001$). The first two canonical axes explained 82% (57% + 25%) of the overall variation in skeletal mor-

phology. The third axis explained the remaining 18%. Table 2 shows the correlations between the original variables and each canonical variate axis. The first canonical axis (CAN1) was negatively correlated with gape, head length and quadrate–coronoid, and positively correlated with head depth and head width. Axis two (CAN2) was described by high negative loadings for quadrate width and jaw width, and high positive loadings for jaw length and out lever length. Axis three (CAN3) was highly positively correlated with retroarticular process length and coronoid–tip length.

To illustrate how species occupied the multivariate space, the means of the canonical variate scores for each species are plotted three dimensionally in Figure 2. It was expected that the SW species (*M. suborbitalis*, *P. lineocellata*) and the WF species (*H. lugubris*, *P. namaquensis*) would occupy similar regions of the morphological space. However, this was not the case. For example, along the first canonical axis (CAN1), *H. lugubris* (WF), *M. suborbitalis* (SW) and *P. lineocellata* (SW) have deep heads and small gapes. By contrast, *P. namaquensis* (WF) has a thin

head and large gape. On axis two (CAN2), the congeners *P. lineocellata* and *P. namaquensis* have intermediate values for quadrate width, jaw length and jaw width whereas *H. lugubris* has high values for these variables and *M. suborbitalis* low values. On axis three (CAN3), two wide foraging species (*H. lugubris*, *P. namaquensis*) have values very similar to one (*M. suborbitalis*) but not the other (*P. lineocellata*) SW species.

To quantify whether species occupied unique portions of the morphological space, Mahalanobis' D^2 distances were computed (Table 3). The largest distances were between *P. namaquensis* and the remaining species, indicating that it was the most morphologically distinct species. Although the D^2 value between them was significant, *H. lugubris* (WF) and *P. lineocellata* (SW) occupied positions closest to one another within morphological space even though they differ in foraging modes. Thus, the analysis of skull morphology

demonstrated species-specific patterns of morphological variation; however, this variation did not covary with predictions made regarding foraging mode.

BITE FORCE

Mean voluntary bite force was most similar between the two SW species (*P. lineocellata*, *M. suborbitalis*) (Table 1). Without controlling for body size differences, bite force differed significantly among the species (ANOVA; $F_{3,93} = 30.77$; $P < 0.001$). Post hoc tests revealed that *P. namaquensis* differed from all other species and that *P. lineocellata* was significantly different from *H. lugubris* (Fig. 3; Table 1, underlining). After adjusting for body size differences, significant differences existed among the species (ANOVA $F_{3,93} = 12.45$, $P < 0.01$). However, post hoc tests showed that *H. lugubris* had significantly greater bite force than *M. suborbitalis* and *P. namaquensis* but not

Table 2. Results of canonical variates analysis on 11 size-corrected skull measurements taken for sit-and-wait and widely foraging lacertid lizards. Values in the table are the variable-variante correlations with the percentage variance explained on each canonical axis at the bottom. Each axis was significant ($P < 0.01$)

	Can1	Can2	Can3
Head Depth	0.806	0.578	-0.126
Retroarticular Process	-0.078	-0.608	0.790
Quadrate-Coronoid	-0.606	0.501	-0.618
Coronoid-Tip	0.210	0.094	0.973
Jaw Length	0.253	0.905	0.342
Jaw Width	-0.333	-0.889	0.314
Head Width	0.696	-0.662	-0.280
Head Length	-0.716	0.631	0.299
Quadrate Width	-0.032	-0.975	-0.220
Gape	-0.909	-0.308	0.282
Out lever	-0.388	0.742	-0.546
Eigenvalue	1.279	0.549	0.411
Per cent Variance	57.1	24.5	18.4

