COMPARATIVE STUDIES IN THE FUNCTIONAL MORPHOLOGY OF LIZARD FEEDING: KINEMATICS, BEHAVIOR, AND BIOMECHANICS

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This dissertation entitled

COMPARATIVE STUDIES IN THE FUNCTIONAL MORPHOLOGY OF LIZARD FEEDING: KINEMATICS, BEHAVIOR, AND BIOMECHANICS

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In fish, mammals, and birds the functional morphology of the feeding apparatus has been well studied. However in lizards (non-ophidian squamates), much less is known about the functional variation that may result from their diverse cranial morphologies. Here, I present four functional studies of the lizard feeding apparatus.

Initially, the feeding kinematics of lizards were quantified and used to test two existing models of prey transport for all amniotes. To do so, I devised a method to quantitatively test for differences in kinematic phases of mouth opening. This method, slope analysis, demonstrated that feeding kinematics were highly variable intra- and interspecifically and that one model accurately characterized prey transport in lizards.

Next, variation in feeding behavior was quantified to understand how members of two clades (Iguania, Autarchoglossa) process their prey. Iguanian lizards processed their prey using mostly a palatal crushing behavior while autarchoglossans used puncture crushing. Iguanians also engaged in significantly fewer processing behaviors per feeding bout. Autarchoglossans processed prey extensively and interspersed processing behaviors with transport behaviors. In fact, three behaviors, puncture crushing, prey transport and the total number of behaviors, are coevolving based on independent contrasts analysis. Interestingly, patterns in feeding behavior closely paralleled the dichotomy seen in foraging mode between these clades.
Because feeding behavior and foraging mode are likely related, I investigated how feeding morphology and foraging mode evolve in a group of closely related species. I tested the hypothesis that feeding biomechanics and performance coevolve with foraging mode in Kalahari lacertids. The head length and width variables supported this hypothesis; however, the remaining variables and biting performance did not. Given the extreme dependence of all Kalahari lizards on termites, it is likely that this dietary constraint prevents morphological specialization.

Finally, the tradeoffs between lizard skull form and biting performance are explored. Lizards exceeded predictions regarding the position of the most posterior tooth and muscle resultant. Head width and depth were highly correlated with biting performance within species, however among species, lever mechanics were better predictors. Consequently further studies of functional tradeoffs are required to understand how they might influence lizard ecology and evolution.

Approved: Stephen M. Reilly

Associate Professor of Biological Sciences
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GENERAL INTRODUCTION

From the initial planning of this research, I was challenged to narrow my varied research interests into a cohesive body of work that would set the stage for a career in academia. Then and now, my research interests include behavior, ecology, and functional morphology. In addition to trying to integrate these disciplines, I was advised to construct a project that would ask broad questions and test existing theoretical models. The work contained herein represents my effort to answer questions regarding the ecology and evolution of lizards via integrative and comparative approaches.

The general topic of lizard feeding was chosen as the focus of this dissertation for several reasons. Lizards are a diverse clade ecologically and morphologically. Specifically, tongue morphology has diverged substantially between the two major clades of extant lizards (Iguania and Scleroglossa) (Schwenk, 1989) and is well known to be important in both the acquisition and processing of prey. Various clades of lizards also differ in the presence, absence or degree of cranial kinesis, and most lizard clades have complex jaw adductor morphologies. Ecologically, the locomotor patterns lizards employ in the acquisition of prey (i.e. foraging mode) has diverged between these two large clades as well (Cooper, 1994). Finally, our understanding of lizard feeding function is limited in that most previous research has been conducted on species within one clade (the Iguania). Therefore, the lizard feeding apparatus is a model system for detailed investigations of adaptation, exaptation, and functional variation among species or higher taxa.

Preview

Chapter one is a broad analysis of prey transport kinematics in lizards. Prey transport is a specific behavior common to all vertebrates. Two models of prey transport have been proposed for all amniotes (Bramble and Wake, 1985; Reilly and Lauder, 1990).
However, neither of these general models has been adequately tested due to the lack of a rigorous methodology to quantify and compare the kinematic phases defined by each model (Smith, 1994). Here, a diverse sample of lizard species was used to test if either model sufficiently characterizes how lizards transport their prey. To do so, a method to objectively quantify and compare kinematic phases was devised. The results indicate that lizard transport kinematics are highly variable and that one of the two models best characterizes lizard behavior.

Chapter two is the first detailed analysis of prey processing in lizards. Lizards are generally regarded as swallowing prey whole with little or no processing. This study quantifies the variation in prey processing among 12 lizard species from the iguanian and autarchoglossan clades. Iguanian lizards use more palatal crushing behaviors per feeding bout than autarchoglossans. Autarchoglossans have a higher total number of behaviors per bout due to increases in the number of puncture crushing and transport behaviors. Comparative methods (independent contrasts analysis) demonstrate that three of the behaviors are coevolving and seem to relate to other phylogenetic patterns in tongue morphology, foraging mode and metabolic rate.

Chapter three relates feeding biomechanics to foraging mode in four species of lacertid lizards. Foraging mode (sit-and-wait or wide foraging) is significantly correlated with diet in these species (Huey and Pianka, 1981). The sit-and-wait species tend to eat more mobile prey (e.g. grasshoppers), while the wide foraging species tend to eat smaller, sedentary prey (e.g. termites). Biomechanically, one expects these dietary preferences to lead to morphological specialization for the preferred prey type. Instead, this study shows an extreme degree of morphological conservatism among four Kalahari lacertid species. In fact, head length and width are the only variables of 11 measured that evolved in the
predicted direction. The similar morphologies of these species may be due to a dietary constraint for termite consumption; however, the results are striking given that these species were the taxa originally used to describe the sit-and-wait/wide foraging paradigm in lizard ecology.

Chapter four describes the first phase of a project to understand the functional tradeoffs resulting from variation in cranial morphology. Five species of lizards are used as representative taxa to explore how variation in skull form influences biting performance. The results show that across species lever arm mechanics are good predictors of bite force, however within species, they are not. Instead, general measures of skull size are better predictors. This study will be expanded by both the addition of taxa and data on jaw muscle architecture. Once complete, this study will yield a better understanding of lizard skulls as form-function complexes and thereby lay the groundwork for future studies into the ecological and evolutionary significance of lizard skull form.

Each chapter has strived to tackle questions that have either not been posed or have not been addressed in sufficient detail. However collectively, these chapters not only contribute to the existing body of knowledge regarding lizard functional morphology but also open new avenues of research by integrating behavioral, functional, and comparative methods. The four chapters herein are intentionally broad and comparative so as to help direct more focused investigations in the future. It is my hope that they will serve this purpose both in my future endeavors as well as those of other scientists interested in the causes and/or consequences of morphological diversification in lizards.
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Chapter 1. Testing amniote models of prey transport kinematics: a quantitative analysis of mouth opening patterns in lizards

INTRODUCTION

Prey transport is a specific feeding behavior common to all vertebrates in which the prey item is moved posteriorly in the mouth for further processing or swallowing (Hiiemae et al., 1979; Schwenk, 2000a). The transport behavior is complex in that the jaws, jaw musculature, and tongue musculature must be coordinated in order to perform this behavior (Bels et al., 1994). Aspects of the prey can be important in shaping transport behavior (Throckmorton, 1980; Bels and Balthus, 1988; Urbani and Bels, 1995; Herrel et al., 1999) and the universal use of prey transport in terrestrial vertebrates has made it the subject of many studies of functional and behavioral evolution (Hiiemae, 1978; Reilly et al., 2001).

Two models have been proposed to describe generalized gape movement patterns during prey transport in terrestrial vertebrates. Bramble and Wake (1985) presented a hypothetical model for a generalized tetrapod in which the transport gape cycle (one cycle of opening and closing of the jaws during prey transport) consisted of 3 proposed kinematic ‘phases’ during mouth opening (Figure 1.1a). The first phase of the Bramble and Wake (B-W) model is termed slow opening I (SO-I). It is defined by “a comparatively low gape angle” while the tongue slides beneath the prey item. The second phase, slow opening II (SO-II), “is recognized by a distinct decline in the rate of change of gape” (p. 237) and thus was represented by a plateau in the gape cycle. Bramble and Wake propose that the SO-II phase may be longer in duration than SO-I and that this phase “may have actual as well as theoretical importance”. The fast opening (FO) phase follows SO-II. During FO, the prey item moves posteriorly on the tongue and hyobranchial apparatus. After FO, the mouth
closes rapidly and then more slowly as the jaws contact the prey item (Fig. 1.1a: FC, SC/PS). At its inception, the B-W model was proposed as an hypothesis for generalized tetrapods and was based largely on data from the literature on generalized salamanders, turtle, and lizards.

Reilly and Lauder (1990) proposed second model of prey transport kinematics for amniotes (Fig. 1.1b). The Reilly and Lauder (R-L) model was based upon a quantitative analysis of transport kinematics in fishes, salamanders (outgroups), and data available in the literature for amniotes. The R-L model differs from the B-W model by dividing the opening portion of the gape cycle into only 2 phases (slow opening (SO) and fast opening (FO), Fig. 1.1b). These authors reasoned that because they found no evidence of a distinct change in the rate of mouth opening (i.e. a ‘plateau’) within the gape cycle of fishes, salamanders, and most published amniote transport cycles, that it was not a characteristic of a generalized tetrapod transport cycle (Reilly and Lauder, 1990; Lauder and Reilly, 1994). To date however, neither model has been empirically tested at the amniote level because sufficient data from non-mammalian amniotes (such as lizards) has not been available (Smith, 1994).

Both the B-W and R-L models assume that the change in gape angle throughout the gape cycle is reflective of not only the change in gape, but also the behavior of the tongue (stationary, protracting/retracting) during mouth opening. The key difference between the models is the presence or absence of a SO-II phase in the gape profile. This difference is significant because it implies different functions and/or kinematics for the tongue during the transport behavior. The B-W model specifically states that the tongue is “fitted” to the prey item during SO-II and a plateau in the gape profile (i.e. when the jaws stop opening momentarily) was hypothesized to be result of this tongue fitting behavior. Furthermore, Bramble and Wake argued that the tongue fitting behavior is necessary in order to increase
adhesion between the tongue’s surface and the prey. In contrast, Reilly and Lauder showed that adequate tongue-prey adhesion is attained during SO in all salamanders and most published amniote transport cycles without an associated static phase in jaw opening.

The B-W and R-L models attempted to identify components of a plesiomorphic transport gape cycle that are proposed to exist across amniotes. This effort was based on the fact that many amniotes use similar feeding behaviors, homologous muscles, and presumably some similar motor patterns while feeding (Smith, 1994). Each model has been qualitatively applied to lizard feeding kinematics in several species. However, lizard transport kinematics have not been quantified sufficiently to understand variation among lizards and to test which model best describes lizard transport behavior (Herrel and De Vree, 1999; Elias et al., 2000).

Most of the published kinematic work on lizard feeding has focussed on a limited number of taxa, primarily those from one lineage (Iguania) (reviewed in Schwenk, 2000b). Considerable variation in skull, tongue, and hyobranchial morphology exists across the lepidosaur clade and little comparative kinematic data exists for the non-iguanian taxa (the Scleroglossa) comprising the rest of the lizard phylogeny (Schwenk, 2000b; but see Urbani and Bels, 1995; Delheusy and Bels, 1999; Herrel et al., 1999). A few studies have applied the B-W and R-L transport models to the kinematics of prey transport (Herrel et al., 1996; Herrel and De Vree, 1999; Elias et al., 2000). More often, however, these transport models have been applied to other behaviors, such as prey ingestion (the strike) and reduction (chewing) (Bels and Goosse, 1990; Bels and Delheusy, 1992; Delheusy et al., 1995; Herrel et al., 1995). Although these studies have further explored the utility of these models, the current understanding of how lizards move their skull, jaws, and tongue during prey transport is inadequate. Thus, the utility of the models for prey transport has not been
broadly tested in lizards and currently is confounded by the application of prey transport models to other behaviors. Furthermore, to date, an empirical method of defining, analyzing, and comparing specific kinematic profiles (e.g. gape phases) has not been used to quantify feeding kinematics (Smith, 1994). How does one quantify transitions between a slow or fast movement in order to ascertain their presence or absence or to compare them across taxa? When taken together, these factors have resulted in considerable confusion and disparity in the literature about the patterns of jaw movements during feeding and the applicability of these models (Smith, 1994).

The purpose of this study is to test the utility of the transport kinematic models by mathematically quantifying the phases of the gape cycle during prey transport in a broad taxonomic sample of lizards. First, I quantified gape cycle kinematics from multiple individuals from each of one iguanian and six autarchoglossan lizard species to sample the breadth of transport behavior across lizards. Second, I developed a method to objectively analyze gape movement profiles by using explicit mathematical criteria to define the kinematic phases in prey transport. Finally, I applied the results of this quantitative methodology to describe the phases of transport kinematics observed in lizards and to test the utility of the B-W and R-L models as descriptors of amniote prey transport kinematics.

**MATERIALS AND METHODS**

*Transport kinematics*

Kinematic data were collected for seven species of lizard from six different lizard families. This was not a phylogenetic analysis of the evolution of transport behavior within lizards. I sampled taxa that have not been studied extensively (i.e. autarchoglossans; Schwenk, 2000b) to better understand transport behavior for all lizards. In doing so, I was
able to identify how well each kinematic model fit the entire clade. Species studied were *Physignathus cocincinus, Eumeces schneiderii, Gerrhosaurus major, Cnemidophorus lemmiscatus, Tupinambis teguixin, Elgaria coerulea,* and *Varanus exanthematicus.* Lizards were obtained through commercial dealers and housed in glass terraria on a 12:12 light:dark cycle (I.A.C.U.C protocol #U99-03). Water was available *ad libidum.* They were maintained on a diet of domestic crickets and mealworms. The lizards were trained to feed in a glass aquarium under strobe lights while being filmed in lateral view with a NAC HSV-400 high-speed video camera at 200 frames s\(^{-1}\). A heat lamp was mounted from above to maintain an air temperature of 27-30°C. During filming five species were fed crickets standardized to the head length of individual lizards. The remaining two species, (*Tupinambis teguixin, Varanus exanthematicus*), were fed freshly killed mice standardized to head length. All lizards were fed to satiation.

For the analysis, a subset of the transport sequences were selected that had clear lateral views of the jaw landmarks and were similar in duration. Three to five transport sequences for each individual of each of the seven species were analyzed for a total of 118 prey transport gape cycles used in the quantitative kinematic analysis. Transports were defined as gape cycles in which the prey was centered in the oral cavity and moved posteriorly in the mouth (no prey processing or chewing was involved and most transport cycles immediately preceded swallowing cycles). Images for each transport sequence were downloaded to a PC and two-dimensional coordinates for landmarks were digitized using MeasurementTV (MTV: Updegraff, 1990). The landmarks used were the tip of the premaxilla, the angle of the jaw, and the tip of the mandible. Time zero of a gape cycle was defined as the frame before visible mouth opening. Images were sampled every two frames (10 ms) throughout the gape cycle.
From two-dimensional coordinates, gape angle was computed for each frame throughout each gape cycle. Gape angle was calculated as the angle between the tip of the upper jaw and mandible using the angle of the jaw as the vertex. Kinematic profiles for each cycle were plotted to visualize the general patterns in the data.

Analysis of Mouth Opening Phases

The B-W and R-L models describe kinematic phases based on gross patterns in the transport gape cycle. Neither model set forth specific criteria to distinguish between the end of one opening phase and the beginning of the next opening phase. Thus, the transitions between SO-I and SO-II or SO and FO are not straightforward (Herrel et al., 1996). To test the applicability of the B-W and R-L models, one must be able to identify where the slope of the gape plot is shallow and positive (SO, SO-I), where it is flat (slope = 0; SO-II), and where it is steep and positive (FO). To empirically describe mouth opening, I developed a methodology to discriminate between the kinematic phases (SO, SO-II, etc.) based on specific slope parameters that describe both the slopes within phases and their end points. I did not test for slope differences within the closing phase (i.e. FC or SC/PS), however closing phases were identified by negative slopes.

