Prey capture kinematics of ant-eating lizards

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Summary

While morphological and behavioral feeding specializations are obvious in many vertebrate groups, among lizards there appear to be few dietary specialists. By comparing the prey capture kinematics and overall feeding behavior in two highly specialized ant-eating lizards (*Moloch horridus* and *Phrynosoma platyrhinos*) with those of two closely related dietary generalists (*Pogona vitticeps* and *Uma notata*), we investigate whether dietary specialization has been accompanied by changes in the function and use of the feeding system. We quantified kinematic variables from high-speed video recordings (200–250 frames s^{-1}) of each species feeding on ants. Prey capture was strikingly different in *M. horridus* to that of other species, being characterized by a suite of unusual behaviors including the lack of a body lunge, faster tongue protrusion, reduced prey processing and, most notably, the ability to modulate the slow open phase of the gape cycle. In concert, these traits make a single feeding event in *M. horridus* faster than that in any other iguanian lizard studied to date. Prey capture behavior in *P. platyrhinos* is kinematically more similar to *U. notata* and *P. vitticeps* than to *M. horridus*, but the ant specialists are similar in that both lack distinct prey processing behaviors, resulting in faster overall capture and feeding events. While ant feeding in *P. vitticeps* is faster than feeding on other prey, the duration of a single feeding event is still four times longer than in either ant specialist, because of extensive prey processing. Additionally, a phylogenetic comparison of ant specialist lizards with dietary generalists revealed that ant-eating lizards require significantly less time to capture and process prey. Thus there are not only significant behavioral modifications in these ant-eating lizards, but also multiple strategies among specialists, suggesting differing selective pressures or phylogenetic constraints in the evolution of ant eating in lizards.

Key words: lizard, iguania, prey capture, feeding, ant eating, myrmecophagy, *Moloch*, *Phrynosoma*, *Pogona*, *Uma*.

Introduction

Over the past two decades, the feeding behavior of lizards has received increasing attention (reviewed by Schwenk, 2000; Bels, 2003). Much of the focus of this body of research has been on testing the generalized tetrapod feeding model of Bramble and Wake (1985), which suggested a general pattern underlying feeding behavior in 'lower' tetrapods. Most studies of lizard feeding behavior have since supported the presence of a basic pattern, but have also identified significant variation in feeding movements (e.g. Schwenk and Throckmorton, 1989; Kraklau, 1991; Urbani and Bels, 1995; Delheusy and Bels, 1999; McBrayer and Reilly, 2002a). While these studies have laid a foundation for comparisons of lizard groups, they also reveal a striking gap in the literature regarding the feeding movements of dietarily specialized lizards. Whereas studies on generalized lizards are ideal for providing insights into basic patterns, studies on feeding systems associated with ecological specialization may allow us to identify evolutionary innovations or point towards constraints on the evolution of phenotypic diversity.

In many organisms, ecological specialization is reflected in morphological and behavioral adaptations (e.g. Losos, 1990; Grant, 1999). Although feeding specializations are obvious in many vertebrate groups such as mammals (e.g. herbivores, ant-eaters, carnivores, etc…), few dietary specialist groups appear to exist among lizards. While reviewing lizard diets, Greene (1982) found it difficult to describe a set of common features characterizing dietary specialists among lizards, primarily because of the preponderance of morphological generalists that appear to have specialized diets. Although Greene (1982) and later Schwenk (2000) suggested there were likely few adaptive characters in the feeding system of lizards related to ecological specialization, they agreed with Pianka and Parker (1975) that many of the unique morphological features exhibited by the North American horned lizards (*Phrynosoma*) and the Australian thorny devil *Moloch horridus* Gray 1841 are likely adaptive traits, related to a specialized ant-eating diet.

Because most lizards include a diversity of prey (in both size and type) in their diet, relatively few items need to be eaten

daily. However, due to the relatively small size and low caloric value of ants (Withers and Dickman, 1995), large quantities have to be consumed daily (e.g. up to 2000 ants per day by *M. horridus*). With the time constraints inherent in eating so many prey, we might expect ant-eating lizards to show distinct specializations, allowing them to minimize the duration of a feeding bout. Thus, myrmecophagous lizards appear ideally suited for investigating functional specializations of the feeding system in lizards.