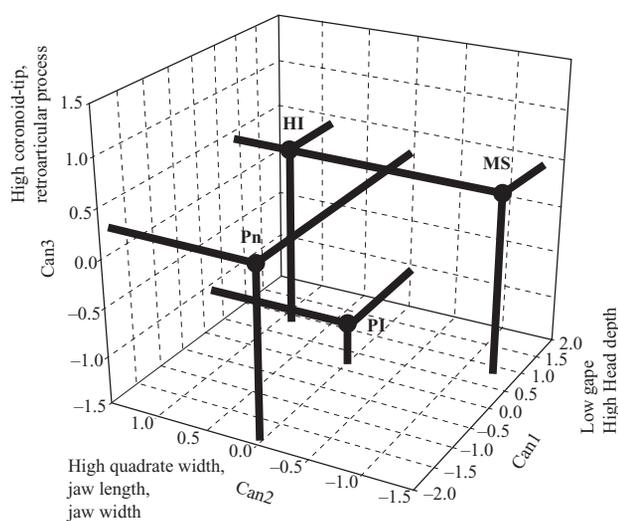


Figure 2. Three-dimensional plot of mean canonical scores of each lacertid species. HI = *Heliobolus lugubris* (WF); MS = *Meroles suborbitalis* (SW); Pl = *Pedioplanis lineocellata* (SW); Pn = *Pedioplanis namaquensis* (WF).

Table 3. Mahalanobis' squared distances (D^2) between species centroids based on size-free morphological variables. Asterisks (*) indicate significance at $P < 0.01$

	<i>H. lugubris</i> WF	<i>M. suborbitalis</i> SW	<i>P. lineocellata</i> SW	<i>P. namaquensis</i> WF
<i>H. lugubris</i>	–			
<i>M. suborbitalis</i>	4.63*	–		
<i>P. lineocellata</i>	3.52*	4.14*	–	
<i>P. namaquensis</i>	8.62*	9.06*	6.01*	–

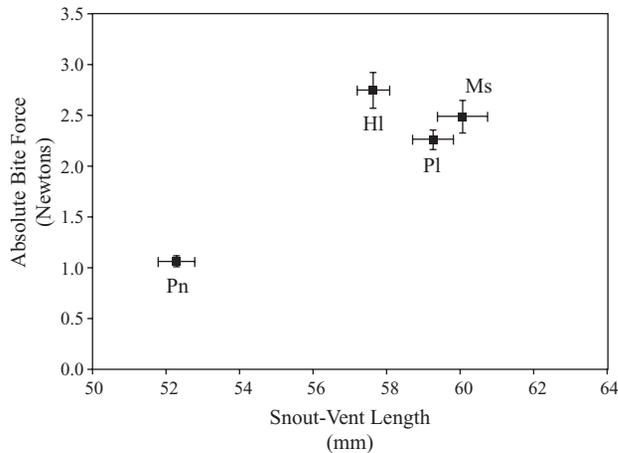


Figure 3. Scatterplot of snout-vent length (mm) and bite force (Newtons). Without correcting for body size differences, *P. namaquensis* was significantly different from all other species and *P. lineocellata* was significantly different from *H. lugubris*. After correcting for body size, *H. lugubris* was significantly different from the other species. The error bars represent standard error. HI = *H. lugubris*, Ms = *M. suborbitalis*, Pl = *P. lineocellata*, Pn = *P. namaquensis*.

P. lineocellata (Table 1, lettering). *Meroles suborbitalis* was not significantly different from either *P. lineocellata* or *P. namaquensis*; but *P. lineocellata* had significantly greater bite force than *P. namaquensis*.

PHYLOGENETIC MAPPING

Changes in both raw and size-corrected traits were mapped on the phylogeny of the four SW and WF species (Fig. 4). Support for the coupling of skull morphology, feeding performance and foraging mode would exist if morphology and performance changed in concert with foraging mode. The raw morphological data suggest that *M. suborbitalis* (SW) has increased its head width relative to the WF *H. lugubris* (Table 1; Fig. 4A). The other SW species, *P. lineocellata*, was no different from *H. lugubris* in head width. For head depth, the SW species had thinner heads than *H. lugubris*. The other WF species, *P. namaquensis*, has drastically reduced its overall size, bite force and many components of its head shape (Table 1; Fig. 4A). Thus *P. namaquensis* has radically changed many aspects of its morphology and is distinct from any of the other species. The results of the size-corrected ANOVAs on the skull variables (bars) and the CVA results (boxes) are mapped in Figure 4B. The CVA results suggest that morphology tracked taxonomic diversification, i.e. overall head morphology changed