Slope Analysis

Kinematic data are typically presented as plots of angular or distance changes over time (e.g. Fig. 1.1). Within gape plots, it is possible to measure the slope (change in gape / change in time) of the profile over short intervals. By calculating the slope of each short interval over the entire plot, one can quantify slopes throughout the gape cycle. This approach precisely distinguishes where the slope changes from being relatively shallow to relatively steep, and the exact timing of these ‘inflection points’ within the gape profile. Thus, the presence of the kinematic phases described by the B-W and R-L models can be
tested by mathematically describing patterns of slope change within the gape plot during the
gape cycle.

Using slopes to delineate transport phases

Using the SLOPE function in MS Excel, the slope patterns for each transport cycle
were analyzed by calculating the array of slope values for each 30 ms bin throughout the
gape cycle (from 0-30, 10-40, 20-50, and so on). Slopes between 0 and 0.01 were considered
to be SO-II phases because this range included distinct decreases in the rate of mouth
opening as well as zero slopes (i.e. plateaus) as hypothesized by the B-W model. This
threshold for the SO-II phase was chosen for two reasons. First, the lowest possible
resolution at which distinct changes in the rate of mouth opening could be detected was the
30 ms sampling bin. Shorter sample bins resulted in a high number of falsely positive SO-II
phases due to digitizing measurement error ($\pm 1^\circ$). (For example, shorter bins and $\pm 1^\circ$
measurement error often yielded “SO-II” phases during FO or FC). Second, slopes
between 0 and 0.01 were within the noise of measurement error—i.e. given the 30 ms
sampling bin and the $\pm 1^\circ$ measurement error, it is mathematically impossible to detect
whether slopes between 0 and 0.01 are increasing, decreasing, or flat. At this resolution,
however, this means I could detect slopes starting at 0.1 degree in 10 ms. The ‘slope limits’
of 0 and 0.01 for SO-II phases are congruent with the BW model—the transition between
SO-I and SO-II is indicated by a distinct decrease in slope and the slope of the gape profile
during SO-II may be slightly increasing, decreasing, or zero. Slopes greater than 0.01 and
less than 0.2 were considered to be slowly increasing slopes. Slopes greater than 0.2 were
considered fast increasing slopes. The slope of 0.2 indicating the threshold between slow
and fast opening is the point at which the opening rate passes 2 degrees in 10 ms. A slope of
0.2 closely matched the SO and FO transition in those gape profiles where this phase change
was obvious visually. Although somewhat arbitrary, this threshold was also chosen because a review of the literature indicated that most authors have placed the beginning of the FO phase at a slope value similar to 0.2.

To mathematically delineate the phases, I simply read down the array of bin values for each gape profile, using these slope thresholds to indicate the ‘inflection points’ between phases (Fig. 1.2). Any time the slope for at least one 30 ms bin, or a series of 30 ms bins, was less than 0.01 it was scored as an SO-II phase (right column, Fig. 1.2). Similarly, bins with slopes between 0.01 and 0.2 were scored as an SO phase. Slopes over 0.2 were scored as an FO phase.

Choosing the bin duration

Deciding on the time interval (i.e. the bin duration) to compute the slope values is important in slope analysis. For events longer than 60 ms, one can easily observe both the beginning and end of the event on high-speed video and in the gape plot. However for events shorter than 60 ms, and/or those involving very slow rates of change (and thus, not readily observable on the video), slope analysis should be employed. Slopes can be measured over any time interval that is meaningful to the investigator and is allowed by the data set. I encourage investigators employing this kind of kinematic analysis to measure slopes over a range of time intervals (e.g. 10, 20, 30, 40 ms, as I did initially) to understand how their slope data may be interpreted (slopes = +/− or 0) over different time intervals.

Because the goal was to correctly identify SO-II phases within a gape plot, I conducted the slope analysis over a 30 ms interval for three reasons. First, the 30 ms interval allowed for better discrimination between a very shallow slope (i.e. a plateau) and slightly increasing slope due to the influence of ± 1° measurement error. Second, this interval yielded the most realistic estimates of a plateau in the gape profile during mouth opening. Measuring the
slope over 10 ms bins yielded nonsense because zero slopes were misidentified throughout the gape cycle owing to measurement error. Measuring slopes over 20 ms resulted in a high number of falsely positive zero slopes (and some negative slopes) being identified. In addition, a 20 ms ‘plateau’ is biomechanically too short of time to expect musculoskeletal control to be possible. Finally, the 30 ms interval was neither too conservative nor too liberal to test for the presence of a SO-II phase within a gape plot. This duration consistently identified SO-II phases where they occurred visually. Intervals longer than 30 ms mathematically missed SO-II phases less than 30 ms long and failed to find any SO-II phases within the 118 lizard profiles.

Scoring gape profile patterns

Using the mathematical criteria of the slope analysis (bin duration = 30 ms, SO = 0.01-0.2, SO-II = 0-0.01, FO > 0.2), I determined the kinematic phases contained within each of the 118 profiles. Tallies of all possible patterns were made to describe the variation in transport kinematics observed. The frequency of each kinematic phase was calculated both within and across species used to describe the range of transport kinematics among lizards and to examine the utility of the generalized tetrapod transport models.

RESULTS

Lizard prey transport kinematics

Representative kinematic profiles for entire feeding bouts and individual transport sequences are presented in Figures 3 and 4 respectively. Although transports generally occur in series at the end of feeding bouts just prior to swallowing (Fig. 1.3 A, B), some species also transported the prey item as part of prey processing behaviors (Fig. 1.3, C). Little visual
evidence of a SO-II phase was apparent in any single raw gape profile (Fig. 1.4) or throughout entire feeding bouts (Fig. 1.3).

Plots of individual transports across individuals reveal the visual extent of intra- and interindvidual variation in transport movements (Fig. 1.4). Peak gape angles among transports within individuals can vary considerably (e.g. Fig. 1.4, A) and vary among species (Fig. 1.4). Visual patterns of transport profiles also appear to vary among individuals within species (Fig. 1.4, B) and across species (compare Fig. 1.4 A, B). Based on the visual observation of the gape profiles across species, lizards appear to fall into two predominant categories: opening, (e.g., Fig. 1.4 A, left individuals on B); and SO + FO (e.g., Fig. 1.4 C, and right individual on Fig. 1.4 B).

**Slope analysis of gape profile patterns**

Twelve different gape cycle patterns were found using the mathematical criteria of slope analysis (Fig. 5). These patterns were divided into those without (A-H) and with (I-L) a SO-II phase occurring after detectable mouth opening began. Only 4 patterns (I-L) had SO-II phases once the mouth began to open and these comprised 12.7% of the total. The remainder of the profiles lacked SO-II phases during the opening phase (A-K). Among these, two patterns (D, G) had initial opening rates that, though perceptible on film by eye, were within measurement error, and thus, technically scored with initial plateaus. Because these plateaus indicate the mouth is mathematically not opening, these two patterns are therefore the same as two more common patterns (D = C, and G = A). Pooling these two patterns, the most common pattern was SO + FO (A) with 37.3% of the total sampled. The FO-only pattern (B) was found in 22.9% of the sample. The SO-only pattern occurred in 21.2 % of the sample. Three transport patterns (E, F, & H), involving only 6 of the 118
sampled, scored as having multiple shifts between SO and FO phases during mouth opening. Overall 87.2% of the profiles sampled lacked SO-II phases during opening.

The slope analysis also revealed both intra- and interspecific specific variation in transport gape patterns among the seven lizard species (Fig. 1.4, Table 1.1). Individuals had between one and four different gape cycle patterns. Within species, some individuals were stereotyped (Fig. 1.4 A) while others were not (Fig. 1.4 B,C). For example, some individuals of a species might possess an SO phase while others might not (Fig. 1.4 B). Among species some exhibited 2-3 patterns while others were highly variable (Table 1.1). *Elgaria coerulea* showed a very consistent pattern of SO-FO across all individuals. *Tupinambis teguixin* and *Varanus exanthematicus* showed the most variability of all species studied. Across species, however, patterns A, B, and C were the dominant gape profiles comprising 40% or more of all profiles within species and 95 - 100% in *Eumeces schneideri, Gerrhosaurus major, Cnemidophorus leminscatus*, and *Elgaria coerulea*.

**DISCUSSION**

The data demonstrate that prey transport kinematics in lizards are highly variable both intra- and interspecifically in the form and duration of the gape cycle. Thus, there clearly is no single predominant prey transport pattern characteristic of all lizards. However, the vast majority (87.2%) of the profiles sampled had some form of constantly opening gape pattern with no SO-II phase (Fig. 5 A-H). The most common pattern was the SO-FO pattern that occurred in over a third (patterns A + G, 37.3%) of the transports. The FO-only (pattern B, 22.9%) and SO-only (patterns C + D, 21.2%) patterns were also common. These patterns accounted for 81.4% of the transports studied. Overall, 87.2% of the profiles (A-H) had constantly opening gapes during prey transport. Continually opening gape
profiles (like patterns A-H) are observed (visually) in every lizard prey transport gape profile that has been published (Smith, 1984; Schwenk and Throckmorton, 1989; Delheusy and Bels, 1992; Herrel et al., 1995; Urbani and Bels, 1995; Herrel et al., 1999; Herrel and DeVree, 1999; Schwenk, 2000b). Thus, it is clear that across the lepidosaur clade, lizards variably open, then close, their mouths during transport.

Some of the variability in lizard mouth opening patterns in general may be due to differences in prey characteristics. As it is processed, prey items change size, shape and consistency and thus, feeding kinematics may change in tandem. However to date, these effects have only begun to be explored in detail. Delheusy and Bels (1999) and Herrel et al. (1999) showed that kinematic timing variables were different among different food items, but that the general form of the gape cycle was very similar between types. Because this was a broad survey of feeding kinematics and prey size was controlled, I did not address the issue of prey effects, however, this topic certainly warrants further investigation. In fact, slope analysis may prove to be an effective technique to quantify how feeding kinematics are modulated among various type of prey.

Testing the utility of transport models

The usefulness of models is their ability to predict patterns observed in the taxa for which the model is proposed. To date, studies of lizard feeding kinematics have applied the prey transport models to kinematic data rather than testing how kinematic profiles fit those predicted by the models (Smith, 1994). The specific problem here is that kinematic phases are simply drawn on ‘representative’ kinematic profiles, without any concern for slope or demonstration of the frequency at which the phases occur. Thus, data are forced to fit a model rather than letting the data test it.
Using patterns determined by slope analysis I can test how well lizard prey transport kinematics fit either of the two models for amniote prey transport. In general terms, the transport models differ primarily in the presence (B-W) or absence (R-L) of a SO-II phase during the opening phase. Lizards lacked a SO-II phase in 87.2% of the transports sampled, thus at this general level, the R-L model was valuable in predicting the transport kinematics of lizards. Slow open II phases anywhere within the mouth opening phase were so infrequent in lizards (occurrence = 12.8%) that the SO-II phase cannot be considered a general feature of lizard prey transport. A more explicit evaluation using slope analysis and the precise predictions of each model shows that the R-L pattern (SO, FO) occurred 37.3% of the time while the B-W (SO, SO-II, FO) pattern was found in 3.4% of the profiles. Thus, at both the general and specific levels, the R-L model predicted the predominant (i.e. most common) gape patterns in lizards. The rarity of the explicit B-W pattern (3.4%), the low occurrence of SO-II phases overall (12.8%), and the fact that SO-II phases were absent in two species (*G. major*, *C. lemniscatus*) indicates that the SO-II phase is a rare component of the gape cycle of lizards. Thus, the Bramble and Wake model is not supported for lizards, and hence, is not supported as a model for amniotes or generalized tetrapods (Reilly and Lauder, 1990; Lauder and Reilly, 1994).

*What is the SO-II phase?*

Clearly, the SO-II phase during mouth opening is not a consistent characteristic of lizard prey transport, but it does occur in 4.7-23.8% of all gape cycles within a given species. Plateaus in transport cycles occasionally occur in turtle (Bels et al., 1997) and mammal (the “O2 phase”; Fig. 13.5; Hiiemae, 2000) transport cycles as well. In addition, Delheusy and Bels (1999) found that the gekkonid lizard *Phelsuma madagascariensis* exhibit long SO-II phases between transport cycles, but because the frequency of this phase in relation to all transports
was not reported, I cannot estimate its overall prevalence. However, the fact that these lizards consistently showed an SO-II phase warrants further study. Regardless, the rarity of the SO-II phase in my data (and the literature) is striking considering that it was hypothesized by the B-W model to be a component of the generalized tetrapod transport cycle and necessary for prey adhesion. This analysis demonstrates that the SO-II phase is not necessary for prey adhesion during prey transport because 1) of the low frequency of SO-II phases across species, 2) the absence of SO-II phases in two species, and 3) no gape cycles were observed in which lizards had trouble holding on to prey items during opening. Therefore, I agree with the R-L model that proposed that ample prey adhesion in amniotes occurs during SO or FO. This conclusion might be criticized because data on the kinematics of tongue movements are not presented. These data are not presented because the mouth or prey item frequently obscured the tongue. Regardless, any specific tongue function hypothesized to be associated with a plateau phase, cannot be considered a common or generalized feature of tetrapod transport, given that plateaus are so infrequent in lizards and absent in salamanders.

Interestingly, a plateau phase is occasionally seen in the gape profiles of lizards that use their tongues in prey capture (the strike). In a manner similar to many salamanders, some lizards (the Iguania and a few Autarchoglossans) project the tongue out of the mouth to capture small prey items. Often they will protract the tongue just beyond the margin of the jaws where it remains stationary until the lizard lunges toward the prey while further protracting the tongue. Upon contact or pinning the prey to the substrate, the prey item is retracted on the tongue into the mouth (pers. obs.; Schwenk 2000b). A plateau phase is sometimes associated with the initial delay in tongue protraction during prey capture. A plateau during tongue projection has been reported in a variety of iguanian lizards
(Dipsosaurus dorsalis, and Uromastyx aegyptius: Schwenk and Throckmorton, 1989; Anolis equestris, Opleurus cuvieri: Bels and Delheusy, 1992; Agama stellio: Herrel et al., 1995) and two autarchoglossans known to use lingual prehension to capture prey (Tiliqua scincoides, Scincidae: Smith et al., 1999; Gerrhosaurus major, Gerrhosauridae: pers. obs.). I know of no published record of a clear plateau phase in the gape profiles of lizards that do not use lingual prehension. It is likely that a broad analysis of gape and tongue movements that quantified the frequency of a plateau phase during ingestion across lizards would reveal that the plateau phase is a consequence of the tongue not being prepared for protraction or the prey not being quite within range as has been proposed by Bels and Delheusy (1992).

Similarly, the occasional plateau phases occurring during prey transport may be a consequence of tongue effects related to prey size or position or a delay produced by sensory feedback.

*Generalized patterns of prey transport in tetrapods*

Salamanders differ from the amniotes in that transport gape cycles (consisting of an opening and closing phase when the prey is transported) are separated by long periods (multiple seconds of time) in which the mouth remains closed. The closed phase is divided into the recovery phase, when the tongue is recycled forward under the prey item, and the preparatory phase, when the animal sits there for a while before the onset of the next prey transport gape cycle (Reilly and Lauder, 1990; Lauder and Reilly, 1994). Interestingly, this is the same pattern seen in the gekkonid Phelsuma madagascariensis (Delheusy and Bels, 1999). Amniotes differ in having more or less contiguous transport cycles with little to no time between successive transport cycles. The action of recycling the tongue under the prey item has been compressed into the gape cycle. Salamanders do not have a clear slow opening phase as in most amniotes (Lauder and Gillis, 1997) and a plateau (or a SO-II phase) is not
present in gape cycle of this group (Lauder and Reilly 1994). Thus, the ancestral condition for transport gape cycles in tetrapods is that the mouth is simply opened and then closed (Reilly and Lauder 1990, 1991; Reilly, 1996; Lauder and Gillis, 1997).

Similar gape profiles consisting of only an open (fast or slow) and a closing phase were a common gape cycle pattern (41.1%). In addition, many published records show representative gape profiles of entire lizard feeding bouts that contain open-close cycles along with some cycles having an SO and FO phases (Smith, 1984; Schwenk and Throckmorton, 1989; Kraklau, 1991; Delheusy and Bels, 1992; Herrel et al., 1995; Urbani and Bels, 1995; Herrel and De Vree, 1999; Herrel et al., 1999). These simple, bell-shaped profiles, with basically opening and closing phases, appear almost identical to many salamander gape profiles, and thus, it is unquestionable that the primitive open-close gape movements characteristic of salamanders are retained in moderate frequencies in most lizard taxa (Table 1.1).