Lizards of the genera *Phrynosoma* and *Moloch* have been considered a classic example of convergent evolution, both genera sharing a suite of morphological and behavioral characters considered to be 'adaptations' to their myrmecophagous diet (Pianka and Parker, 1975; Pianka, 1986). Strikingly, relatively few of these 'adaptations' (e.g. spiny body, cryptic coloration, reduced dentition, large stomach, dorso-ventrally flattened body) have been examined quantitatively in an explicit comparative or experimental framework. Only Montanucci's examination of *Phrynosoma* dentition (Montanucci, 1989) found any relationship between morphology and diet. Besides Montanucci's study, and a statement that *Phrynosoma* exhibit diet-based tongue modifications (Schwenk, 2000; Schwenk and Sherbrooke, 2003), there have been few predictions of what morphological or behavioral modifications of the feeding system might be exhibited by ant-eating lizards.

In this study, we examine the kinematics of prey capture and some aspects of ant-eating feeding behavior in four species of lizards. Two of the species, *Moloch horridus* (Agamidae) and the desert horned lizard *Phrynosoma platyrhinos* Girard 1852 (Phrynosomatidae) are considered ant specialists. Whereas the diet of *M. horridus* is exclusively ants (Withers and Dickman, 1995; Pianka and Pianka, 1970), non-ant prey may at times dominate the diet of *P. platyrhinos* (Pianka and Parker, 1975; J. J. Meyers and A. Herrel, personal observation). In addition, we include kinematic data for two non-ant-specialized lizards to test specifically for differences between each specialist and a closely related generalist species. The Australian bearded dragon *Pogona vitticeps* Ahl T1926 (Agamidae) and the fringe-toed lizard *Uma notata* Baird 1858 (Phrynosomatidae) are typical dietary generalists, including ants only occasionally in their diet (Greer, 1989; Cogger, 2000; Turner, 1998). By comparing the specialist species with these generalists, we will attempt to identify functional novelties in the feeding system that have allowed these lizards to successfully exploit ant prey as their dominant dietary resource.

Materials and methods
Specimens and high-speed videography
The *Moloch horridus* Gray 1841 (*N*=4; snout–vent length, SVL=88.2, 94.7, 95.0, 99.1 mm) used in this study were housed at the Alice Springs Reptile Centre, Alice Springs, NT, Australia. Animals were kept in a large outdoor enclosure where ant prey were attracted using dead cockroaches. Unrestrained prey capture events were recorded using a

portable JVC high-speed digital camera (Victory Company, Japan; 200 frames s^{-1}). A ruler serving as a scale bar was placed in view whenever the animal or camera changed position. Juvenile *Pogona vitticeps* Ahl T1926 (*N*=3; SVL=72.0, 73.5, 77.5) and *Phrynosoma platyrhinos* Girard 1852 (*N*=3; SVL=71.0, 77.5, 78.0) were purchased from commercial animal dealers, while the *Uma notata* Baird 1858 (*N*=2; SVL 85, 97.25) were collected in the Yuma sand dunes in Arizona, USA. Unrestrained prey capture events of these individuals feeding on ants were filmed using a digital high-speed camera (Redlake Motionscope, San Diego, CA, USA; 250 frames s^{-1}).

Kinematic analyses
A total of 27 kinematic variables were computed from the *x,y* coordinates obtained from seven anatomical landmarks digitized on each frame. Landmarks were located at the eye, the tip of the upper jaw, the jaw vertex, the tip of the lower jaw, the throat surface directly below the jaw vertex, the tongue tip and a fixed point on the prey (Fig. 1). Feeding sequences were digitized using Didge Image Digitizing software (A. J. Cullum, 1999; Parthenogenetic Products). Only sequences in which the lateral aspect of the animal's head was approximately perpendicular to the camera were digitized.