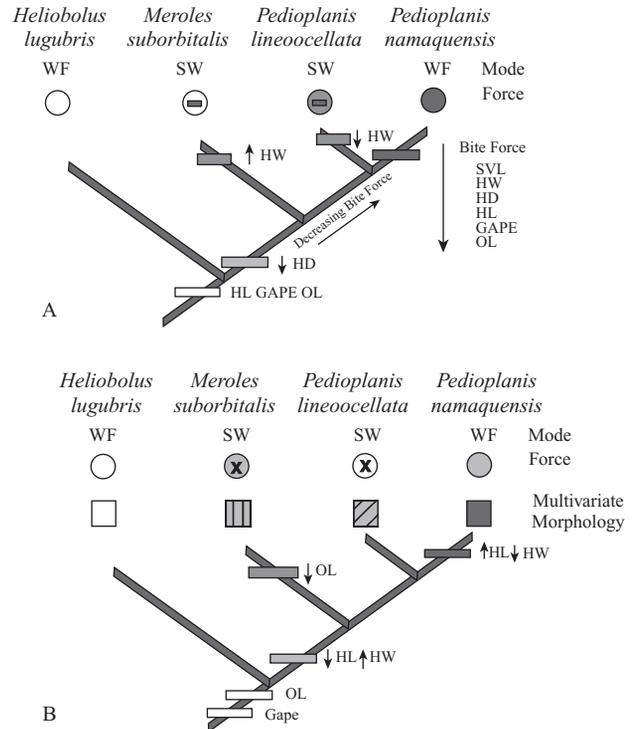


Figure 4. Phylogenetic mapping of skull morphology, biting performance, and foraging mode in four lacertid species. A, evolutionary transitions based on the analysis of the raw morphological and bite force data (Table 1, underlining). B, evolutionary changes based on the canonical variates analysis (boxes; Table 3) and size-corrected ANOVAs (bars and circles; Table 1, lettering). Shared shading or symbols within the circles or boxes indicates no significant difference. The SW and WF species were expected to covary in morphology and biting performance; however, only size-corrected head length and head width met those predictions. See text for details.

at each bifurcation of the phylogeny (Fig. 4B, shaded boxes). The univariate tests showed a different pattern. Each species was significantly different in size-corrected head depth whereas relative gape (GAPE) remained unchanged across the four species. The out lever length (OL) decreased in *M. suborbitalis* but not in any other species. Certain morphological traits appear to have evolved in tandem with foraging mode as predicted. *Meroles suborbitalis* and *P. lineocellata* have short, wide heads as was expected in SW foragers (light grey bar). These traits then change back again in *P. namaquensis*; this WF species has a long, narrow head as predicted for a WF (black bar).

Biting performance decreased from the ancestral condition of *H. lugubris* (high bite force) to similar values in the two SW species (Fig. 4A, B, circles). Not surprisingly, the smaller *P. namaquensis* had even lower bite force values. Thus, although they were similar in

size-corrected bite force, the two SW species unexpectedly had lower biting performance than the WF ancestor *H. lugubris*.

In summary, the two SW species were similar in bite force (Table 1; Fig. 3) and morphology (Table 3). However, they were not always more similar to one another than to a WF species (Fig. 2). The same was true of the WF species. Thus, except for head width and head length, skull morphology and performance did not provide reliable predictors of dietary and foraging mode differences in these lacertid species.

DISCUSSION

MORPHOLOGICAL AND PERFORMANCE VARIATION

In order to feed efficiently on highly mobile and large prey, the SW species (*M. suborbitalis* and *P. lineoocellata*) were predicted to be more similar to one another in skull and gape characteristics than to the WF species (Toft, 1981; Emerson, 1985). This prediction was not supported in the multivariate analysis of head shape. However, by comparing size-corrected trait values, SW species did have significantly wider heads and WF species significantly longer heads (Table 1, lettering). Aside from head width and head length, other aspects of skull morphology that were expected to reflect biomechanical differences had little explanatory value for the differences in foraging mode between these SW and WF species. Because diet has been repeatedly cited as a substantive difference between SW and WF lizards, this study tried to choose morphological (biomechanical) variables that would reflect differences in performance and thus diet and ecology. However, the overall poor correspondence between skull morphology and foraging mode when mapped on the phylogeny demonstrated that this was not the case, especially in biomechanically relevant measures.