However, all species in this study had some transport gape cycles containing both the SO and FO phases, and overall, it was the predominant pattern observed in lizards as predicted by the R-L model. An SO phase has been observed in at least some gape cycles in most lizards investigated to date (reviewed in Schwenk, 2000b), and the outgroup to lizards, rhynchocephalians, show a slow opening phase in reduction and repositioning movements (Fig. Fig. 6-9, Gorniak et al., 1982; simple transport cycles have not been analyzed in this taxon). Although the data are limited to a few species, turtles also have SO phases during prey transport (Bels et al., 1997). Therefore, lizards and turtles not only retain the pleisomorphic open-close transport cycle but also commonly insert an SO phase during prey transport.
The feeding apparatus of mammals has been studied extensively (Bramble, 1978; Hiemae and Crompton, 1985; Smith, 1992; Herring, 1993; Weijs, 1994). Mammals usually have a clear SO phase (Hiemae, 2000). Mammals have a derived jaw joint and teeth (tribosphenic molars) that improve jaw mobility and chewing ability compared to other tetrapods. Consequently, mammals can process prey in the mouth to a greater degree than most other amniotes (Reilly et al., 2001). Increased prey processing in turn creates a functional need for a well-developed tongue to reposition the prey in the mouth. Compared to other tetrapods, most mammals have robust, complex tongues that are used extensively in prey processing. Thus, the derived condition of the mammalian tongue, jaw joint, and teeth allow for increased prey processing and thereby increase the functional need for a consistent SO phase in the gape cycle when food is controlled (Smith, 1994).

An SO phase does not exist in salamanders (Reilly and Lauder, 1990), is variably present in most turtles (Bels et al., 1997) and lizards (this study; Bels and colleagues, Herrel and colleagues), and is common in mammals (Hiemae, 2000). I suggest that the increased role of the tongue in prey manipulation and transport, and thus a SO phase, arose in the common ancestor of the amniotes as proposed by Reilly and Lauder (1990). The appearance of the SO phase may be due to the emergence of an increasingly more developed tongue, the new functional demand created by lingually based prey processing behavior, or both. I agree with Smith’s (1994) hypothesis that the similarities in jaw movements across tetrapods may be due as much to the functional demands of prey transport as to the evolutionary retention of homologous kinematic or neuromuscular activity patterns as implied by the B-W and R-L models.

Given the extreme variability in lizard transport kinematics, it seems that a single kinematic model does not fully describe lizard transport behavior. The R-L model predicted
the principal gape cycle pattern (SO, FO, Close) but the great extent to which lizards retain
the basic open-close transport cycle was unexpected. Future studies should focus on
particular taxa, like Tupinambis and Varanus, which show extreme variability in the gape
profile during transport (Elias et al., 2000). Interesting questions regarding tongue
morphology, prey size, prey position, and the consequences of a tradeoff with the
chemosensory function of the tongue should be probed to understand why these taxa are so
variable. Conversely, why is Elgaria so stereotyped? This species shows many interesting
patterns related to prey processing (i.e. chewing) that are not typical of the rest of the
Autarchoglossa (Reilly et al., 2001).

I encourage future comparative work to test models (by reporting the frequency with
which behaviors or kinematic phases occur) rather than forcing their data to fit models.
Specific models for prey ingestion in lizards or other amniotes should be developed, rather
than describing prey ingestion with prey transport models. In doing so, the applicability of
the model and its testability are lost (Smith, 1994). Finally, in testing these or other
kinematics models, or in the detailed analysis of kinematic data, I strongly encourage the use
of slope analysis. Performing this straightforward technique adds little increased effort and
allows investigators to better quantify and interpret kinematic data. In addition, the
influence of measurement error and event duration can be included in the analysis and
interpretation of the data. Similar slope analyses on other taxa will increase the
comparability of independent data sets because the criteria used for defining kinematic
events would be empirically based and repeatable. Therefore, I feel slope analysis represents
a useful tool in all forms of kinematic data analysis that can be used for novel applications in
studies of feeding and locomotion.
LITERATURE CITED


Table 1.1. Patterns of prey transport gape kinematics in seven species of lizard. The letter for each gape profile pattern corresponds to those in Figure 1.5. The number of each gape profile pattern identified by slope analysis is presented for each species. Sample sizes per individual are listed in parentheses below the species abbreviation. Abbreviations: Pc = *Physignathus cocincinus*; Es = *Eumeces schneiderii*; Gm = *Gerrhosaurus major*; Cl = *Cnemidophorus lemniscatus*; Tt = *Tupinambis teguixin*; Ec = *Elgaria coerulea*; Ve = *Varanus exanthematicus*.

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SO-II
Figure 1.1. Proposed models for the generalized amniote prey transport cycle. The Bramble and Wake (1985) model (A) requires a plateau in the opening phase (termed the SO-II phase) and the Reilly and Lauder (1990) model (B) does not. See text for explanation.
Figure 1.2. An example array showing how slope analysis was used to identify kinematic phases within each gape cycle. Slopes calculated for each 30 ms segment of the kinematic curve (shaded cells) are used to quantify slopes throughout the gape cycle. The presence of gape cycle phases (indicated to the right of the slope column) was then based on trends in the slope column. Slopes less than 0.01 were within digitizing measurement error and were considered to be decreasing or zero slopes indicating a SO-II phase. Slopes between 0.01 and 0.2 were scored as slow opening phases (SO) and slopes greater than 0.2 were scored as fast opening phases (FO). When the slope becomes negative the closing phase (C) begins. See text for further explanation.
Figure 1.3. Representative gape profiles for entire feeding bouts for *Caenidophorus lemniscatus* (A), *Eumeces schneiderii* (B), and *Physignathus cocincinus* (C). The strike is followed by a series of contiguous puncture crushing (PC) and prey transport (T) cycles before the prey is swallowed (SW). Note that only slow opening and fast opening phases are visually obvious.
Figure 1.4. Interindividual and interspecific variation in prey transport gape profiles from *Cnemidophorus lemniscatus* (A), *Eumeces schneideri* (B), and *Physignathus cocincinus* (C). Note the interindividual variation in peak gape and cycle duration, and that, visually, species have basically opening phases (A), slow opening plus fast opening phases (C), or both (B). See results of slope analysis (Table 1.1 and Figure 1.5) for details of variation in transport kinematics.
Figure 1.5. Transport gape profiles patterns identified by slope analysis listed by relative occurrence. Patterns A-H (above the line) have profiles with continuous mouth opening (no plateaus) and fit the Reilly and Lauder model. Patterns I-L (below the line) exhibited SO-II phases in the gape profile after mouth opening has begun and fit the Bramble and Wake model. The number observed (N out of 118), percentage of the total sampled (%), and cumulative percentages for each general pattern (Cum %) are indicated on the right. Patterns A and G, and patterns C and D, were combined because the analysis revealed a phase with zero slope at the beginning of the gape cycle. Accordingly, 37.3% of the profiles (patterns A and G) fit the Reilly and Lauder model while 3.4% of the profiles (pattern K) fit the Bramble and Wake model.
Chapter 2. Prey processing in lizards: Behavioral variation in sit-and-wait and wide foraging taxa

INTRODUCTION

Describing and explaining the functional significance of feeding mechanisms and behaviors within and among taxa has long been a goal of many ecologists and functional morphologists. Often, this work seeks to explain differences in diet and/or morphology in terms of behavioral variation in obtaining or using resources (Pianka 1981; Schwenk and Throckmorton 1989; Illius and Gordon 1993; Lauder and Reilly 1994; Robinson and Wilson 1998; Herrel et al. 1999a; Nakano et al. 1999; Shipley et al. 1999). Rarely however, is the range of behaviors (the behavioral repertoire) that organisms use during the acquisition and processing of food adequately described and quantified in a comparative context (Reilly et al. 2001).

Mastication and transport cycles have been reviewed for several mammalian taxa processing various types and/or sizes of food (Hiemae and Crompton 1985; Hiemae 2000). The mammalian feeding repertoire is composed of chewing cycles that prepare the food for swallowing and digestion (e.g. puncture crushing and the tribosphenic chewing strokes), and transport cycles to reposition the food for further chewing (e.g. side-to-side transports) or shift it posteriorly for swallowing (Hiemae et al. 1979; Hiemae and Crompton 1985). Thus, a basic understanding of mammalian feeding behavior exists. However, analogous, detailed investigations of prey processing and general behavioral patterns have yet to be fully described for other amniote groups. This lack of data leaves the false impression that non-mammalian taxa engage in little prey processing (Schwenk 2000a; Reilly et al. 2001). The focus of this paper is to take the first broadly comparative look at prey processing in lizards.
Extant lizards are an ecologically and dietarily diverse group of over 4500 species and therefore are well suited to investigate variation in prey processing behaviors. Within squamates, numerous morphological studies have revealed major dietary, morphological, and functional differences among lizard groups (Herrel et al. 1999b; reviewed in Schwenk 2000b). Tongue morphology, a factor likely to be important in prey processing, is known to vary substantially across the group as a whole (Schwenk 1988, 2000b). The iguanian clade retains the ancestral condition of heavily papillose, short thick tongues with a round tip and wide base. Tongue morphology is more variable and derived in various ways in the autarchoglossan clade; however, these lizards typically have a narrower, triangular shaped foretongue with distinct tips and a reduced base compared to iguanians (Schwenk 2000b).

The iguanian and autarchoglossan clades have also diverged in foraging mode (e.g. Cooper 1994, 1995a; Perry 1999). Foraging mode describes the movement patterns of lizards as they forage and can be split broadly into two major categories. Sit-and-wait foragers are ambushers while wide foragers tend to move through the habitat in search of food items. These modes expose lizards to different prey types resulting in different diets. Sit-and-wait foragers tend to eat more mobile prey items and wide foragers encounter more sedentary prey items (Huey and Pianka 1981). Thus, key components of morphology and ecology covary across lizards and suggest that feeding behavior might also covary with these characters.

This study makes the first attempt to quantify and compare the feeding repertoire of lizards using a phylogenetically diverse sample of species. Basic chewing and transport behaviors are defined and their relative frequencies across a diversity of taxa are quantified. The results show that particular behaviors are used more frequently by certain taxa and that
this parallels a broad dichotomy in foraging mode, tongue morphology, and metabolic rate among lizards.

**MATERIALS AND METHODS**

The phylogenetic relationships of the 12 species studied are shown in Figure 2.1. *Sphenodon* (Rhynchocephalia) is the outgroup to lizards and snakes (Squamates) (Estes et al. 1988). It has been classified as a sit-and-wait predator (Cooper 1995a, 1999) and thus this foraging mode is considered to be primitive for lizards. Squamates are split into the Iguania and Scleroglossa (Gekkota + Autarchoglossa). This study focuses on representatives of the Iguania and Autarchoglossa. The Gekkota, the sister taxon to the Autarchoglossa were not included in this study because most are nocturnal (difficult to film with strobes) and their foraging mode may be sit-and-wait, wide foraging or mixed (Perry 1999). With few exceptions, autarchoglossans are widely considered to have evolved a wide foraging feeding mode (Cooper 1995a).

Lizards were purchased from commercial dealers and housed in glass terraria on a 12h:12h light-dark cycle. Each terrarium contained a water dish, shelter, and a heat and UV source. Water (supplemented with vitamins) was available *ad libitum*. Lizards were maintained on a variety of commercially available reptile food (primarily crickets and mealworms).

Lizard feeding bouts were filmed in lateral view with a NAC high-speed video system at 200fs\(^{-1}\). Because the body sizes of the lizards under study varied greatly, the smaller lizards were fed crickets standardized to lizard head length. The much larger, *Tupinambis teguixin* and *Varanus exanthematicus*, were fed mice standardized to head length. During each filmed feeding bout, lizards were fed to satiation. Data collection began
immediately following the strike (prey capture) and ended with the first swallowing cycle (i.e. when prey was no longer seen in oral cavity but had entered the pharynx). This sequence, strike to swallowing, defines one feeding bout. Only behaviors involved in prey manipulation and processing once the prey was within the mouth were considered. I defined transport behaviors as any behavior during which the prey item was moved anteroposteriorly within the mouth without any attempt to alter its shape or form. Prey processing behavior, i.e. chewing (sensu Schwenk 2000b; Reilly et al. 2001), was defined as any behavior during which the size, shape, and/or structural integrity of the prey item was changed via contact with the tongue, palate, jaws and/or teeth. Finally, side-to-side prey movements were classified as a separate category.

Videotapes were initially reviewed and the types of feeding behaviors that occurred consistently across all species were defined. All videotapes were then reviewed in greater detail and the order and number of each defined feeding behavior was tallied for each feeding bout for each individual. The raw occurrence data for each behavior for each bout were pooled across individuals within species to calculate mean occurrences of each behavior and the mean total number of behaviors per bout (TOT). Percentages were then calculated to quantify the relative frequency of each behavior for each lizard family. Variation in the sequence of chewing and transport behaviors used during a bout was quantified by creating another variable, interspersion. Interspersion is the mean number of times a lingual transport behavior (T) was followed by a chewing behavior (either puncture-crushing (PC) or palatal crushing (PLC)) indicating how often prey items are repositioned for further chewing.

Our sample of lizards included one species representative per family except for the families Iguanidae and Teiidae, for which three species of each were filmed. Thus, for
familial comparisons, the means for the three species within each family were pooled to generate a family mean. The iguanian species *Ctenosaurus quinquecarinata, Oplurus cuvieri,* and *Sceloporus clarkii* were considered to be monophyletic based on the analyses of Macey et al. (1997) and Schulte et al. (1998). I recognize that feeding behavior is not a family level phenomenon; however, this level was used because few phylogenetic hypotheses exist for relationships within many autarchoglossan families, teiids in particular. Furthermore, data on branch lengths within lizard families (see below) are scarce. Therefore, the level of family was deemed appropriate for comparison because key aspects of lizard feeding biology [foraging mode (Cooper 1994); tongue morphology (Schwenk 1988)] are highly conserved at this taxonomic level and because phylogenies with branch lengths are available.

Because tongue morphology is conserved phylogenetically (Schwenk 1988) and is likely to be an important factor in determining variation in feeding behavior, phylogenetic effects within the data were also assessed. The effects of phylogeny (i.e. the statistical non-independence of comparative data) were removed by computing phylogenetically independent contrasts (IC’s) on family means for five of the behavioral variables (Felsenstein 1985). Assuming a Brownian motion model of evolution, IC’s were calculated for numbers of lingual transports (T), puncture crushing (PC), palatal crushing (PLC), interspersion (INT), and total (TOT). Correlation coefficients between each of these variables were then computed for the raw family means and for the IC’s. The phylogeny used in these analyses is based on Estes, de Queiroz, and Gauthier (1988). Data on branch lengths (in millions of years before present) were obtained from Cooper (1997; and references therein), except for the lengths between the Scincidae and Gerrhosauridae. Time since divergence of these families is not known, thus this branch length was arbitrarily set at 10 mybp.
Calculations of IC values were conducted in COMPARE 4.4 (Martins 2001). The absolute value of each IC was plotted against its standard deviation to check for appropriate branch length standardization (Garland et al. 1992). No significant trends were observed for any variable.

In order to visualize how feeding behaviors might have evolved across the squamate clade, ancestral character states were reconstructed along the phylogeny with branch lengths shown in Figure 2.1 for total, INT, T, PC, and PLC. The side-to-side (SS) variable was of low and relatively uniform occurrence and therefore was not included in this analysis. Calculations of ancestral states follow the generalized least squares (GLS) approach described in Martins and Hansen (1997) and were performed in COMPARE 4.4. The GLS approach calculates ancestral state values as a weighted average of the other taxa on the phylogeny. A Brownian motion model of evolution was assumed. The within-family variation was assumed to be zero, thus, the values reported are the sum-of-squared-changes parsimony estimates of ancestral state values.

RESULTS

Prey manipulation and transport behaviors

A total of 337 feeding bouts were analyzed from a sample of 12 lizard species (sample sizes per species in Table 2.1). Two transport behaviors were found to be common and easily observable from the video records. These were side-to-side transports (SS) and posteriorly directed lingual transport movements (T) of the prey item. The SS transports were manipulative movements whereby the prey item was transferred, either lingually or inertially, to the opposite side of the jaws (e.g. right→left, left→right). Processing behaviors and/or transport behaviors may follow SS movements. The SS behavior was highly variable
and no patterns were detected in its use or frequency in any species studied. The use of this behavior likely depends on properties of the prey, particularly position, size, and degree of struggling.