All timing variables were computed relative to the onset of mouth opening, and included (1) the time until the onset of tongue protraction, (2) the time of prey contact, (3) the time of maximum tongue protrusion, (4) the time of maximum gape, (5) the time of the onset of tongue retraction, (6) the time of the onset of mouth closing, (7) the time to completion of tongue retraction, (8) and the time to completion of mouth closing. A total of 7 durations were calculated from timing variables: (1) the duration of mouth opening, calculated as the time from the onset of mouth opening until the time of maximum gape, (2) the duration of tongue protraction, calculated as the time from the onset of tongue protraction until the time of maximum tongue protraction, (3) the duration of tongue retraction, calculated as the time from the onset of tongue retraction until the completion of tongue retraction, (4)
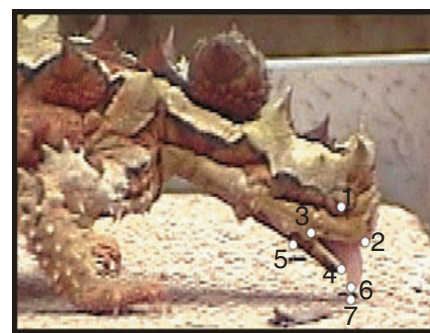

Fig. 1. *M. horridus*: points digitized and used to calculate kinematic variables. 1, eye; 2, tip of the upper jaw; 3, jaw vertex; 4, tip of lower jaw; 5, throat below jaw vertex; 6, tongue tip; 7, prey. Note the relatively long neck, especially when compared to the other species (see Figs 3A–5A).

the duration of mouth closing, calculated as the time from the onset of mouth closing until the completion of mouth closing, and (5) the duration of prey capture, calculated from the onset of mouth opening until completion of mouth closing. In addition to these variables associated specifically with prey capture, we also calculated two duration variables associated with the duration of the entire feeding event: (6) the duration of prey processing, from the completion of prey capture to the completion of mouth closing after the last processing event, and (7) the duration of the entire feeding sequence, calculated as before, but including the duration of the capture event.

Maximal excursions and displacements were calculated directly from the *x,y* coordinates of the digitized points: (1) maximum gape angle, defined as the maximum angle between the upper jaw tip, vertex, and lower jaw tip, (2) maximal gape distance, calculated as the maximal linear distance between upper and lower jaw tips, (3) tongue reach, calculated as the maximal distance from the lower jaw tip to the tongue tip, (4)

prey distance, calculated as the rectilinear distance from the upper jaw tip to the prey at the onset of the lunge, and (5) number of processing movements, calculated as the total number of gape cycles after prey capture. In addition, we calculated maximum velocities and accelerations of the lower jaw during opening (1,2) and closing (7,8) and of the tongue during protraction (3,4) and retraction (5,6). Raw displacement profiles were smoothed using a low-pass filter employing a zero phase shift, fourth-order Butterworth digital filter at 10 Hz (Winter, 1990). Velocities and accelerations were calculated from the filtered displacement data by taking the first and second derivative.

Statistical analysis

To visualize species differences in feeding kinematics, we performed a principal components analyses on the kinematic data set for all four species. We excluded the timing variables (variables 1–8 in Table 1) since they are mainly used to derive