There was some evidence for covariation between skull morphology and foraging mode within the two *Pedioplanis* species. *Pedioplanis lineoocellata* and *P. namaquensis* were virtually identical along CAN2 (Fig. 2); however, they differ substantially along CAN1 and CAN3. The first axis, CAN1, was correlated with head depth and gape; *P. lineoocellata* had higher values of head depth whereas *P. namaquensis* had lower values. The deeper skull of *P. lineoocellata* may permit increases in bite force (via increased muscle volume) and relative gape size – important variables to an SW forager that eats large prey. *Pedioplanis namaquensis*, by contrast, had longer components of the lower jaw (coronoid-tip, part of the closing velocity out lever; retroarticular process, part of the opening velocity in lever). These variables would assist in increasing the velocity of mouth opening and closing and thereby aid

in the rapid cycling of the jaws and processing of small prey (Emerson, 1985). Although these patterns may reflect substantive ecological differences, they must be interpreted with caution owing to the lack of similar covariance in the other SW and WF species. Further analyses on more species, however, would enable testing these observations. Nevertheless, as quantified here, it appears that variation in skull morphology may be related more to phylogenetic differentiation (albeit small) than to differences related to diet and foraging mode (Fig. 4).

Bite force was predicted to be higher in the SW species because they capture and process larger, active prey items. However, bite force did not covary between the SW and WF species as predicted. Without correcting for body size differences, the larger SW species did not have the highest bite forces; rather the WF *H. lugubris* did. *H. lugubris* also had the highest size-corrected bite force of all species. In terms of diet, *H. lugubris* takes the highest percentage of termites (a soft prey item) of all species studied (Huey & Pianka, 1981). Therefore, its high bite force capability is probably not related to resource use but may be beneficial for other ecological tasks (intraspecific agonistic encounters, mating, etc.).

The high bite forces of *H. lugubris* may be an example of 'excessive construction' (Gans, 1979). Often, organisms possess morphological or performance capacities beyond what are generally required by their environment. Such capacity provides more degrees of freedom for an individual to respond to fluctuating environmental conditions and thereby potentially lead to increased survival or even adaptive shifts (Gans, 1979). Even though *H. lugubris* apparently eats mostly termites, times of fluctuating termite abundance could require a shift in resource utilization to harder, or at least different, prey items (see below).

Gape size, rather than bite force, may be the critical aspect of skull morphology related to resource use in sit-and-wait and widely foraging lizards. The SW species had shorter and wider heads than the WF (Table 1, lettering). Having a wider head will increase both absolute and relative prey sizes that may be eaten (Emerson, 1985), and furthermore, large prey may be 'preferred' because it will presumably yield more energy than a smaller prey item. However, some data suggest that most arthropod prey is relatively similar in energetic content (Cummins & Wuycheck, 1971). Thus, a tradeoff may exist between gape size and handling time. Lizards may select the largest prey item with the shortest handling time (and thus energetic cost) rather than selecting the largest possible prey item that may be consumed (Herrel *et al.*, 2001b). Such a scenario may explain the dietary differences in these Kalahari lizards. The SW species have a larger gape that enables them to handle large active prey

items more easily, whereas the WF species may reject these because of increased handling times. The SW species are still able to find and process small prey items like termites, but their wider heads enable them to exploit larger, active prey as well.

Although the percentage by number and volume of active prey items in the diets of the study taxa differ (Huey & Pianka, 1981), the diet of *M. suborbitalis* contains 51% termites by volume in summer whereas *H. lugubris* contains 93%. In winter, termites comprise 52% and 84% of the diet, respectively (Huey & Pianka, 1981). In fact, all Kalahari lizard species show an increased dependence on termites (Ricklefs, Cochran & Pianka, 1981). Compared with North American and Australian deserts, the Kalahari has the lowest prey diversity (Pianka, 1986), and thus the abundance of termites in the Kalahari is probably of critical importance to these lacertid species. Furthermore, the Kalahari saurofauna (and lacertids in particular) is less morphologically diverse than either the Australian or the North American fauna. This conservatism has been hypothesized to be due to the 'specialization' of Kalahari lizards on termites (Ricklefs *et al.*, 1981). The importance of being able efficiently to capture and consume this staple prey item may constrain the degree to which Kalahari lacertids may specialize on different prey types.