The T behaviors were transports during which the prey item was moved posteriorly within the mouth by the tongue in preparation for further processing or swallowing. They were usually in series at the end of each feeding bout; however, they were occasionally interspersed between chewing behaviors. Three autarchoglossan taxa also used inertial transports (I). During this behavior, the head was thrust forward over the prey item with no associated movement of the tongue (Gans 1969). These simple inertial transports were observed only in the autarchoglossan families Teiidae (Ameiva ameiva, Tupinambis teguixin) and Varanidae (Varanus exanthematicus). Tupinambis teguixin and V. exanthematicus also used inertial feeding behaviors that involved the protraction and retraction of the tongue in tandem with the inertial movements of the head. These behaviors have been described in detail elsewhere (Elias et al. 2000). In this analysis, the inertial transport with tongue behaviors were pooled with normal lingually based transports (T) because each behavior involved the use of the tongue as in normal transports (T).

**Chewing behaviors**

The chewing behaviors observed were puncture crushing (PC) and a behavior I have termed palatal crushing (PLC). The PC behavior involves the piercing and/or crushing of the prey by the jaws and marginal teeth such that the structural integrity of the prey is changed. The teeth frequently penetrate the prey item and its shape was obviously changed by the forces imposed on it by the jaws and teeth. This behavior is essentially the same as the puncture crushing observed in mammals because the jaws of lizards approach each other vertically and the upper and lower teeth do not come into contact because the prey item
impedes them from doing so (Reilly et al. 2001). In the PLC behavior the prey item is compressed or crushed between the tongue and palate (i.e. inside the marginal tooth rows) such that it was fractured and/or its shape changed. This behavior is further defined by a lack of anterior/posterior or side-to-side movement of the prey item. Several PLC's were most often observed in sequence.

*General behavioral patterns*

Behavioral occurrence data are presented in Table 2.1. Figure 2.2 summarizes the frequencies of each behavior across all feeding bouts for each species. All species exhibited T and PC behaviors. The number of T behaviors (Fig. 2.2: open bars) per bout was greater in autarchoglossans than in iguanians except in three species (*E. schneideri, G. major, A. ameiva*). Only three species, *V. exanthematicus, T. teguixin, and A. ameiva*, were observed to use simple inertial transports (Fig. 2.2: open bar I). The SS behavior (Fig. 2: gray bars) was used infrequently and was not observed in *E. coerulea* or *E. schneideri*.

Among iguanian taxa, PLC (Fig. 2.2: stippled bars) clearly dominated prey crushing behaviors while PC (Fig. 2.2: black bars) dominated in autarchoglossans. The PLC behavior was not observed in *E. coerulea, V. exanthematicus or T. teguixin*. The total number of behaviors (i.e. transport and chewing behaviors combined) in iguanians ranged from 6 - 8.4 per bout (Table 2.1). In five of the autarchoglossans the total number of behaviors was much greater than in iguanians ranging from 14 - 18 per bout. However, three autarchoglossan species, *E. coerulea, E. schneideri, and A. ameiva*, had values similar to iguanians, with *E. schneideri* having the lowest total of any species in the study. The autarchoglossan taxa showed high interspersion values compared to iguanians (> 1.3 vs. < 0.9) (Table 2.1; Fig 3). Note however, *E. coerulea* (Anguidae) and *E. schneideri* (Scincidae),
again, were more similar to iguanians in the degree to which T’s were interspersed between chewing behaviors.

The iguanian families Agamidae and Iguanidae used the PLC behavior more than any other behavior (Fig. 2.4). These iguanians used PC infrequently and T to an even lesser degree. Conversely, the autarchoglossan families employed a higher frequency of T and PC behaviors. The anguid *E. coerulea* used a very high percentage of T’s, few PC’s, and no other behaviors while feeding.

*Evolution of behaviors*

Significant correlations were observed before and after accounting for phylogenetic effects (Table 2.2) in three pairs of the variables (TOT vs. PC, TOT vs. INT, PC vs. INT). This indicates that increases in the total number of behaviors used in prey consumption is achieved by adding more PC's and INT's and that both of them increase together. Transports (T) were negatively correlated with PLC showing that these variables are inversely related.

Ancestral character state reconstructions for total, INT, T, PC and PLC are presented in Figure 2.5. The mean value of each variable for each family is given at the tips of the phylogenies and the estimated ancestral state values are given at the corresponding nodes. The shading pattern along the branches indicates trends in trait values between nodes. From the Iguania—Autarchoglossa node, values for TOT, INT, T, and PC, increase within the Autarchoglossa and decrease within the Iguania (Fig. 5, A-D). For PLC, the reverse is true (Fig. 5, E) with the Iguania evolving higher values, and Autarchoglossa lower values. Note that for the familial means of TOT, INT, and PC, the Scincidae and Anguidae are more similar to iguanian family means than they are to other autarchoglossans. Values
DISCUSSION

Historically, lizards have been portrayed as swallowing prey items whole with little or no processing (i.e. chewing). Chewing, in the functional sense, is the reduction of material to a condition suitable for swallowing and/or to facilitate the penetration of digestive enzymes so as to expedite the chemical breakdown of the food (Hiiemae and Crompton 1985; Schwenk 2000a; Reilly et al. 2001). This study is the first to quantify chewing and transport behaviors and their relative frequencies across a diverse sample of lizards. The data confirm that lizards do in fact chew; they use their teeth (and jaws, tongues, and palates) to puncture, compress, and/or reduce food items within the oral cavity. The shape, size, and structural integrity of the prey item are changed by this behavior, which prepares the prey item for swallowing and digestion. Thus, these behaviors meet the functional definition of chewing.

This analysis revealed an interesting and widely used lizard feeding behavior, the PLC. Although palatal crushing has been noted for lizards feeding on eggs (Herrel et al. 1997), it has not previously been thought to be so common. During the PLC behavior, the prey item was stationary. Had the prey item moved laterally or posteriorly, this behavior would have been interpreted as repositioning (SS) or transport (T). However, during PLC's the prey did not move as it was visibly crushed and frequently parts of it were broken off, falling out of the mouth. Depending on prey position (how far posterior the prey was positioned in the oral cavity during PLC), the prey could often be seen clearing the palate between sequential PLC cycles. The presence of pterygoid teeth in Ctenosaura quinquecarinata and Oplurus cuvieri (and many other iguanians) further suggests that the palatal region serves a
chewing function (Etheridge and de Queiroz 1988). Finally like PC’s, many PLC’s were used in succession prior to the onset of final transport movements. Thus, PLC’s and PC’s are undoubtedly chewing behaviors. If each PLC was followed by a T behavior, this could have been interpreted as some sort of "pre-transport" behavior whereby prey adhesion to the tongue is facilitated by pressing the tongue up against the prey item (as hypothesized as a function of T's by Bramble and Wake 1985). But PLC’s preceded PLC’s far more than they preceded T's. Furthermore if PLC’s were prey adhesion behaviors then the values for interspersion would have been higher in the iguanian taxa where the PLC is the dominant chewing behavior. Although the PLC behavior is clearly a chewing behavior, it is possible that tongue adhesion could be facilitated in those few PLC's that directly precede T's prior to swallowing.

Comparisons of iguanians and autarchoglossans

The most striking finding in this study is the degree to which the lizard feeding repertoire appears to have evolved in concert with tongue morphology and foraging mode. The robust fleshy tongues of iguanians are covered with long papillae and are very important in prey capture and transport of food (Schwenk 2000b), and in some species for pheromone detection (Cooper 1994). Autarchoglossans have more elongate, often forked tongues that are not used at all during prey capture (Schwenk and Throckmorton 1989; Schwenk 2000b) but which are used extensively for chemoreception (Schwenk 1993; Cooper 1994, 1997; Schwenk and Wagner 2001). Behaviorally, iguanian and autarchoglossans differ in their mode of foraging as well. With few exceptions, foraging mode follows phylogenetic lines with the iguanian taxa being ambush or sit-and-wait foragers while the autarchoglossan taxa are more active or widely foraging (Perry 1999). Morphological and physiological correlates of these foraging modes include tongue morphology (Schwenk 1994; Copper 1994), body
and tail size (Huey and Pianka 1981; Perry et al. 1990), locomotor performance (Huey et al. 1984), diet (Huey and Pianka 1981; Gasnier et al. 1994), habitat use (Belliure and Carrascal 1996), metabolic rate (Anderson and Karasov 1981; Nagy et al. 1999), reproduction (Vitt 1990; Vitt and Price 1982), and learning ability (Day et al. 1999). Assuming the sit-and-wait foraging mode is the primitive condition for squamates (because the outgroup Sphenodon is a sit-and-wait forager (Cooper 1995a, 1999)), the Iguania can be interpreted as retaining the primitive mode and the Autarchoglossa appear to have evolved a different mode.

Autarchoglossan (wide foraging) species in this study differed substantially from iguanian (sit-and-wait) species in total number of behaviors, INT, and PC (Fig 2, 2.5). In contrast, the iguanian species showed much higher numbers and percentages of PLC’s (Fig. 2.2, 2.4). Thus, the widely foraging autarchoglossan taxa seem to have evolved a longer and more complex feeding repertoire than the sit-and-wait iguanians, having higher values for total, interspersion, and puncture crushing. On the other hand, the sit-and-wait iguanians have evolved a repertoire that focuses primarily on PLC’s and T’s. The significant correlation of TOT, INT, and PC in the IC analysis suggests that these behaviors are evolving together.

Evolutionary reversals in the Autarchoglossa

Three autarchoglossan species clearly did not follow the patterns of behavioral evolution seen in the group in general. First, Ameiva ameiva, a medium sized teiid, showed a reduction in the total number of behaviors used (Fig. 2.2). However, this reduction in total behaviors per feeding was driven by a decreased use of transports. Like other teiids, this lizard has a very elongate, protrusible tongue and is a known wide forager (Magnusson et al. 1985). Its decreased use of T’s is hard to explain given its morphological and ecological similarity to the other teiids, and suggests that the feeding biology of this species deserves
more detailed analyses. Furthermore, behavioral variation within the family Teiidae is clearly evident. I chose the taxonomic level of ‘family’ for these comparisons because of its relevance to foraging mode and tongue morphology, however, it is likely that feeding behavior within particular clades or dietary groupings (e.g. herbivores) would be equally as informative.

Second, *Eumeces schneideri* (Scincidae) trended toward lower values for PC, interspersion, and total behaviors (Figs. 2, 5). The patterns observed in skink feeding behavior may be explained by evidence that some skink species have reversed to the iguanian condition. In terms of foraging mode, some skinks have secondarily evolved the sit-and-wait foraging mode from wide foraging ancestors (Cooper 2000). *Eumeces schneideri* is known to tongue flick plant and insect material extensively and on this basis is believed to be a wide forager (Cooper et al. 2000). However, no data on foraging patterns in *E. schneideri* are available to evaluate if it may have changed its foraging mode. Variation in tongue morphology may also explain the apparent behavioral reversals of *E. schneideri*. Iguanians are well known to engage in lingual prehension of small prey and so are some skink species (Smith et al. 1999), including *E. schneideri* (pers. obs.). Skinks have rather broad hindtongues compared with many other autarchoglossans (Schwenk 1995, 2000b). This enlarged hindtongue may contribute towards shaping feeding behavior in that prey items can be manipulated differently due to its increased surface area and adhesive abilities (Schwenk 2000b).

Finally, *Elgaria coerulea* (Anguidae) also trended toward the iguian patterns of lower values for the PC, interspersion, and total behaviors (Fig. 2.2, 2.5). As in some skink species (*E. laticeps, E. fasciatus*), the tongue of *E. coerulea* has a more generalized form than most autarchoglossans in its relative surface area (relative to its tip width) (Cooper 1995b;
Schwenk 2000b). Although, *Elgaria* has been classified as wide foraging on the basis of chemoreceptive abilities (Cooper 1990, 1994, 1995b), it has also been classified as sit-and-wait based on other characteristics (Vitt and Price 1982). Even more compelling is the fact that its sister taxon, *E. multicarinata*, has been suggested to be a sit-and-wait forager because most of its diet consists of free moving prey, it relies primarily on crypsis for predator avoidance, and it has a low field metabolic rate (Kingsbury 1994, 1995). The sit-and-wait strategy is often coupled with metabolic costs and sit-and-wait lizards tend to have lower field and resting metabolic rates than wide foragers owing to decreased locomotor costs (Anderson and Karasov 1981; Nagy et al. 1999). Although no movement data are available for *E. coerulea*, the best available reproductive, behavioral, and metabolic evidence suggest that it may have secondarily evolved the sit-and-wait foraging mode.

**CONCLUSIONS**

The data for PC, PLC and INT show clearly different evolutionary patterns of change in the iguanian and autarchoglossan lizard lineages (Fig. 5) that parallel known contrasting patterns of foraging mode (Perry 1999), tongue morphology (Schwenk 1988, 2000b), and chemosensory behavior (Schwenk 1993; Cooper 1994). Thus, feeding behavior seems to be diverging in concert with changes in these other aspects of the lizards feeding biology. In addition, two species (*E. coerulea* and *E. schneideri*), appear to have reverted to more iguanian patterns in these systems and also may have reverted to the iguanian feeding repertoire. Thus, tongue morphology and foraging mode appear to play a role in shaping how various feeding behaviors evolve. Indeed if *E. coerulea* and *E. schneideri* do represent secondarily derived sit-and-wait foragers, then the apparent covariation between foraging mode, tongue morphology, and feeding behavior is truly remarkable. However, explicit tests
of the relationships among these variables need to be conducted to verify these general patterns.

This study has shown that lizards do chew and exhibit some processing behaviors similar to, but not as extensive as, those seen in mammals. Mammals and birds have very different and highly efficient chewing behaviors (Reilly et al. 2001). A potential benefit resulting from increased oral processing is that digestive efficiency may be increased and thereby may allow for an increase in metabolic rate. My data show that compared to the iguanians, autarchoglossan lizards have evolved a more complex feeding repertoire with more emphasis on puncturing the prey (PC's), more interspersion, and about twice as many prey processing cycles involved per feeding bout. Is this increase in prey processing related to an increase in the metabolic demands of an active foraging strategy? Interestingly, resting and field metabolic rates have been shown to be higher in wide foraging autarchoglossan lizards (Anderson and Karasov 1981; Nagy et al. 1999). Future work must quantify the strength of the relationship between foraging mode, metabolic rate and prey processing. However, it appears that the more extensive prey processing behavior of autarchoglossan lizards may be correlated with a higher metabolic rate, just as in mammals and birds (Reilly et al. 2001). Although the data in this study cannot unequivocally support this hypothesis, lizards may provide a glimpse into how feeding function evolves in response to the demands of increasing metabolic rate.

Finally, this study suggests that tongue morphology, foraging mode, diet and feeding behavior may be coevolving as a highly integrated character complex. Autarchoglossan lizards, with their elongate chemosensory tongues have evolved a more complex feeding repertoire compared to their iguanian relatives. This increased complexity may be related to changes in foraging mode and metabolic rate. Thus, tongue morphology, chemoreception,
feeding behavior, and metabolic rate may all be fundamentally linked (this paper; Schwenk 2000b; Wagner and Schwenk 2000; Schwenk and Wagner 2001). Although I studied lizard feeding behavior across a diverse sample of taxa, these behaviors should be quantified in more species and with different types of prey to verify the general patterns I have described and to assess the relationships between the different components of lizard ecology. In particular, feeding behavior must be explored in gekkotans, chamaeleonids, and snakes. These taxa, although strikingly different from most lizards, will provide important information about the evolution of feeding behavior across all squamates. Given that the gekkotan clade is positioned ‘between’ the iguanian and autarchoglossan clades, data from representatives of this group are of particular importance for understanding the evolution of these behaviors and their relevance to foraging mode and metabolic rate. Equally interesting will be further study focussing on taxa such as *Elgaria* that appear to have reversals in foraging mode or tongue morphology. Such data would elucidate in greater detail the covariation among and between these behavioral characters and foraging mode, tongue morphology, and metabolic rate.