Table 1. *Kinematic variables for each species feeding on ant prey*

	Moloch horridus	*Pogona vitticeps*	*Phrynosoma platyrhinos*	*Uma notata*
Time from onset of mouth opening (s)				
(1) Onset of tongue protraction	0.025±0.018	0.108±0.018	0.113±0.074	0.095±0.021
(2) Prey contact	0.055±0.019	0.241±0.061	0.218±0.100	0.166±0.028
(3) Maximum tongue protrusion	0.059±0.019	0.244±0.062	0.220±0.101	0.166±0.031
(4) Maximum gape	0.065±0.017	0.269±0.070	0.235±0.101	0.179±0.035
(5) Onset of tongue retraction	0.064±0.017	0.249±0.065	0.228±0.102	0.174±0.029
(6) Onset of mouth closing	0.074±0.017	0.277±0.072	0.241±0.100	0.185±0.034
(7) Completion of tongue retraction	0.087±0.017	0.282±0.018	0.247±0.103	0.191±0.032
(8) Completion of mouth closing	0.116±0.017	0.307±0.078	0.263±0.102	0.200±0.031
Duration of stage				
(1) Mouth opening	0.064±0.018	0.239±0.088	0.216±0.107	0.179±0.035
(2) Tongue protraction	0.035±0.004	0.136±0.043	0.106±0.031	0.071±0.010
(3) Tongue retraction	0.023±0.003	0.033±0.006	0.019±0.004	0.017±0.002
(4) Mouth closing	0.040±0.006	0.030±0.007	0.022±0.003	0.016±0.003
(5) Prey capture	0.115±0.018	0.277±0.095	0.244±0.107	0.200±0.031
(6) Prey processing	0.257±0.058	1.764±0.276	0.164±0.061	1.148±0.439
(7) Feeding sequence	0.350±0.054	2.109±0.339	0.416±0.130	1.353±0.441
Maximal excursions and displacements				
(1) Gape angle (degrees)	47.21±2.82	29.45±8.06	50.87±3.93	24.11±0.58
(2) Absolute gape (cm)	0.529±0.045	0.752±0.165	0.657±0.036	0.609±0.020
(3) Tongue reach (cm)	0.375±0.040	0.547±0.025	0.459±0.048	0.440±0.038
(4) Distance to prey (cm)	0.684±0.045	1.757±0.287	1.462±0.398	3.434±1.394
(5) Number processing/transport movements	2.350±0.054	8.125±1.552	0.222±0.666	6.900±1.197
Maximal speed variables				
(1) Mouth opening velocity (cm s^{-1})	11.92±1.69	10.16±4.22	9.00±0.43	7.44±0.24
(2) Mouth opening acceleration (cm s^2)	578.99±92.12	531.57±109.81	509.46±132.21	554.32±400.65
(3) Tongue protraction velocity (cm s^{-1})	16.20±0.82	9.39±1.24	10.00±1.94	9.232±0.05
(4) Tongue protraction acceleration (cm s^2)	2135.29±365.49	376.86±161.49	651.55±95.60	595.32±4.90
(5) Tongue retraction velocity (cm s^{-1})	15.38±2.21	25.13±14.24	19.03±7.41	7.06±1.06
(6) Tongue retraction acceleration (cm s^2)	2385.62±188.17	3094.70±2081.95	2703.98±800.25	915.45±202.78
(7) Mouth closing velocity (cm s^{-1})	13.63±2.01	29.28±5.71	28.570±2.12	22.872±4.20
(8) Mouth closing acceleration (cm s^2)	825.88±247.35	1701.69±752.71	2530.30±60.25	1469.46±510.66

The numbers in each section refer to text descriptions.

Values are means ± S.D. The number of individuals (number of sequences digitized) for all individuals are 4(20) for *M. horridus*, 3(8) for *P. vitticep,* 3 (9) *P. platyrhinos* and 2 (10) for *U. notata*.

relevant duration variables. The Broken Stick method (Jackson, 1993) was used to determine the number of factors explaining a significant amount of variation in kinematic space. To determine how species differed in behavioral space, a MANOVA and subsequent univariate *F*-tests coupled with simultaneous Bonferonni *post-hoc* tests were performed on the factor scores using all significant axes. All variables were logarithmically transformed ($\log_{10}$) prior to analysis. Statistical analyses were performed using SPSS-PC v10.0.5 (Maria J. Norusis/SPSS Inc.).

To address whether the feeding kinematics of ant-eating lizards has diverged from that of dietary generalists, we analyzed a subset of variables within an explicit phylogenetic framework. We assembled a data set for a select set of variables (Duration variables in Table 1), including the duration of mouth opening, duration of mouth closing, duration of prey capture and the duration of the entire feeding event. These variables were chosen because they loaded highly on the PC axes and most importantly, we could obtain similar values in the literature for other species. In addition to the species examined in this study, we were able to extract data for the following taxa using both literature data and personal, previously unpublished data: *Anolis carolinensis*, *Anolis sagrei*, *Chamaeleo jacksonii*, *Crotaphytus collaris*, *Dipsosaurus dorsalis*, *M. horridus*, *Phrynosoma cornutum*, *P. platyrhinos*, *P. vitticeps*, *Pseudotrapelus sinaitus*, *Sceloporus undulatus*, *U. notata* and *Urosaurus ornatus* (see Fig. 2). Since our goal is to compare ant-eaters to non-ant eaters, in the subsequent analyses we coded the ant-eaters (*M. horridus*, *P. cornutum*, *P. platyrhinos*) and non-anteaters (all others) differently. For many other species, we were able to find data for all variables except total feeding duration. While these species were not included in the phylogenetic analysis, we included them in Table 3 for comparative purposes.