A reliance on an abundant food source like termites may be critical during particular seasons or periods of environmental variability (Pietruszka, 1986; Taylor, 1986; Bullock, Jury & Evans, 1993). The Kalahari is unique in that it receives no winter rains. During the winter months, lizard diets contain few active prey items (e.g. beetles and locusts) and instead mostly termites are consumed (Pianka, 1986: fig. 4.3). Thus, Kalahari lacertids must survive this period of decreased resource abundance by switching to the most readily available food resource, termites. Wiens & Rotenbury (1980) suggest that selection is relaxed during periods of high resource abundance and subsequent episodic periods of low resource availability do not allow for substantial morphological evolution. This may be the case in Kalahari lacertids – foraging modes and diets converge during the winter because termites are the only available resource. Therefore, selection for change in skull form to increase capture and processing success on active prey is constrained by low availability of this prey type each winter.

The observed similarity of the species studied may also be due to phylogenetic effects (Miles & Dunham, 1993). Lineage effects may have any number of causes (diet, population structure, climate, etc.), but often result in all the members of a particular group having minor variation on a central theme (Arnold, 1994). For example, Jaksic, Nunez & Ojeda (1980) found that lizards of the genus *Liolameus* show striking morpholog-

ical similarities even though the group is speciose and occupies a wide variety of habitats. Here, the SW and WF species are comparable in body size and most head dimensions; however, they differ in variables related to gape (i.e. head length, width). Thus, these species, and possibly other members of this derived lacertid clade, could be phylogenetically and/or developmentally canalized and may vary only slightly in key, ecologically important traits.

It is also possible that the species studied here have not been separated long enough for substantial morphological specialization to occur. Unfortunately, divergence times are not known for members of this clade, and thus this possibility cannot be ruled out. Whether the cause is lineage effects, lack of sufficient evolutionary time or an ecological constraint for termite consumption, it is striking that the species that defined the SW–WF paradigm show such similarity in overall head morphology and lack covariation between morphology and ecology.

IMPLICATIONS FOR THE SW–WF PARADIGM

To date, most ecomorphological studies of lizards have largely centred on the covariation between limb morphology, locomotor performance and microhabitat choice (e.g. Losos, 1990; Miles, 1994; Irschick & Losos, 1999). Although none has specifically addressed foraging modes, many of these studies have been successful in demonstrating a relationship between morphology and ecology. By contrast, ecomorphological relationships of feeding in lizards have seen less study. Herrel *et al.* (1999) revealed patterns of covariation between skull morphology and herbivory; however, the current study is the first to test for relationships between foraging mode and specific aspects of skull morphology.

My results indicate that only head length and head width change as expected with foraging mode. In general, however, skull morphology is not a good predictor of foraging mode for these taxa, but can reveal interesting differences among species. Whether ecological differences result from the observed species-specific morphological differences remains unknown. Most likely the observed variation is more related to phylogenetic diversification than foraging mode. Possibly, another suite of morphological or feeding performance characters is related to foraging biology in these lizards (e.g. feeding behaviour or handling time; Motta, 1989; McBrayer & Reilly, 2002). However, it is equally likely that other factors (e.g. dietary flexibility) guide (or constrain) significant morphological evolution in these species.

A central element in the SW–WF paradigm in lizards is that each foraging mode results in differing exposure to the prey spectrum (active vs. sedentary prey) and, consequently, different diets. Vitt *et al.*

(2003) demonstrated that a detectable shift in diet occurred at the Iguania–Scleroglossa transition and it may be that this dietary shift coincides with the SW–WF transition. The present study demonstrates that observations of dietary differences are not a result of considerable morphological specialization in the skull. Thus for lacertids, the continuum of SW–WF (Pietruszka, 1986; Perry, 1999) may have less to do with prey capture and processing abilities and diet selection than with other important aspects of lizard biology. Although a diet–foraging mode relationship seems intuitive, factors like seasonal fluctuations in prey availability or life history may alter selection regimes such that morphological specialization is not viable (Wiens & Rotenbury, 1980). Therefore, dietary differences between SW and WF may primarily be by-products of other ecological factors rather than a direct consequence of foraging mode. However, given the findings of Vitt *et al.* (2003), it may also be that a diet–foraging mode relationship exists at a higher taxonomic level. The relationship between skull morphology, diet and foraging mode should be explored across higher taxa like families or suborders to assess this hypothesis.