Table 2.1. Mean number of individual behaviors, total number of behaviors per bout, and interspersion data (± standard errors) for prey processing behaviors in lizards feeding on the same relative size prey. Percent occurrence of a behavior for a species is indicated below each entry in parentheses. Interspersion is the mean number of times transport movements (side-to-side, transports or inertial transports) are followed by prey crushing behaviors (palatal crushing or puncture crushes). Iguanidae = Oplurus cuvieri, Ctenosaurus quinquecarinata, and Sceloporus clarkii; Teiidae = Tupinambis teguixin, Cnemidophorus lemniscatus, and Ameiva ameiva.

<table>
<thead>
<tr>
<th>Species</th>
<th>Side-to-side (SS)</th>
<th>Palatal Crushing (PLC)</th>
<th>Transports (T)</th>
<th>Inertial Transports (I)</th>
<th>Puncture-crushes (PC)</th>
<th>Total (TOTAL)</th>
<th>Interspersion (INT)</th>
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<tbody>
<tr>
<td>Agama agama</td>
<td>0.56 ± 0.15</td>
<td>4.50 ± 0.44</td>
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<td>(13)</td>
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<td>Oplurus cuvieri</td>
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<td>0.84 ± 0.13</td>
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<td>(25)</td>
<td>(0)</td>
<td>(14)</td>
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<td>(14)</td>
<td>(0)</td>
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<td>Sceloporus clarkii</td>
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<td>8.40 ± 0.24</td>
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<td>(14)</td>
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Table 2.1: continued.

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<th>Species</th>
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<td><strong>Elgaria coerulea</strong></td>
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<td><strong>Varanus exanthematicus</strong></td>
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<td><strong>Eumeces schneideri</strong></td>
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<td><strong>Tupinambis teguixin</strong></td>
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Table 2.1: continued.

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<tr>
<td>Ameiva ameiva</td>
<td>0.15 ± 0.09</td>
<td>1.96 ± 0.34</td>
<td>2.08 ± 0.23</td>
<td>0.31 ± 0.14</td>
<td>3.00 ± 0.46</td>
<td>7.50 ± 0.47</td>
<td>1.65 ± 0.14</td>
</tr>
<tr>
<td>(7, 10, 9)</td>
<td>(2)</td>
<td>(29)</td>
<td>(29)</td>
<td>(3)</td>
<td>(37)</td>
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Pooled family means:

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<tr>
<td>Iguanidae</td>
<td>0.42 ± 0.16</td>
<td>4.22 ± 0.43</td>
<td>1.25 ± 0.11</td>
<td>0.00 ± 0.00</td>
<td>1.38 ± 0.31</td>
<td>7.27 ± 0.28</td>
<td>0.46 ± 0.17</td>
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<tr>
<td>(3)</td>
<td>(55)</td>
<td>(24)</td>
<td>(0)</td>
<td>(18)</td>
<td></td>
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<tr>
<td>Teiidae</td>
<td>0.31 ± 0.07</td>
<td>1.89 ± 0.29</td>
<td>3.85 ± 0.29</td>
<td>0.88 ± 0.28</td>
<td>5.81 ± 0.44</td>
<td>12.7 ± 0.57</td>
<td>1.65 ± 0.17</td>
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<td>(3)</td>
<td>(16)</td>
<td>(31)</td>
<td>(7)</td>
<td>(43)</td>
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Table 2.2. Matrix of correlation coefficients on raw data (above diagonal) and on independent contrasts (below diagonal). Total, interspersion, and puncture crushing are significantly correlated. INT = interspersion, PC = puncture-crushing, PLC = palatal-crushing, T = transport, TOT = total.

<table>
<thead>
<tr>
<th></th>
<th>PLC</th>
<th>T</th>
<th>INT</th>
<th>PC</th>
<th>TOT</th>
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<tbody>
<tr>
<td>PLC</td>
<td>--</td>
<td>-0.645</td>
<td>-0.264</td>
<td>-0.058</td>
<td>-0.099</td>
</tr>
<tr>
<td>T</td>
<td>-0.559</td>
<td>--</td>
<td>0.582</td>
<td>0.176</td>
<td>0.571</td>
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<tr>
<td>INT</td>
<td>0.073</td>
<td>0.108</td>
<td>--</td>
<td>0.736*</td>
<td>0.920**</td>
</tr>
<tr>
<td>PC</td>
<td>0.190</td>
<td>-0.260</td>
<td>0.828*</td>
<td>--</td>
<td>0.765*</td>
</tr>
<tr>
<td>TOT</td>
<td>0.211</td>
<td>-0.035</td>
<td>0.928**</td>
<td>0.934**</td>
<td>--</td>
</tr>
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(df = 5; *P < 0.05, **P < 0.01)
Figure 2.1. Phylogeny and general foraging modes of taxa used in this study. Numbers along branches indicate estimates of branch lengths (in millions of years before present). The phylogeny and branch lengths are based on Estes, de Queiroz, and Gauthier (1988) and Cooper (1997). Data on branch lengths were obtained from Cooper (1997) and references therein.
Figure 2.2. Mean occurrence data for prey processing behaviors in lizards from high-speed video recordings of individual feeding bouts of lizards feeding on prey sizes adjusted to the same relative head length (N=337). Note the relative increase in puncture-crushing and total numbers of prey processing cycles in the autarchoglossans.
Figure 2.3. The “interspersion” of prey processing behaviors. Interspersion (INT) is the mean number of times a transport behavior (T) is followed by a chewing behavior (PC, PLC) indicating the greater degree of prey handling involved in repositioning the prey item for chewing in autarchoglossans.
Figure 2.4. Feeding repertoires of lizard families expressed as the percent usage of each behavior. Note the dominance of PLC's in the iguanian feeding bouts and the dominance of PC's and increase in T's in the autarchoglossan taxa. Abbreviations: I = inertial transport; PC = puncture crushing; PLC = palatal crushing; SS = side-to-side; T = lingual transport.
Figure 2.5. Evolutionary patterns of feeding behavior in lizards for total (TOT), interspersion (INT), transport (T), puncture crushing (PC) and palatal crushing (PLC). Familial means are presented at the tips of the branches. Ancestral nodal values were estimated by the GLS method of Martins and Hansen (1997). Changes in the shading of the branches represent general trends (higher values darker) in the evolution of the trait values. Taxa in bold type indicate values more similar to the iguanian condition than the autarchoglossan condition.
Chapter 3. The relationship between skull morphology, biting performance and foraging mode in Kalahari lacertid lizards

INTRODUCTION

Foraging mode describes the movement patterns of organisms during the acquisition of prey (Pianka 1966; Gerritsen and Strickler 1977). Sit-and-wait foragers (SW) move infrequently and ambush prey as it comes within range, and thus, these predators tend to eat mobile and often fleet prey (e.g. grasshoppers). In 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; Magnuson 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. The “sit-and-wait/wide foraging paradigm” in lizards is based on thousands of foraging observations in the field (e.g. Pianka 1966; Schoener 1971; Huey & Pianka 1981; Pianka 1986; Pietruszka 1986; McLaughlin 1989; Perry 1999) and is widely cited as a general descriptor of lizard ecology.

The 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 et al. 1994), metabolic rate (Anderson & Karasov 1981; Nagy et al. 1984), feeding behavior (McBrayer & Reilly 2002), habitat use (Belliure 2002 Carrascal 1996), reproduction (Vitt & Price 1982; Vitt 1990), and learning ability (Day et al. 1999). Thus for many aspects of lizard biology, considerable support for the SW-WF paradigm exists.

Foraging mode also follows phylogenetic lines. During the squamate radiation, a key behavioral shift among insectivores occurred. One large radiation, the Iguania, has retained
the ancestral condition of sit-and-wait foraging (Cooper 1995, 1997a, 1997b), while virtually all of the members of the other major squamate radiation, the Scleroglossa & Autarchoglossa, evolved wide foraging (Cooper 1994, 1995; Schwenk 1995). 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 clearly dichotomous as has long been thought. Thus, rigorous comparative tests of the SW-FW 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, 1997b; 1999; 2000a, 2000b; Cooper & Whiting 1999; Cooper & Hartdegen 2000). However, other ecological and morphological corollaries of the paradigm have yet to be studied in adequate detail.

While 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 (Cooper 1997b, 2000b). The vertebrate skull is a dynamic structure with several functions—many related to feeding and biting. Thus, it is surprising that the relationship
between skull morphology and foraging mode has not been quantified—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), 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, 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, 1999b). 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’s and the general correlation of skull design with prey type in vertebrates in general, 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 will compare feeding morphology and performance in a group of lizards within the family Lacertidae. The species studied are the SW and WF species from which the paradigm was first described 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 the appropriate phylogenetic context. 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).

MATERIALS 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 et al. 1997; Mouton et al. 2000;
Lacertidae: Huey & Pianka 1981; Cooper & Whiting 1999; Scincidae: Castanzo & Bauer 1993; 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 et al. 1979; Huey & Pianka 1981; Perry & Pianka 1997; Cooper & Whiting 1999). These species are similar in body size (Huey & Pianka 1981; Pianka 1986) and their phylogenetic relationships are known (Fig. 3.1). This group is also very well studied ecologically (Pianka & Huey 1971; Pianka et al. 1979; Huey & Pianka 1981; Pianka 1981; Bennett et al. 1984; Huey et al. 1984; Pianka 1986). 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 Appendix 1). The following external measurements were taken from each specimen: snout-vent-length (SVL), mass (g), and depth of the head (skull and mandible) at the quadrate 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 sec.) 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 insure 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.

The 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).

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) (Emerson 1985, Radinsky 1981). However, ratios
are often difficult to interpret in statistical tests (Packard & Boardman 1987). Therefore, I
analyzed 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*). 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 variable 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 needed to consumer 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 prey handling times 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 handling time (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 *et al.* 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
(Anderson & McBrayer, in prep.; Sinclair 1983). This change in resistance was output 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. Field captured lizards were measured for mass (g), SVL (mm). Each individual was then induced to bite the transducer a minimum of three times to achieve a maximal bite from each individual (Anderson & McBrayer, in prep). The largest force value from these trials was used for further analysis. Maximum compressive 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 et al. 1984). In terms of feeding performance, I predicted maximum in vivo bite force would be greater in SW species due 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 in 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 centered by adding a value of two to each observation. Finally, each log-transformed, size-removed, centered variable for each species was then scanned for outliers and checked to ensure that it conformed to a normal distribution.

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 onto 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 ANOVA’s and the canonical variates analysis. The performance differences mapped were taken from the results of the raw and size corrected ANOVA’s of bite force.

Ideally, several more species of *Meroles* and *Pedioplanis* would have been included in this study. However, the foraging modes of most of these species are not well established and many have isolated or restricted distributions thereby obtaining large samples of them is difficult. Thus I included only the four species originally used to describe the SW and WF paradigm. 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 two times, 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 will assume 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 is that 1) there is very 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 SW (Cooper & Whiting 1999); and 3) *P. lineoocellata* is the basal member of its genus. Thus it
seems likely 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 3.1. The analysis of the raw, non-size corrected morphological data showed mixed support for the specific predictions made regarding head design. The SW species 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. lineoocellata* (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. lineoocellata* 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 3.1, lettering). Size corrected head depth was significantly different in each of the four species, while 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 feeding morphology (Wilks' $\lambda = 0.2007, P < 0.0001$). The first two canonical axes explained 82% (57% + 25%) of the overall variation in skeletal morphology. The third axis explained the remaining 18%. Table 3.2 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 4.2. It was expected that the SW species (*M. suborbitalis, P. lineoocellata*) 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. lineoocellata* (SW) have deep heads and small gapes. In contrast, *P. namaquensis* (WF) has a shallow head and large gape. On axis two (CAN2), the congeners *P. lineoocellata* and *P. namaquensis* have intermediate values for quadrate width, jaw length, and jaw width while *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. lineoocellata*) SW species.

To quantify whether species occupied unique portions of the morphological space, Mahalanobis’ $D^2$ distances were computed (Table 3.3). 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. lineoocellata* (SW) occupied positions closest to one another within morphological space even though they differ in foraging modes. Thus, the analysis of feeding morphology
demonstrated species-specific patterns of morphological variation, however, this variation did not covary with predictions made regarding foraging mode.

Bite force

Mean bite force was most similar between the two SW species (*P. lineoocellata, M. suborbitalis*) (Table 3.1). 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. lineoocellata* was significantly different from *H. lugubris* (Fig. 3.3; Table 3.1 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 *P. lineoocellata* (Table 3.1, lettering). *Meroles suborbitalis* was not significantly different from either *P. lineoocellata* or *P. namaquensis*; but *P. lineoocellata* 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. 3.4). Support for the coupling of feeding 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 3.1; Fig. 3.4a). The other SW species, *P. lineoocellata*, 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 3.1; Fig. 3.4a). 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 ANOVA’s 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 at each bifurcation of the phylogeny (Fig. 3.4b shaded boxes). The univariate tests showed a different pattern. Each species was significantly different in size corrected head depth while 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 gray 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. 3.4a,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 3.1; Fig. 3.3) and morphology (Table 3.3). However, they were not always more similar to one another than to a WF species (Fig. 3.2). The same was true of the WF species. Thus, except for head width and head length, feeding 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 efficiently feed 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 3.1 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. 3.2), however, they differ substantially along CAN1 and CAN3. The first axis, CAN1, was correlated with head depth and gape; *P. lineoocellata* had higher values in head depth while *P. namaquensis* had lower values. The deeper skull of *P. lineoocellata* permits increases in bite force (via increased muscle volume) and relative gape size—important variables to a SW forager that eats large prey. *Pedioplanis namaquensis*, in
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 consumption of prey (Emerson 1985). Although these patterns may reflect substantive ecological differences, they must be interpreted with caution due to the lack of similar covariance in the other SW and WF species. Further analyses on more species, however, would be able to test these observations. Nevertheless, as quantified here, it appears that variation in feeding morphology may be related more to phylogenetic differentiation (albeit small) rather than to differences related to diet and foraging mode (Fig. 3.4).

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), and thus, its high bite force capability is likely not related to resource use.

Gape size, rather than bite force, may be the critical aspect of skull morphology related to resource use in active and wide foraging lizards. The SW species had shorter and wider heads than the WF (Table 3.1, 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 contain 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 lowest 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 more easily handle large active prey items, while 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 also 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), each species diet consists of one half to nearly all termites (M. suborbitalis = 51% by volume vs. H. lugubris = 93% by volume). In fact, all Kalahari lizard species show an increased dependence on termites (Ricklefs et al. 1981). Compared to North American and Australian deserts, the Kalahari has the lowest prey diversity (Pianka 1986), and thus the abundance of termites in the Kalahari is likely of critical importance to these lacertid species. Furthermore, the Kalahari saurofauna (and lacertids in particular) is less morphologically diverse compared to either the Australian or 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 to efficiently 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 et al. 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) instead eating mostly
termites (Fig. 4.3, Pianka 1986). Thus, Kalahari lacertids must survive this ‘crunch’ time by switching to the most readily available food resource. Wiens and Rotenbury (1980) suggest that selection is relaxed during periods of high resource abundance and subsequent periodic environmental crunches 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 (e.g. 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 et al. (1980) found that lizards in the genus *Liolameus* show striking morphological 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 the ‘advanced lacertid’ clade are canalized to reach a similar morphology and 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 centered on the covariation between limb morphology, locomotor performance and microhabitat choice (e.g. Losos 1990; Miles 1994; Irschick & Losos 1999). Although none have specifically addressed foraging modes, many of these studies have been successful in demonstrating a relationship between morphology and ecology. In contrast, ecomorphological relationships of feeding in lizards have seen considerably less study. Herrel *et al.* (1999) revealed patterns of covariation between head morphology and herbivory, however, the current study was the first to test for relationships between foraging mode and specific aspects of feeding morphology.

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

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. This study demonstrates that observations of dietary differences are not a result of considerable morphological specialization in the skull. Because limited differences were found, the strength of the relationship between diet and foraging mode must be called into question. Furthermore, the continuum of SW-WF (Pietruszka 1986; Perry 1999) may have less to do with foraging 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.

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 2000a); (cordylids: Mouton et al. 2000)]. Research on these taxa holds considerable promise in that it will allow for further comparative tests of hypotheses regarding foraging mode evolution in groups whose diets may not be constrained during particular seasons.