Because species share a phylogenetic history, they cannot be considered independent data points and thus species cannot be compared using standard *F*-distributions. To address this concern we used the Phenotypic Diversity Analysis Programs (PDAP; Garland et al., 1992), which allows us to first construct a phylogenetic tree with trait values at the tips, run simulations of character evolution taking these phylogenetic relationships into account, perform ANOVAs on the simulations to create an empirical null distribution of *F*-statistics and, lastly, compute the 95th percentile of the null distribution to compare with the results of traditional analysis of variance (ANOVA).

The method described first requires construction of a phylogenetic tree, which was made in PDTREE and based on literature data depicting the relationships of the species in our analysis (Macey et al., 2000; Schulte et al., 2003; see Fig. 2). Relationships among iguanid clades were considered a hard polytomy (see Schulte et al., 2003). Because divergence times between all groups/species in our analysis were not available, we set all branch lengths to unity (Diaz-Uriarte and Garland, 1998). While errors in branch lengths usually do not have a substantial effect on the analysis (Martins and Garland, 1991;
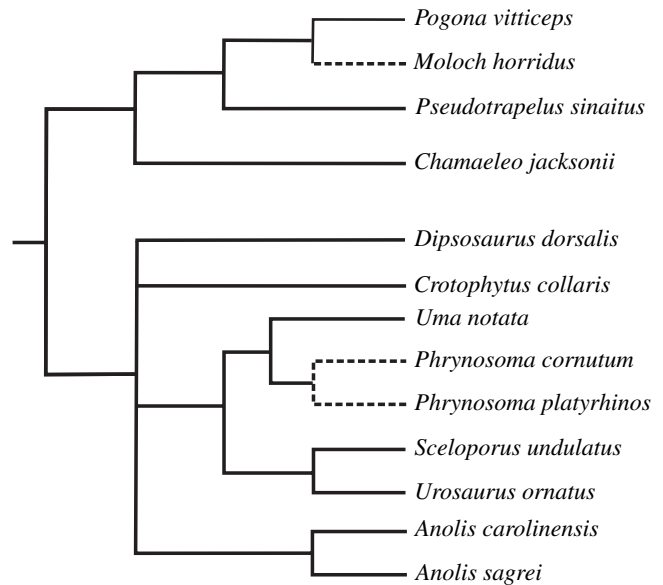

Fig. 2. Composite phylogeny used to address the evolution of feeding behavior (see Table 3) between ant specialists and dietary generalists. Broken branches denote ant specialists, while all others are considered dietary generalists.

Diaz-Uriarte and Garland, 1998), we confirmed that our branch lengths were adequately standardized using the diagnostic tests in PDTREE (Garland et al., 1992).

Simulation analyses were performed using the PDSIMUL and PDANOVA programs of Garland et al. (1993). The tree, with trait values at the tips, was input into the PDSIMUL program where we then selected the Brownian motion model of evolutionary change using the default values (means and variances of the original data). Note that, when the branch lengths are set to unity, this corresponds to a speciational model of evolution, which assumes sudden 'jumps' along the tree during speciation events. We ran 1000 unbounded simulations of character evolution and then performed ANOVAs on these simulations using PDANOVA. *F*-statistics from the phylogenetic ANOVAs were used to create an empirical null distribution from which we computed the 95th percentile and used these phylogenetically corrected critical values ($\alpha=0.05$) to determine significance. A univariate ANOVA was then performed on the original data and the F_{trad}-values from this analysis were compared to the critical F_{phy}-values obtained from the simulation analyses. Values were considered statistically significant if the non-phylogenetic F_{trad}-value was greater than the critical F_{phyl}-value of the empirical *F*-distribution.