Further research is needed in order to quantify the relationships between foraging mode and other such critical aspects of lizard biology. Lacertids are the best model system available because many aspects of their biology have been well studied and a well-supported phylogeny exists for several genera. These aspects greatly improve the interpretations of any patterns observed (Perry, 1999). However, several species of skinks (Scincidae) and cordylids (Cordylidae) also vary in foraging mode [(skinks: Castanzo & Bauer, 1993; Cooper *et al.*, 1997; Cooper & Whiting, 2000); (cordylids: Greeff & Whiting, 2000; Mouton, Geersema & Visagie, 2002)]. Research on these taxa holds considerable promise in that it will allow for further comparative tests of hypotheses regarding foraging mode evolution.

In particular, comparative studies of life history, locomotor morphology and neuroanatomy are needed for lacertids. Clutch size and egg size are known to covary with each foraging mode across lizard families (Vitt & Congdon, 1978; Dunham & Miles, 1985); however, broad, detailed comparative studies of lacertids, skinks or cordylids have not yet been conducted. Consequently, the strength of the relationship between foraging mode and life history is unclear below the taxonomic level of family. Further studies of covariation in locomotor morphology are also desirable. Seminal studies on locomotor performance in Kalahari lacertids have been conducted (Huey *et al.*, 1984; Nagy *et al.*, 1984); however, studies of the covariation of locomotor performance with morphology are yet to be performed. Finally, neu-

roanatomical studies of SW and WF lizards are lacking. Other derived lacertid species (*Acanthodactylus boskianus*, *A. scutellatus*) were shown to vary in the size of the region of the brain associated with spatial memory (Day *et al.*, 1999). Although locomotor morphology and life history presumably share some relationship to foraging mode, neurological studies that demonstrate differences in the ability to locate prey may offer a mechanism by which foraging decisions are controlled.

ACKNOWLEDGEMENTS

This work could not have been completed without the advice and assistance of Steve Reilly, Audrone Biknevičius, Don Miles, Scott Moody, Roger Anderson, Bill Cooper, Ray Huey, Clay Corbin, Rick Essner, Peter Larson, Kristin Hickey and Andrew Parchman. The Ecolunch and Evomorph discussion groups at Ohio University and the Vertebrate Ecology and Evolution Group at Stephen F. Austin provided many helpful discussions, ideas and criticisms of this and other research related to lizard feeding. The advice and logistical knowledge of Aaron Bauer, Alexander Flemming and Mike Griffin made fieldwork on Kalahari lacertids possible. Martin Price was instrumental in the collection of the bite force data. Henke Picard, Fricki Picard, Henne Molle, Sorel Burger, John and Callo provided tremendous assistance during fieldwork in South Africa and Namibia. The fieldwork for this research was supported by an Ohio University Student Enhancement Award. Tents, sleeping bags and clothing used during fieldwork were graciously supplied by Sierra Designs.

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APPENDIX

Natural History Museum of Los Angeles County (NHMLAC) catalogue numbers of the species included in this study.

Heliobolus lugubris:

79898–79901, 79904–79906, 79908, 79911, 79917–79918, 79924, 79934–9939, 79947, 79951, 80025–80035, 80039, 80042, 80047, 80049, 80050–80053, 80055, 80056, 80060–80063, 80065, 80067–80070, 80072, 80074, 80076–80083, 80085, 80087, 80092–80094, 80097–80100, 80143

Meroles suborbitalis:

81840, 81848, 81857, 81858, 81873, 81875, 81877–81879, 81882, 81886, 81889, 81897, 81903, 81918, 81920, 81929, 81938, 81944, 81946, 81951, 81953, 81954, 81956–81958, 81960–81962, 81965, 81967, 81969–81976, 81980–81983, 81986, 81988, 81990–81993, 81995, 81996

Pedioplanis lineoocellata:

78739–78744, 78754–78764, 78766–78773, 78775–78780, 78782, 78784–78794, 78796–78799, 78801–78803, 78806, 78808–78810, 78816–78818, 78820–78822, 78824–78827, 78831, 78885, 78886, 78904, 78916

Pedioplanis namaquensis:

80186–80195, 80197–80204, 80206, 80208–80216, 80219, 80220, 80229, 80230, 80232, 80233, 80235, 80238, 80256, 80262, 80414, 80422–80425, 80428, 80430, 80441, 80443, 80448, 80454, 80457, 80458, 80460, 80461, 80463, 80465, 80471, 80472, 80476, 80480, 80481, 80483, 80484.