In particular, comparative studies of life history, locomotor morphology, and neuroanatomy are needed in lacertids. Clutch size and egg size are known to covary with each foraging mode across lizard families (Vitt & Congdon 1978; Dunham & Miles 1985),
however, to date a broad, detailed comparative studies of lacertids, skinks, or cordylids have not 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 were 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, neuroanatomical studies of SW and WF lizards are lacking. Other advanced 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). While 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.
LITERATURE CITED


Table 3.1. Variation in head morphology and maximum bite force in sit-and-wait (*Meroles suborbitalis*, *Pedioplanis lineoocellata*) and wide foraging (*Heliobolus lugubris*, *Pedioplanis namaquensis*) lizards. The means (± 1 SE) 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 (± 1 SE). 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 in 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 QW = quadrate width; GAPE = gape; OL = jaw closing out lever.

<table>
<thead>
<tr>
<th></th>
<th><em>H. lugubris</em></th>
<th><em>M. suborbitalis</em></th>
<th><em>P. lineoocellata</em></th>
<th><em>P. namaquensis</em></th>
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<tr>
<td></td>
<td><em>WF</em></td>
<td><em>SW</em></td>
<td><em>SW</em></td>
<td><em>WF</em></td>
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<tr>
<td>SVL</td>
<td>56.75 ± 0.40</td>
<td>58.21 ± 0.47</td>
<td>57.26 ± 0.40</td>
<td>49.52 ± 0.42</td>
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<td>HD</td>
<td>6.72 ± 0.10</td>
<td>6.28 ± 0.06</td>
<td>6.43 ± 0.06</td>
<td>5.01 ± 0.05</td>
</tr>
<tr>
<td></td>
<td>(0.066 ± 0.003)(^A)</td>
<td>(0.040 ± 0.003)(^C)</td>
<td>(0.052 ± 0.003)(^B)</td>
<td>(0.026 ± 0.003)(^D)</td>
</tr>
<tr>
<td>HW</td>
<td>7.78 ± 0.06</td>
<td>8.21 ± 0.07</td>
<td>7.93 ± 0.08</td>
<td>6.51 ± 0.05</td>
</tr>
<tr>
<td></td>
<td>(0.127 ± 0.002)(^B)</td>
<td>(0.138 ± 0.001)(^A)</td>
<td>(0.133 ± 0.001)(^A)</td>
<td>(0.122 ± 0.001)(^B)</td>
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<tr>
<td>HL</td>
<td>14.27 ± 0.10</td>
<td>13.99 ± 0.12</td>
<td>13.94 ± 0.13</td>
<td>12.47 ± 0.10</td>
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<td></td>
<td>(0.366 ± 0.002)(^A)</td>
<td>(0.354 ± 0.002)(^B)</td>
<td>(0.359 ± 0.002)(^B)</td>
<td>(0.373 ± 0.002)(^A)</td>
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Table 3.1: continued.

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<th></th>
<th>5.18 ± 0.06</th>
<th>5.34 ± 0.07</th>
<th>5.16 ± 0.09</th>
<th>4.43 ± 0.04</th>
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<tr>
<td>GAPE</td>
<td>(-0.026 ± 0.003)(^A)</td>
<td>(-0.023 ± 0.004)(^A)</td>
<td>(-0.025 ± 0.003)(^A)</td>
<td>(-0.018 ± 0.003)(^A)</td>
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<td>OL</td>
<td>12.36 ± 0.10</td>
<td>12.22 ± 0.12</td>
<td>12.26 ± 0.12</td>
<td>10.58 ± 0.09</td>
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<tr>
<td></td>
<td>(0.307 ± 0.001)(^A)</td>
<td>(0.299 ± 0.001)(^B)</td>
<td>(0.309 ± 0.001)(^A)</td>
<td>(0.307 ± 0.001)(^A)</td>
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<tr>
<td>RAP</td>
<td>2.26 ± 0.03</td>
<td>2.45 ± 0.03</td>
<td>2.15 ± 0.03</td>
<td>1.88 ± 0.03</td>
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<td>QC</td>
<td>4.02 ± 0.06</td>
<td>3.78 ± 0.06</td>
<td>4.23 ± 0.06</td>
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<td>CT</td>
<td>8.35 ± 0.06</td>
<td>8.44 ± 0.07</td>
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<td>JL</td>
<td>14.48 ± 0.10</td>
<td>14.41 ± 0.11</td>
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<td>JW</td>
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<td>0.93 ± 0.03</td>
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<tr>
<td>QW</td>
<td>1.30 ± 0.02</td>
<td>1.43 ± 0.03</td>
<td>1.39 ± 0.02</td>
<td>1.04 ± 0.02</td>
</tr>
<tr>
<td>Newtons</td>
<td>2.75 ± 0.17</td>
<td>2.49 ± 0.16</td>
<td>2.26 ± 0.09</td>
<td>1.06 ± 0.05</td>
</tr>
<tr>
<td></td>
<td>(0.5551 ± 0.1877)(^A)</td>
<td>(-0.0260 ± 0.1156)(^BC)</td>
<td>(-0.1483 ± 0.0728)(^AB)</td>
<td>(-0.4132 ± 0.0719)(^C)</td>
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N 69/26  51/16  69/36  62/21
Table 3.2. Results of canonical variates analysis on 11 size-corrected skull measurements taken in sit-and-wait and wide foraging lacertid lizards. Values in the table are the variable-variate correlations with the percent variance explained on each canonical axis at the bottom. Each axis was significant ($P < 0.01$).

<table>
<thead>
<tr>
<th></th>
<th>Can1</th>
<th>Can2</th>
<th>Can3</th>
</tr>
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<tbody>
<tr>
<td>Head Depth</td>
<td>0.806</td>
<td>0.578</td>
<td>-0.126</td>
</tr>
<tr>
<td>Retroarticular Process</td>
<td>-0.078</td>
<td>-0.608</td>
<td>0.790</td>
</tr>
<tr>
<td>Quadrate-Coronoid</td>
<td>-0.606</td>
<td>0.501</td>
<td>-0.618</td>
</tr>
<tr>
<td>Coronoid-Tip</td>
<td>0.210</td>
<td>0.094</td>
<td>0.973</td>
</tr>
<tr>
<td>Jaw Length</td>
<td>0.253</td>
<td>0.905</td>
<td>0.342</td>
</tr>
<tr>
<td>Jaw Width</td>
<td>-0.333</td>
<td>-0.889</td>
<td>0.314</td>
</tr>
<tr>
<td>Head Width</td>
<td>0.696</td>
<td>-0.662</td>
<td>-0.280</td>
</tr>
<tr>
<td>Head Length</td>
<td>-0.716</td>
<td>0.631</td>
<td>0.299</td>
</tr>
<tr>
<td>Quadrate Width</td>
<td>-0.032</td>
<td>-0.975</td>
<td>-0.220</td>
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<tr>
<td>Gape</td>
<td>-0.909</td>
<td>-0.308</td>
<td>0.282</td>
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<tr>
<td>Out lever</td>
<td>-0.388</td>
<td>0.742</td>
<td>-0.546</td>
</tr>
<tr>
<td>Eigenvalue</td>
<td>1.279</td>
<td>0.549</td>
<td>0.411</td>
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<tr>
<td>Percent Variance</td>
<td>57.1</td>
<td>24.5</td>
<td>18.4</td>
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Table 3.3. Mahalanobis’ squared distances ($D^2$) between species centroids based on size-free morphological variables. Asterisks (*) indicate significance at $P < 0.01$.

<table>
<thead>
<tr>
<th></th>
<th>H. lugubris</th>
<th>M. suborbitalis</th>
<th>P. lineoocellata</th>
<th>P. namaquensis</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>WF</td>
<td>SW</td>
<td>SW</td>
<td>WF</td>
</tr>
<tr>
<td>H. lugubris</td>
<td>---</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M. suborbitalis</td>
<td>4.63*</td>
<td>---</td>
<td></td>
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<tr>
<td>P. lineoocellata</td>
<td>3.52*</td>
<td>4.14*</td>
<td>---</td>
<td></td>
</tr>
<tr>
<td>P. namaquensis</td>
<td>8.62*</td>
<td>9.06*</td>
<td>6.01*</td>
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</table>
Figure 3.1. A) Phylogenetic relationships among major lizard clades showing the evolution of foraging mode across squamates. The cladogram is based on Estes et al. (1988). B) Phylogenetic relationships among the taxa included in this study. Sit-and-wait foraging is presumed to be the basal condition for both *Meroles* and *Pedioplanis*. See text for details. The cladogram is based on Arnold (1991).
Figure 3.2. Three-dimensional plot of mean canonical scores of each lacertid species. Hl = *Heliobolus lugubris* (WF); Ms = *Meroles suborbitalis* (SW); Pl = *Pedioplanis lineoocellata* (SW); Pn = *Pedioplanis namaquensis* (WF).
Figure 3.3. 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. lineoocellata* 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. lineoocellata*, Pn = *P. namaquensis*. 
Figure 3.4. Phylogenetic mapping of skull morphology, biting performance, and foraging mode in four lacertid species. Panel A shows evolutionary transitions based on the analysis of the raw morphological and bite force data (Table 3.1 underlining). Panel B shows evolutionary changes based on the canonical variates analysis (boxes; Table 3.3) and size corrected ANOVA’s (bars and circles; Table 3.1 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.
Chapter 4. Preliminary analyses of lizard skull design and biting performance

INTRODUCTION

Historically, functional and structural (biomechanical) analyses have used a form-function approach to test predictions regarding how morphology affects the life of an organism (Bock and von Wahlert, 1965; Lauder, 1991; Bock, 1994). This approach grew out of comparative anatomy and ranged from purely anatomical descriptions to studies of the relationship between morphology and the performance of a particular task. While such studies provided a means for the description and quantification of morphology, they often did not explicitly test a hypothesis about the ecological or evolutionary significance of the variation observed. In a now classic paper, Arnold (1983) proposed a framework whereby by morphology, performance, and fitness could be integrated to understand how selection might act on morphological variation through performance.

Arnold’s framework brought on tremendous growth in research that uses performance measures to clarify the relationship between ecology and morphology (e.g. Pounds, 1988; Losos, 1990; Wainwright, 1991; Garland and Losos, 1994; Miles et al., 1995; Pough et al., 1997; Barbosa and Moreno, 1999a, 1999b; Irschick and Losos, 1999). The critical component of Arnold’s framework, and much of the subsequent study, was the quantification of performance. Performance measures represent the intersection of morphology with ecological patterns of resource use, habitat selection, etc. (Bock and von Wahlert, 1965; Miles and Ricklefs, 1984; Miles et al., 1987; Pounds, 1988; Bock, 1994; Ricklefs and Miles, 1994; Westneat, 1995). Thus to further our understanding of how performance relates to ecological and evolutionary patterns in nature, analyses of organismal form and function are critical (Arnold, 1983). Form-function analyses play the central role in
the generation of testable hypotheses regarding the performance capabilities of organisms and thus are the groundwork for studies of eco-morphology, selection, and adaptation (Wainwright, 1996).

For many vertebrate groups, the relationship between feeding morphology, diet, and feeding performance has been explored. In fact, key biomechanic elements and regions of the skull are known to be associated with various prey types in a wide range of organisms (Radinsky, 1981; Kiltie, 1982; Lauder, 1991; Zweers et al., 1994; Perez-Barberia and Gordon, 1999). In teleosts, lever arm mechanics and motor patterns are correlated to dietary variation within and among taxa (Lauder, 1991; Turingan, et al., 1995; Wainwright, 1996). In mammals, there is a general trend in cranial shape where as dietary selectivity increases, the rostrum (snout) tends to become narrower and incisor tooth structure changes (Radinsky, 1981; Solounias, 1988; Gordon and Illius, 1994; Biknevicius, 1996). In birds, beak morphology and lever mechanics have been correlated to dietary patterns (Beecher, 1962; James, 1982; Barbosa and Moreno, 1999a).

In lizards (non-ophidian squamates), similar studies relating diet to skull morphology have yet to be conducted. Classic works provide descriptions of lizard skull and muscle morphology (Haas, 1973; Gomes, 1974), but few have tried to relate these to diet. Some functional morphological studies have detailed particularly interesting forms such as the outgroup to lizards, Sphenodon (Gorniak et al., 1982), durophagous species (Wineski and Gans, 1984; Gans et al., 1985, Gans and de Vree, 1986, 1987), carnivorous species (Smith, 1982, 1984; Throckmorton and Saubert, 1982) and herbivorous species (Throckmorton, 1976, 1978, 1980; Herrel and de Vree, 1999; Herrel et al., 1999a). However, these works are far from comprehensive and the study taxa are not representative of the vast majority of lizards.
Most extant lizards are small insectivores that show remarkable diversity in skull morphology, jaw adductor anatomy, and dietary preferences (Schwenk, 2000). Studies of cranial form, function and performance in insectivorous lizards would not only broaden the existing data on lizard skull morphology but also provide a foundation to quantify how variation in cranial morphology may result in ecological differences. Yet little work to date has investigated how variation in skull morphology, jaw muscle anatomy, and feeding performance influences the ecology of insectivorous lizards (Schwenk, 2000). Understanding the nuances between morphology and performance will yield a much broader perspective of lizard skulls as form-function complexes, and therefore direct future research into the ecological or evolutionary consequences of the morphological variation seen in particular clades.

Currently, we know little about the tradeoffs between head form and biting performance in lizards and even less about the tradeoffs between muscle architecture and biting performance. The most comprehensive body of literature on lizard skull function is on the origin and adaptive significance of cranial kinesis (Reipple, 1978; Smith, 1980; Frazzetta, 1983; Smith and Hylander, 1985; Congdon, 1987; de Vree and Gans, 1987; Iordansky, 1990, 1996; Arnold, 1998; Herrel et al., 2000). However, some works have suggested that skull form and muscle architecture are important in shaping the range of dietary specializations in lizards. Gans et al. (1985) provided a detailed analysis of jaw adductor muscle architecture and motor patterns to demonstrate how blue-tongued skinks are able to feed on snails. In addition, Herrel et al. (1999a) showed that motor patterns change with different types of insect prey. Other works investigated motor patterns and kinematics (Schwenk and Throckmorton, 1989; Herrel et al., 1997), and one quantified motor patterns and biting performance simultaneously (McBrayer and White, 2002). Herrel
and colleagues (2001a,b) quantified how variation in head shape corresponds to in vivo biting performance in lacertids and in xenosaurids; however, data from other clades have not been collected.

Therefore, an extensive analysis of lizard head form coupled with data on feeding performance is required to understand the functional tradeoffs in insectivorous lizards. Such information will provide the baseline information to address detailed questions on particularly diverse lineages such as iguanians. Furthermore, it is only after we know the broader patterns of skull form, function and performance that we may test hypotheses about the ecological and/or evolutionary importance of variation in one or all three.

This study is a portion of a larger ongoing project whereby morphological differences are compared in taxa with diverse ecologies and evolutionary backgrounds. The general goal of this work is to provide data that increases our comparative knowledge of morphological variation in squamates. This paper focuses on several independent yet related issues. First, lever mechanics will be compared among five species to test if the in-lever /out-lever ratio of the lower jaw is similar to the values predicted for reptiles by Greaves (1988). Second, patterns of morphological variation will be quantified among the species. The purpose of this analysis is to investigate how species of similar and dissimilar ecologies differ in size corrected skull morphology (i.e. shape). Third, the relationship between external cranial morphology and in vivo bite force will be explored to find which morphological measures are best correlated with maximum biting performance. The primary objective of this study is to develop the framework for further analyses of the tradeoffs between head morphology and biting performance in particular lizard clades.
MATERIALS AND METHODS

Taxa

Five species of North American lizards were chosen as representative species to quantify morphological and functional variation. While the taxa are not representative of all of the morphological variation present in lizards, they serve as an adequate starting point because they span a continuum of body sizes, dietary preferences, morphotypes, foraging modes, and lizard clades.

Lizards were collected between 1998 and 2001. *Callisaurus draconoides* (n = 25) and *Cnemidophorus tigris* (n = 25) were collected two kilometers northwest of Desert Center California (Riverside Co.). *Sceloporus magister* were also collected at Desert Center (n = 4), and along the Verde River Valley in central Arizona ((n = 12); Tonto National Forest, Maricopa Co.). *Gambelia wislizenii* (n = 13) were collected in the Alvord Desert seven kilometers east of Fields Oregon (Harney Co.). *Elgaria coerulea* (n = 23) were collected along on state highway 11, 20 kilometers south of Bellingham Washington (Whatcom Co.).