Results

General feeding behavior

Here we provide a brief description of prey capture in *P. vitticeps* and then describe how the other three species compare to this general pattern. The gape profile during prey capture in *P. vitticeps* is similar to that described for other iguanian
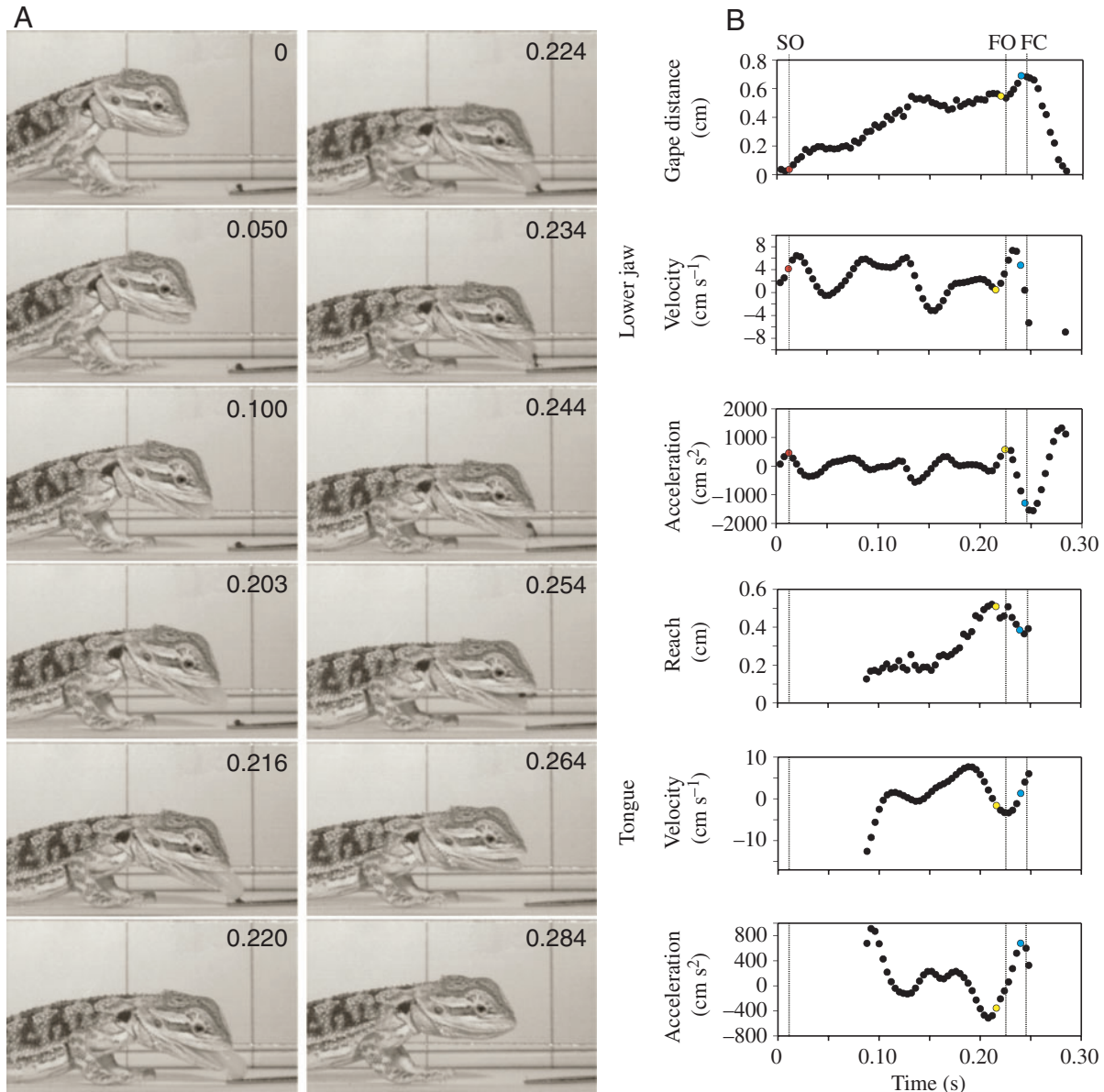
Fig. 3. Typical ant feeding event in *P. vitticeps*. (A) *P. vitticeps* capturing ant prey. Time (s) is given in the upper right of each frame. (B) Selected kinematic profiles. The gape distance profile is similar to all iguanians but very different than *M. horridus*. Colored dots denote onset of mouth opening (red), prey contact with the tongue (yellow) and maximum gape (blue). Onset of slow open (SO), fast open (FO) and fast close phases (FC) are denoted by dotted lines.

lizards (e.g. Schwenk and Throckmorton, 1989; Delheusy and Bels, 1992; Herrel et al., 1995) and displays the kinematic phases characteristic of the generalized lower tetrapod feeding model (Bramble and Wake, 1985). Although this model was originally developed to describe prey processing and transport, it has been aptly applied to prey capture as well (Delheusy and Bels, 1992, 1999; Herrel et al., 1995; Smith et al., 1999) and will be used here to describe the general features of the prey capture cycle in the four species. However, in our descriptions, we combined the slow open I (SOI) and slow open II (SOII) phases, as they were not always clearly distinguishable during prey capture events. To help delineate the kinematic phases, McBrayer and Reilly (2002b) proposed a method using slope

analysis. While useful, the magnitude of differences noted in the animals used in this study was so great that this method was deemed unnecessary.

A typical feeding event in *P. vitticeps* is initiated when the animal sees, recognizes and orients itself toward a prey item. The mouth is then opened slowly and the tongue is protracted slowly (i.e. start of slow open phase, SO). The duration of the first part of this phase can be highly variable while the animal observes the prey and determines whether to capture it or not. During the SO phase, capture events are sometimes aborted. Once the animal decides to capture the prey, however, it lunges forward, rotating over the forelimbs and simultaneously protruding the tongue at increasing speeds. The tongue is

protruded maximally at, or near the time of prey contact (end of SO). As tongue retraction is initiated, the mouth opens rapidly (fast open phase, FO). Maximum gape or mouth opening typically occurs as the prey enters the buccal cavity, after which the mouth closes rapidly around the prey (fast close phase, FC). During the FC phase, the animal moves back to its resting position. When the teeth come into contact with the prey, mouth closing slows (slow close phase, SC) and the prey is crushed (Fig. 3A).

Prey processing and transport occur in the buccal cavity, and these behaviors continue in a rhythmic fashion until the prey is finally transported to the back of the buccal cavity and swallowed. We combined prey processing and transport into one behavioral category because of the lack of these behaviors in ant specialists and because of the difficulties in adequately distinguishing between these behaviors without the use of cineradiography.