Morphology and Bite Force

Linear measurements were chosen to reflect biomechanically informative aspects of the jaws as well as overall variation in skull size and shape. External measurements were taken from individuals in the field and from preserved specimens upon returning to the lab. Each measurement is shown in Figure 4.1. Head length (HL), depth (HD), and width (HW) represent general measures of skull size and shape, while tooth row length (TRL), quadrate to coronoid distance (QC), and the distance between the quadrate and the tip of the snout (QT) characterize the jaw closing lever mechanics.

Bite force is a performance measure that is essential in determining the prey spectrum available to lizards as well as potential winners of agonistic encounters with
conspecifics (Herrel et al., 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 when the lizard bit down upon it (Anderson and McBrayer, in prep.). This change in resistance was output 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 (two mm from the end of bite bars). All lizards bit the transducer at this location so that actual force values could be obtained from the millivolt output using a calibration equation. Lizards were induced to bite the transducer a minimum of five times to try to achieve a maximal bite from each individual. The largest force value from these trails was retained for analysis. Maximum compressive bite forces were measured for each of the five species at their field active body temperature (30°C in \textit{E. coerulca}; 40°C in the other species).

\textit{Statistical analyses}

Because the species are different in body size, all morphological measures were size corrected via the technique of Mosimann and James (1979). For each individual, seven morphological measures (HL, JL, HW, HD, TRL, QT, QC) were log\(_{10}\) transformed, summed, and divided by the total number of measurements. This quotient represents the log-size component. Each measurement for each individual was divided by its log-size value to yield a size free estimate of that measurement. Each log transformed, size corrected variable for each species was then scanned for outliers and checked to ensure that it conformed to a normal distribution.

Six of the size corrected external skull measurements were subjected to a principal components analysis to reveal patterns of morphological differentiation. Head length (HL)
and jaw length (JL) were highly correlated ($r = 0.97$), and thus, JL was excluded from the PCA. The principal component axes were extracted using the covariance matrix. Next, a partial correlation matrix was computed using the raw morphological data to quantify the strength of the relationship between each morphological variable and maximum bite force. Head length was entered as the partial variable and correlations were computed both intra- and interspecifically.

Because the partial correlation analysis could be confounded by inter-correlations among the morphological variables (i.e. collinearity), a stepwise multiple regression analysis was also run to find the best morphological predictors of bite force production. The resulting regression coefficients provide an estimate of the influence of a given morphological variable on maximum bite force while holding the influence of the other morphological variables constant. The analysis was initially run using the size corrected morphological data, however, regression diagnostics (Mallow’s $C_p$) showed a high degree of collinearity among the terms. Therefore, the analysis was run again using the principle component scores. For interspecific comparisons, the first three PC axes were entered into the PCA because they explained 98% of the sample variance in morphology and because the inclusion of more PC axes did not substantially increase the $R^2$ value or decrease $C_p$. The use of PC axes 1-3 was confirmed by running the all-possible regression procedure available in the NCSS software package. This procedure helps identify which variables to include in a multiple regression analysis based upon how each variable influences $R^2$ and $C_p$. For intraspecific comparisons, the all-possible regression procedure was run on all six PC axes. The PC axes that that maximized the variance explained ($R^3$) while minimizing collinearity ($C_p$) were included in the multiple regression analysis of each species. All statistical tests were run using NCSS software.
RESULTS

Morphological and bite force variation is summarized in Table 4.1. Lizards have higher than expected values for the jaw closing in lever/out lever ratio (QC/QT). For all five species, the ratio averaged 0.37 rather than the 0.20 predicted Greaves (1988). In fact one species, *E. coerulea*, had a very high value 0.53. A high value for the in lever / out lever ratio indicates high potential force generation. Thus, I plotted the lever ratio and bite force for each species (Fig. 4.2). Those species with higher bite force values also had higher lever ratios. Across all species, the in lever / out lever ratio was significantly correlated with bite force ($r = 0.79; P < 0.01$).

Patterns of variation in head morphology (size corrected) were initially explored by principal components analysis (Table 4.2). The first three principal components explained 98.3% of the sample variance. Principal component one (PC1) described 57.1% of the variance in morphology. Quadrate-coronoid (QC) distance was highly positively correlated with this component. Head width and depth were also positively correlated with the first component while tooth row length and head length were negatively correlated with it. The second component (PC2) described 31.8% of the variance and had a high positive loading for quadrate-tip (QT) distance and a moderate loading for head length. Head depth and head width had moderate negative loadings on PC2. The third component (PC3) described 9.4% of the variance and had high negative loadings for tooth row length. The fourth, fifth, and sixth components explained 1.25, 0.44, and 0.04% of the variance in morphology, respectively.

Plots of the PCA scores revealed distinct species clusters along the first two components (Fig. 4.3 A-C). Three species (*E. coerulea*, *G. wislizenii* and *S. magister*) were
positioned at the positive end of PC1 while *C. tigris* and *C. draconoides* were at the negative end. On PC2, *E. coerulea* and *C. tigris* were the only species with positive scores. Plots of PC3 described a gradient of species having short tooth row lengths at the positive end (*C. draconoides* and *E. coerulea*) to those with longer ones at the negative end (*G. wislizenii, C. tigris*).

The correlation between bite force and skull morphology was estimated while holding head length constant. When analyzed across all species, the jaw lever variables (QC, QT) were significantly correlated with bite force production (Table 4.3). Head depth, tooth row length, head width and jaw length were all negatively correlated to bite force. Quadrate-coronoid distance was highly correlated ($r = 0.85$) with bite force production. Head width and jaw length were poorly correlated with bite force ($r = -0.17, r = -0.24$, respectively). The remaining variables, although significant, were moderately correlated with bite force ($r = -0.55$ to $0.47$).

Within species, the correlations among bite force and individual morphological variables varied. Quadrate–tip was significantly correlated to bite force in *C. draconoides* while quadrate-coronoid was correlated to bite force in *G. wislizenii*. Tooth row length was only significantly correlated to bite force in *G. wislizenii*. Head depth and head width were significantly correlated with bite force in *C. draconoides, C. tigris,* and *E. coerulea* but not in *G. wislizenii* or *S. magister*. Jaw length was not significantly correlated with bite force in any of the five species.

The interspecific multiple regression analysis revealed that PC1 and PC2 were significantly associated with bite force and explained $71\%$ of the sample variance (Table 4.4). The third principal component axis (PC3) was not significant and did not explain any additional variance. Thus across species, only PC1 and PC2 were good predictors of bite force.
Within species, the patterns varied (Table 4.4). In *C. tigris*, PC1 was the only significant coefficient, while in *C. draconoides*, PC1 and PC3 were significant. In *E. coerulea*, coefficients for PC1, PC2, PC3, PC5, and PC6 were significant. No regression coefficients were significant for either *G. wislizenii* or *S. magister*. Thus cranial morphology was a poor predictor of bite force in *G. wislizenii* and *S. magister*. However in the remaining three species, PC1 was a good predictor while the remaining PC axes variably contributed to bite force production.

**DISCUSSION**

Unlike mammals with specialized teeth for shearing, and crushing, most lizards possess an unspecialized homodont dentition along the entire length of the upper and lower jaws. Thus, lizards do not possess any obvious morphological adaptations to suspect that they use any particular teeth (e.g. molars) or region along the tooth row for powerful biting like mammals do. Instead, it is likely that they optimize bite force production along the entire length of the jaw rather than on particular teeth (Druzinsky and Greaves, 1979). Using this logic, the position of the muscle resultant was predicted to be 20% of jaw length for reptiles and 30% for mammals (Greaves, 1988). Greaves found some support for his predictions in both mammals (Greaves, 1982) and turtles (Druzinsky and Greaves, 1979). As an approximation of the muscle resultant, I used the in lever / out lever ratio (QC/QT) to test his prediction for reptiles. The in lever / out lever ratio corresponds roughly to the 0muscle resultant and is the point along the jaw that Greaves identified as the point where bite force could be maximized without disarticulating the lower jaw.

This study was the first to test Greaves' predictions for any squamate. Four of the five lizard species examined had very similar lever ratios (0.32-0.37) that were greater than
those predicted. In the case of *E. coerulea*, the ratio was even greater than that predicted for mammals. Although Greaves’ prediction for reptiles was smaller than that observed in lizards, the similarity of lever ratio values across four of the species suggests that most lizard species maintain a lever ratio around 0.35 regardless of body size or dietary preference. Greaves also predicted that the position of the most posterior tooth in the tooth row would be at approximately one-third jaw length in mammals (Greaves, 1982). The QC/QT ratio is equal to the position of the most posterior tooth along the jaw, and for these lizard species, it closely approximates this ‘one-third’ position.

The morphological analysis of skull form revealed several interesting patterns. For example, *C. tigris* has a long, narrow head while *G. wislizenii* has a relatively long, wide head (Table 4.1; Fig. 4.3). These differences may reflect each species’ diet; *C. tigris* probes for and consumes lots of termites while *G. wislizenii* eats larger, more fleet prey like lizards and grasshoppers (Pianka, 1986). In both species, having a long head and jaws will potentially increase the velocity of movement of the jaws during prey capture and/or processing. Increased mouth opening or closing velocity would be beneficial in rapidly processing many tiny prey items like termites (*C. tigris*) and in rapid attacks on fast moving prey like lizards (*G. wislizenii*). However, the wide skull and thus larger gape of *G. wislizenii* also enable it to eat large prey like lizards.

Other patterns may be seen by closely examining the species positions in morphological space. Sexual dimorphism in head size and shape was detected in one species, *C. tigris*. Large male *C. tigris* form a distinct cluster separate from females and small males along PC1 (Fig. 4.3). The PCA was performed using size corrected data, and thus, differences along PC1 may be considered shape differences. Although *G. wislizenii* and *E. coerulea* are reported as being dimorphic in body size (Stebbins, 1985), males and females of
these species did not cluster together based on head morphology in this sample. Thus for species other than *C. tigris*, differences between the sexes in head morphology are likely related to size differences rather than differences in head shape.

For some species, the morphological variation also reflected performance variation. *E. coerulea* had high positive scores on PC1 and PC2 (Fig. 4.3) and had high bite force values. In contrast, *C. draconoides* had low scores on PC1 and PC2 and low bite force (Table 4.1; Fig. 4.3). The QC and QT variables were strongly correlated with PC1 and PC2, respectively, (Table 4.2) and with bite force (Table 4.3). Although other studies (Herrel et al., 1999b; Herrel et al., 2001a,b) have relied on measures like skull length, width, and depth, my results suggest that the inclusion of lever arm estimates (QC, QT) may be helpful in predicting potential bite force production among species.

Better evidence for a relationship between QC, QT, and bite force was found in the partial correlation and multiple regression analysis. Quadrate-coronoid distance had the highest partial correlation coefficient among all species. In the multiple regression, QC had a high loading on PC1 (0.93), and PC1 was a significant predictor of bite force in three of the five species. Thus, QC and QT are good predictors of biting performance when considered among species.

However within species, the relationship between QC, QT, and bite force was different. Head depth and head width were significantly correlated to bite force in *C. draconoides*, *C. tigris*, and *E. coerulea* (Table 4.3). The QT variable was only significantly correlated with bite force in *C. draconoides*. Herrel et al. (2001a) found that head depth was significantly related to bite force in three species of xenosaurid lizards. In a separate study of lacertids, head width was found to be important (Herrel et al., 2001b). Unfortunately, lever
mechanics were not quantified in either of these studies and thus comparisons among this study and those of Herrel and colleagues are difficult.

However, the data from this and Herrel’s studies demonstrate that head size and shape are important for bite force production in lizards. Given the current data, it appears that for any given species, either head width or head depth are the best general predictors of biting performance. Across species, lever arm estimates may be better indicators biting performance. These patterns highlight how the combination of morphological traits influences biting performance.

For example, *E. coerulea* occupies a unique portion of the morphological space in each panel of Fig. 4.3. It also has the highest bite force. Thus this species possesses a combination of traits (wide, deep head coupled with large in lever / out lever ratio) that enables it to produce large forces. If these morphological traits were to change, the performance capabilities of the jaw system must also change.

Because the feeding apparatus is a composite of many morphological traits, functional tradeoffs exist among the traits and their performance capacity (Wainwright, 1996). To illustrate this, I constructed a schematic of how the morphological variation observed in this study mapped onto performance variation (Fig. 4.4). I summarized the morphological variation among the species by plotting the species means along PC1 and PC2 (Fig. 4.4, bottom). Performance variation was portrayed by plotting the species means for the in lever / out lever ratio and bite force (Fig. 4.4, top). Differences among the species were tested via GLM ANOVA coupled with the Tukey posthoc procedure in SAS. This ‘multilevel’ approach (*sensu* Miles, 1994; Lauder and Reilly, 1996) allows one to visualize the relationships among classes of traits (i.e. morphology and performance) and explore the functional tradeoffs that exist across levels.
At the morphological level, clear patterns are present. On PC1, *E. coerula*, *G. wislizenii*, and *S. magister* are equal to one another yet significantly different from *C. draconoides* and *C. tigris* (Table 6). The former species have long QC distances and wide, shallow heads while the latter have shorter QC distances and narrow, deep heads. On PC2, *C. draconoides* and *G. wislizenii* are not different, but all of the other species are different. Thus at the morphological level, each species has a unique morphology—all species are significantly different across both axes.

In performance space, the lever ratio is the same in *S. magister*, *C. tigris* and *G. wislizenii* and in *S. magister* and *C. draconoides*. For bite force, *C. tigris* is equal to *S. magister*; *S. magister* is also equal to *C. draconoides* (Table 6). *Callisaurus draconoides* and *S. magister* are not significantly different on either performance axis and thus are circled.

Mapping these patterns across each space shows some of the potential tradeoffs in morphology and performance. *Elgaria coerula* has high values within the morphospace (upper right) and maps to the highly positive region of performance space as one might predict. *Gambelia wislizenii* follows a similar pattern. *Cnemidophorus tigris* has a relatively short QC and longer QT, thus it maps to the lower left region of the performance space. In *S. magister*, the reverse is true; it has a long QC but short QT.

By mapping patterns across the performance and morphological spaces, other functional patterns may be exposed (Lauder and Reilly, 1996). For example, *C. draconoides* has low scores within the morphospace. Because the morphological variables making up the morphospace reflect performance potential, it is not surprising that *C. draconoides* also has low scores in the performance space. However, it is interesting that *S. magister* is not significantly different from *C. draconoides* in either performance variable but is different morphologically. These species are members of the same iguanian subfamily.
(phrynosomatinae; Macey et al., 1997), and although they are radically different morphologically, they must share similar jaw muscle morphologies to explain their similarity in biting performance. Therefore, this multilevel analysis demonstrates a tradeoff between their skeletal morphology and performance ability as well as generates testable morphological and biomechanical predictions for other variables like jaw adductor muscle morphologies.

*Future work*

This study represents a portion of a larger study comparing head form and biting performance in lizards. The data presented here are from a limited number of taxa and thus any inferences made regarding lizards in general would be tenuous. Furthermore, no attempt has been made to account for the influence of the phylogenetic relationships among the taxa. Finally, and most importantly, this study demonstrates that external morphological data are good general indicators of the form-function relationship between lizard head morphology and biting performance but that muscle morphology also plays a critical role. Therefore, additional data on muscle morphology must be incorporated into this analysis before any general patterns will emerge regarding the tradeoffs between lizard head form and biting performance.

The major finding of this portion of the study is that some species show very similar patterns of bite force production yet are obviously different in skull morphology (Table 4.1; Fig 3, 4.4). Beyond adding more species, the future emphasis of this work will be to add data on muscle moment arms, fiber lengths, fiber orientations, and cross sectional areas. The addition of muscle architecture data will reveal exactly how changes in head depth and/or head width affect muscle morphology, and thus, force production. Furthermore by
increasing the number of taxa within the study, a range of possible evolutionary ‘solutions’ to the functional demands of feeding and biting can be identified.

Therefore this study will be expanded through the addition more species and muscle architecture data. I will focus on members of the family Iguanidae first, before making more phylogenetically broad comparisons as has been done here. Iguanids were chosen for several reasons. They are speciose and diverse morphologically and ecologically. The family is currently thought be monophyletic and eight subfamilies are proposed to lie within it (e.g. the phrynosomatinae; Macey et al., 1997). Finally, two of the three iguanid species examined here are from iguanid subfamilies that are monophyletic (G. wislizenii, crotaphytinae; S. magister, C. draconoides phrynosomatinae; Schulte et al., 1998) and thus provide a good foundation to begin to examine variation among the subfamilies. By quantifying the functional tradeoffs between skull form and biting performance across the family, this analysis will serve as a springboard for future ecological or evolutionary work within this large clade.

Although functional tradeoffs are known to exist, they are often implicated in studies rather than being investigated in their own right. Furthermore, tradeoffs are rarely quantified at the skeletal, muscular and whole organism levels, however, Herrel et al. (1999b) have provided an excellent example of how such studies should be conducted in lizards. Furthermore, lizard skulls are model systems for such work because they have diverse skeletal and muscular morphologies and most will readily bite. A detailed analysis of the lizard feeding apparatus will provide a valuable test of the theoretical predictions of muscle structure and performance (Gans, 1988; Gans and Gaunt, 1991) and identify how each change with skull morphology.
Integrating these three data types will provide a basis to ask refined functional questions that have ecological importance. For example, many lizards are sexually dimorphic in both body size and head size (Anderson and Vitt, 1990). In many species, males not only engage in fights where they aggressively bite each other, but they also ritualistically bite the head, neck, or torso of females during copulation, and often, these bite are powerful enough to leave sizable scars. For many species, the ecological basis of sexual dimorphism is not well understood (Shine 1989; Anderson and Vitt, 1990). Thus, a broad analysis of skull form may reveal important functional differences between males and females and thereby provide insights into the maintenance of the dimorphism.

In conclusion, the data presented here and the forthcoming muscle architecture data represent the foundation of a long-term research program on the form and function of the lizard skull and jaws. By quantifying the functional tradeoffs in a range of species from particular lineages, patterns of evolutionary change can be assessed. For example, by completing a survey of iguanids, hypotheses regarding the evolutionary significance of variation in cranial morphology may be tested using comparative methods (e.g. independent contrasts). Precise comparative data on jaw adductor morphology in iguanids or other groups (e.g. teiids or sciromorphs) may ultimately help reveal phylogenetically informative characters for the group under study or the clade as a whole. Ultimately however, the study will yield new insights into how variation in morphology results in performance variation, and as such, provide the context to direct field related studies of resource use, mating success, and/or fitness in the framework proposed by Arnold (1983).
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Table 4.1. Variation in cranial morphology and biting performance in five lizard species. The species mean in mm (± 1 S.E.) are presented. Numbers in parentheses are sample sizes. Abbreviations: SVL = snout-vent length; HL = head length; JL = jaw length; HW = head width; HD = head depth; TRL = tooth row length; QT = quadrate to snout tip; QC = quadrate to coronoid; QC/QT is the ratio of the jaw in lever to out lever. Each measure is explained in Figure 4.1.

<table>
<thead>
<tr>
<th></th>
<th>C. draconoides</th>
<th>C. tigris</th>
<th>E. coerulea</th>
<th>G. wislizenii</th>
<th>S. magister</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(25)</td>
<td>(25)</td>
<td>(23)</td>
<td>(13)</td>
<td>(16)</td>
</tr>
<tr>
<td>SVL</td>
<td>68.08 ± 1.31</td>
<td>83.88 ± 1.90</td>
<td>93.80 ± 1.57</td>
<td>97.34 ± 2.24</td>
<td>84.94 ± 3.59</td>
</tr>
<tr>
<td>HL</td>
<td>11.85 ± 0.20</td>
<td>19.24 ± 0.42</td>
<td>16.59 ± 0.22</td>
<td>20.50 ± 0.29</td>
<td>16.38 ± 0.51</td>
</tr>
<tr>
<td>JL</td>
<td>14.33 ± 0.25</td>
<td>21.72 ± 0.54</td>
<td>18.63 ± 0.25</td>
<td>23.71 ± 0.39</td>
<td>19.97 ± 0.66</td>
</tr>
<tr>
<td>HW</td>
<td>10.79 ± 0.18</td>
<td>10.90 ± 0.32</td>
<td>10.94 ± 0.22</td>
<td>17.08 ± 0.31</td>
<td>16.99 ± 0.70</td>
</tr>
<tr>
<td>HD</td>
<td>7.77 ± 0.16</td>
<td>9.51 ± 0.28</td>
<td>7.75 ± 0.14</td>
<td>11.10 ± 0.23</td>
<td>11.22 ± 0.39</td>
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<tr>
<td>TRL</td>
<td>8.60 ± 0.16</td>
<td>11.83 ± 0.25</td>
<td>8.71 ± 0.15</td>
<td>14.95 ± 0.29</td>
<td>12.03 ± 0.32</td>
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<tr>
<td>QT</td>
<td>12.74 ± 0.20</td>
<td>18.70 ± 0.46</td>
<td>18.63 ± 0.25</td>
<td>23.71 ± 0.39</td>
<td>18.17 ± 0.52</td>
</tr>
<tr>
<td>QC</td>
<td>4.13 ± 0.13</td>
<td>6.83 ± 0.23</td>
<td>9.92 ± 0.19</td>
<td>8.75 ± 0.17</td>
<td>6.14 ± 0.31</td>
</tr>
<tr>
<td>QC/QT</td>
<td>0.32 ± 0.01</td>
<td>0.37 ± 0.01</td>
<td>0.53 ± 0.01</td>
<td>0.37 ± 0.01</td>
<td>0.34 ± 0.01</td>
</tr>
<tr>
<td>Bite Force</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Newtons)</td>
<td>3.50 ± 0.17</td>
<td>6.21 ± 0.50</td>
<td>16.88 ± 1.01</td>
<td>11.62 ± 0.50</td>
<td>4.77 ± 0.43</td>
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Table 4.2. Factor loadings from a principal components analysis on size corrected morphological data.

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
<th>PC5</th>
<th>PC6</th>
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<tr>
<td>Head Length</td>
<td>-0.413</td>
<td>0.644</td>
<td>-0.464</td>
<td>-0.132</td>
<td>0.426</td>
<td>0.006</td>
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<tr>
<td>Head Width</td>
<td>0.728</td>
<td>-0.601</td>
<td>-0.278</td>
<td>0.177</td>
<td>0.026</td>
<td>-0.016</td>
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<tr>
<td>Head Depth</td>
<td>0.629</td>
<td>-0.701</td>
<td>-0.311</td>
<td>-0.122</td>
<td>-0.015</td>
<td>0.028</td>
</tr>
<tr>
<td>Tooth Row Length</td>
<td>-0.556</td>
<td>0.349</td>
<td>-0.739</td>
<td>-0.139</td>
<td>-0.059</td>
<td>-0.033</td>
</tr>
<tr>
<td>Quadrate – Tip</td>
<td>0.076</td>
<td>0.924</td>
<td>-0.347</td>
<td>0.138</td>
<td>-0.027</td>
<td>0.026</td>
</tr>
<tr>
<td>Quadrate – Coronoid</td>
<td>0.934</td>
<td>0.349</td>
<td>0.064</td>
<td>-0.042</td>
<td>-0.001</td>
<td>-0.006</td>
</tr>
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<td>Eigenvalue</td>
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<td>0.2070</td>
<td>0.0061</td>
<td>0.0008</td>
<td>0.0003</td>
<td>0.00002</td>
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<tr>
<td>Percent Variance</td>
<td>57.10</td>
<td>31.78</td>
<td>9.39</td>
<td>1.25</td>
<td>0.44</td>
<td>0.04</td>
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</table>
Table 4.3. Partial correlation matrix between maximum bite force and six skull measures with head length held constant.

<table>
<thead>
<tr>
<th></th>
<th>Jaw Length</th>
<th>Head Width</th>
<th>Head Depth</th>
<th>Tooth Row Length</th>
<th>Quadrate Tip</th>
<th>Quadrate – Coronoid</th>
</tr>
</thead>
<tbody>
<tr>
<td>Interspecific</td>
<td>-0.24</td>
<td>-0.17</td>
<td>-0.43*</td>
<td>-0.55*</td>
<td>.47*</td>
<td>0.85*</td>
</tr>
<tr>
<td>C. draconoides</td>
<td>0.40</td>
<td>0.50*</td>
<td>0.55*</td>
<td>0.17</td>
<td>0.51*</td>
<td>0.34</td>
</tr>
<tr>
<td>C. tigris</td>
<td>0.26</td>
<td>0.48*</td>
<td>0.46*</td>
<td>-0.08</td>
<td>0.12</td>
<td>0.21</td>
</tr>
<tr>
<td>E. coerulea</td>
<td>0.33</td>
<td>0.49*</td>
<td>0.65*</td>
<td>0.29</td>
<td>0.33</td>
<td>0.13</td>
</tr>
<tr>
<td>G. wislizenii</td>
<td>0.004</td>
<td>-0.09</td>
<td>-0.15</td>
<td>-0.62*</td>
<td>0.004</td>
<td>0.67*</td>
</tr>
<tr>
<td>S. magister</td>
<td>0.18</td>
<td>-0.35</td>
<td>0.04</td>
<td>-0.05</td>
<td>-0.18</td>
<td>-0.12</td>
</tr>
</tbody>
</table>

*P < 0.05
Table 4.4. Results of interspecific and intraspecific multiple regression analyses using bite force as the dependent variable and principal component axes as independent variables. Principal component axes were used due to high collinearity within the size-corrected morphological data. Table 4.2 shows the morphological variables that loaded each principle component (PC) axis. Empty cells indicate that a given variable was omitted from the model because it neither increased $R^2$ nor decreased Mallow’s $C_p$.

<table>
<thead>
<tr>
<th></th>
<th>$R^2$</th>
<th>Intercept</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
<th>PC5</th>
<th>PC6</th>
</tr>
</thead>
<tbody>
<tr>
<td>Interspecific</td>
<td>0.71</td>
<td>8.42</td>
<td>3.55**</td>
<td>3.46**</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C. draconoides</em></td>
<td>0.66</td>
<td>5.689**</td>
<td>1.329**</td>
<td>-0.967**</td>
<td>0.075</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C. tigris</em></td>
<td>0.79</td>
<td>6.082**</td>
<td>2.798**</td>
<td>-1.361</td>
<td>1.023</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>E. coerulea</em></td>
<td>0.74</td>
<td>23.006**</td>
<td>7.541**</td>
<td>-4.731**</td>
<td>-7.160**</td>
<td>1.618**</td>
<td>1.711**</td>
<td></td>
</tr>
<tr>
<td><em>G. wislizenii</em></td>
<td>0.55</td>
<td>10.063</td>
<td>3.430</td>
<td>4.493</td>
<td>-1.968</td>
<td>-1.650</td>
<td>0.981</td>
<td></td>
</tr>
<tr>
<td><em>S. magister</em></td>
<td>0.19</td>
<td>4.388**</td>
<td></td>
<td>-0.470</td>
<td>0.339</td>
<td>1.083</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**$P < 0.01$
Table 4.5. Results of Tukey post hoc tests from individual ANOVA’s on morphology (PC1, PC2) and performance (In / Out lever, Bite force) variables. Underlining indicates no significant difference among the species.

<table>
<thead>
<tr>
<th></th>
<th>C. draconoides</th>
<th>S. magister</th>
<th>C. tigris</th>
<th>G. wislizenii</th>
<th>E. coerulea</th>
</tr>
</thead>
<tbody>
<tr>
<td>PC 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PC 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>In / Out Lever</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bite Force</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

PC1: $F = 47.1, df = 4.97, P < 0.0001$; PC2: $F = 214.2, df = 4.97, P < 0.0001$

In/Out lever: $F = 153.8, df = 4.97, P < 0.0001$; Bite Force: $F = 85.4, df = 4.97, P < 0.0001$
Figure 4.1. External measurements taken from each lizard. Head length = number of mm from the tip of the snout to the posterior edge of the parietal. Tooth row length = number of mm from the tip of the snout to most posterior tooth in the upper tooth row. Jaw length = number of mm from the tip of the lower jaw to the tip of the retroarticular process (including skin and muscle). Head depth = the depth of the head and lower jaw at the anterior curvature of the quadrate. Quadrate-tip = number of mm from the posterior surface of the quadrate at the tympanum to the tip of the snout. Quadrate-coronoid = number of mm from the posterior surface of the quadrate at the tympanum to the most posterior tooth.
Figure 4.2. Scatterplot of bite force (Newtons) and the in lever / out lever ratio (QC/QT). *Elgaria coerulea, G. wislizenii,* and *C. tigris* have the highest bite force values and high lever ratios.
Figure 4.3. Plots of the principal component scores from the first three principal components of a PCA run on six size corrected skull variables measured in five lizard species. Note that distinct species clusters are formed and that in *C. tigris*, sexual dimorphism in head shape is apparent. See text for details.
Figure 4.4. Multilevel visualization of interspecific variation in skull morphology and biting performance in five lizard species. The species abbreviations within each plane approximate the position of the species’ mean on each axis. Circled species are not significantly different from one another on both axes. See Table 4.5 for significant differences among species on individual axes. See text for an explanation of the functional tradeoffs between morphology and performance in individual taxa.
CONCLUSIONS AND FUTURE WORK

This dissertation had three principle objectives. First, I tried to ask questions that had significant evolutionary and/or theoretical importance. Second, I tried to develop novel techniques and/or approaches that would further our ability to test these kinds of broad questions. And finally, I wanted to integrate biological subdisciplines to develop a niche for myself as a scientist. This dissertation developed a useful analytical tool (slope analysis, Chapter 1), strengthened our understanding of the interrelationships between form and behavior (Chapter 2), demonstrated that morphology and ecology are not always closely associated (Chapter 3), and tested frequently cited theoretical predictions (Chapters 4 and 1). Thus either in whole or in part, I believe this work has achieved its goals. Moreover, this work now provides the philosophical and pragmatic underpinnings for more detailed investigations of lizard ecology and functional morphology.

Future work

The influence of variation in head form and muscle anatomy on biting performance will continue to be explored, particularly in iguanid species. Iguanids are monophyletic, speciose, and diverse morphologically and ecologically. Thus, this group is ideal for examinations of functional and ecological tradeoffs among species. Quantifying tradeoffs in head form and biting performance will serve as a springboard for further ecological and evolutionary studies within this large clade.

This type of functional work will also be extended into questions regarding sexual dimorphism in iguanids. Many iguanid species are sexually dimorphic in head size (and/or overall body size). In most species, males ritualistically bite females during copulation. Thus, the role of bite force and/or gape size may be very important in individual male
fitness. However to date, little work has attempted to relate any functional differences associated with sexual dimorphism to ecological differences in lizard mating success.

The work on prey processing will be expanded with more taxa within particular lineages. The chapter included here was intentionally broad in order to gain insight into what patterns might be present. Now, it is imperative to narrow the focus of this work to species within families to test the strength of the patterns shown here. Furthermore, a study of prey processing variation will be conducted on members of the Gekkota. This clade is a “transitional” group between the Iguania and the Autarchoglossa, and thus will also provide a test of the patterns shown here.

Finally, I plan to continue studying foraging mode evolution in the lacertid genera *Merides* and *Pedioplanis*. The data presented here showed that feeding morphology and performance were not related to foraging mode. Therefore, other factors must be investigated. The interspecific scaling relationships in hindlimb morphology will be studied in several *Pedioplanis* species. Anecdotal reports of several sit-and-wait *Pedioplanis* species exist; hence, higher numbers of taxa and other analytical techniques (e.g. concentrated changes test) can be included. This approach will strengthen the inferences made regarding the evolution of these traits with foraging mode, and hopefully, provide better insight into the traits associated with foraging mode evolution across all lepidosaurs.
Appendix A. Natural History Museum of Los Angeles County (NHMLAC) catalog numbers of the species included in this study

**Heliobolus lugubris:**
79898-79901,79904-79906,79908,79911,79917-79918,79924,79934-9939,79947,79951,80025-80035,80039,80042,80047,80049,80050-80053,80055,80056,80060-80063,80065,80067-0070,80072,80074,80076-80083,80085,80087,80092-80094,80097-80100,80143

**Meroles suborbitalis:**
81840,81848,81857,81858,81873,81875,81877-81879,81882,81886,81889,81897,81903,81918,81920,81929,81938,81944,81946,81951,81953,81954,81956-81958,81960-1962,81965,81967,81969-81976,81980-81983,81986,81988,81990-81993,81995,81996

**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