Of the other three species, *U. notata* is the most similar in feeding movements to *P. vitticeps*, exhibiting the same capture and processing movements. However, *U. notata* is substantially faster during prey capture as well as prey processing (Fig. 4A), making a single feeding event shorter in duration when compared to *P. vitticeps*. Like in *U. notata*, the prey capture movements of *P. platyrhinos* are faster than those of *P. vitticeps*, with the most pronounced difference in *P. platyrhinos* occurring near the end of prey capture and during
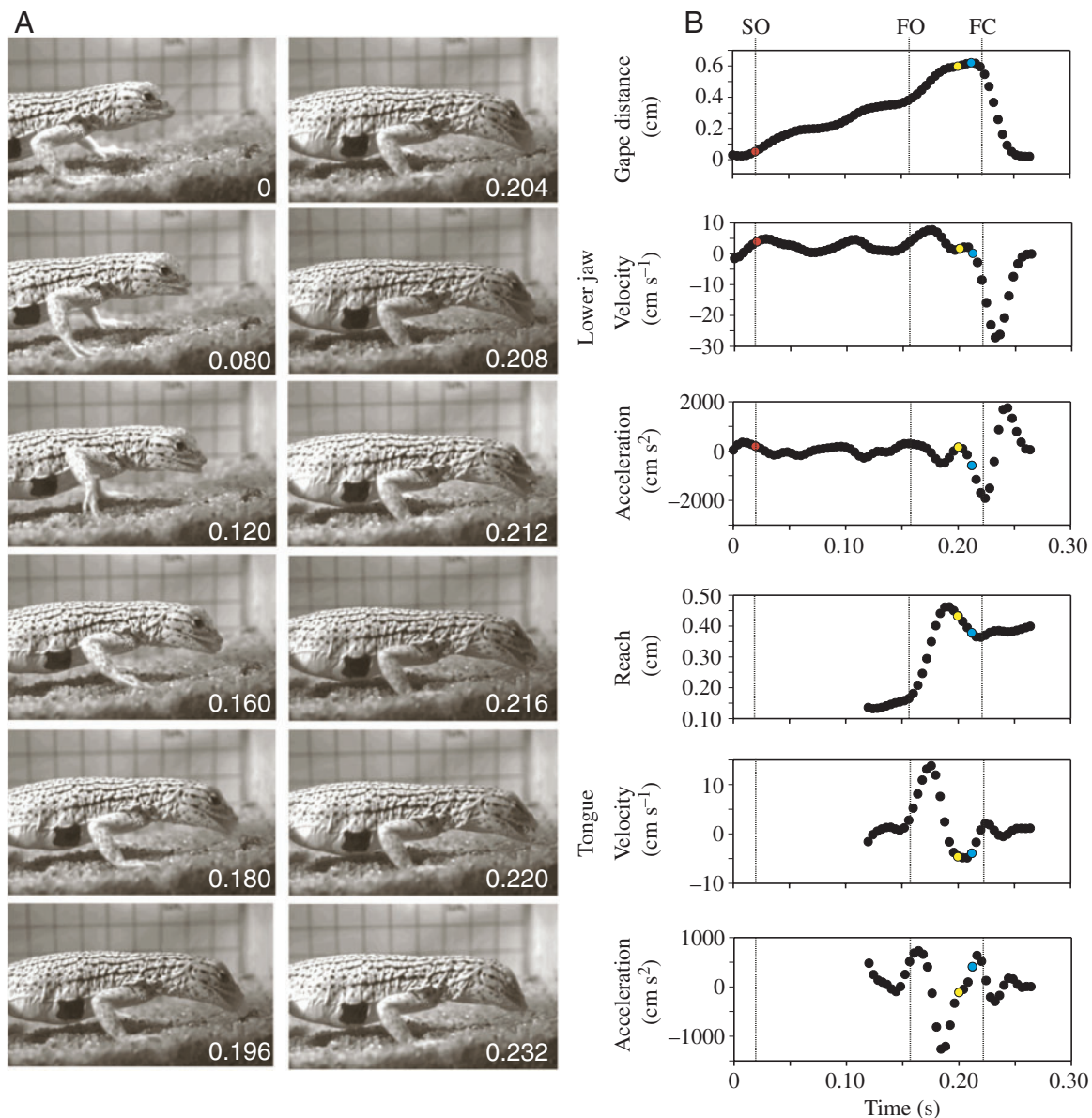

Fig. 4. Typical ant feeding event in *U. notata*. (A) *U. notata* capturing ant prey. Time (s) is given in the lower right of each frame. (B) Selected kinematic profiles. The gape distance profile is similar to *P. vitticeps* and *P. platyrhinos* but very different than *M. horridus*. Colored dots denote onset of mouth opening (red), prey contact with the tongue (yellow) and maximum gape (blue). Onset of slow open (SO), fast open (FO) and fast close phases (FC) are denoted by dotted lines.

prey processing. Unlike *P. vitticeps* and *U. notata*, which close their mandibles around the prey, *P. platyrhinos* transports the prey directly into the posterior buccal cavity after the capture event, and no crushing bites are performed (Fig. 5A). Because processing does not occur in *P. platyrhinos* the overall duration of the feeding sequence is highly reduced (see Table 1).

A feeding event in *M. horridus* is strikingly different from those observed for the other three species. First, *M. horridus* does not lunge during prey capture. Instead, the body generally remains stationary while the long neck swivels the head within range of the prey (Fig. 6A). Furthermore, the jaws open quickly and the tongue is protruded rapidly. During the initial

stages of mouth opening, *M. horridus* frequently modulates its behavior. In most cases, the SO phase was not discernable (more than 80% of the sequences) and the gape cycle merely consisted of FO and FC phases. When present, the slow open phase was typically associated with stationary ant prey (e.g. ants that were slightly injured or attempting to move a food item), which appears atypical of most ant prey eaten by *M. horridus* (see Discussion). Interestingly, in the few capture events in which a distinct SO phase was present, we did not see simultaneous slow tongue protraction, as in the other species. In *M. horridus*, prey contact always occurred close to maximum gape and was not typically followed by the initiation
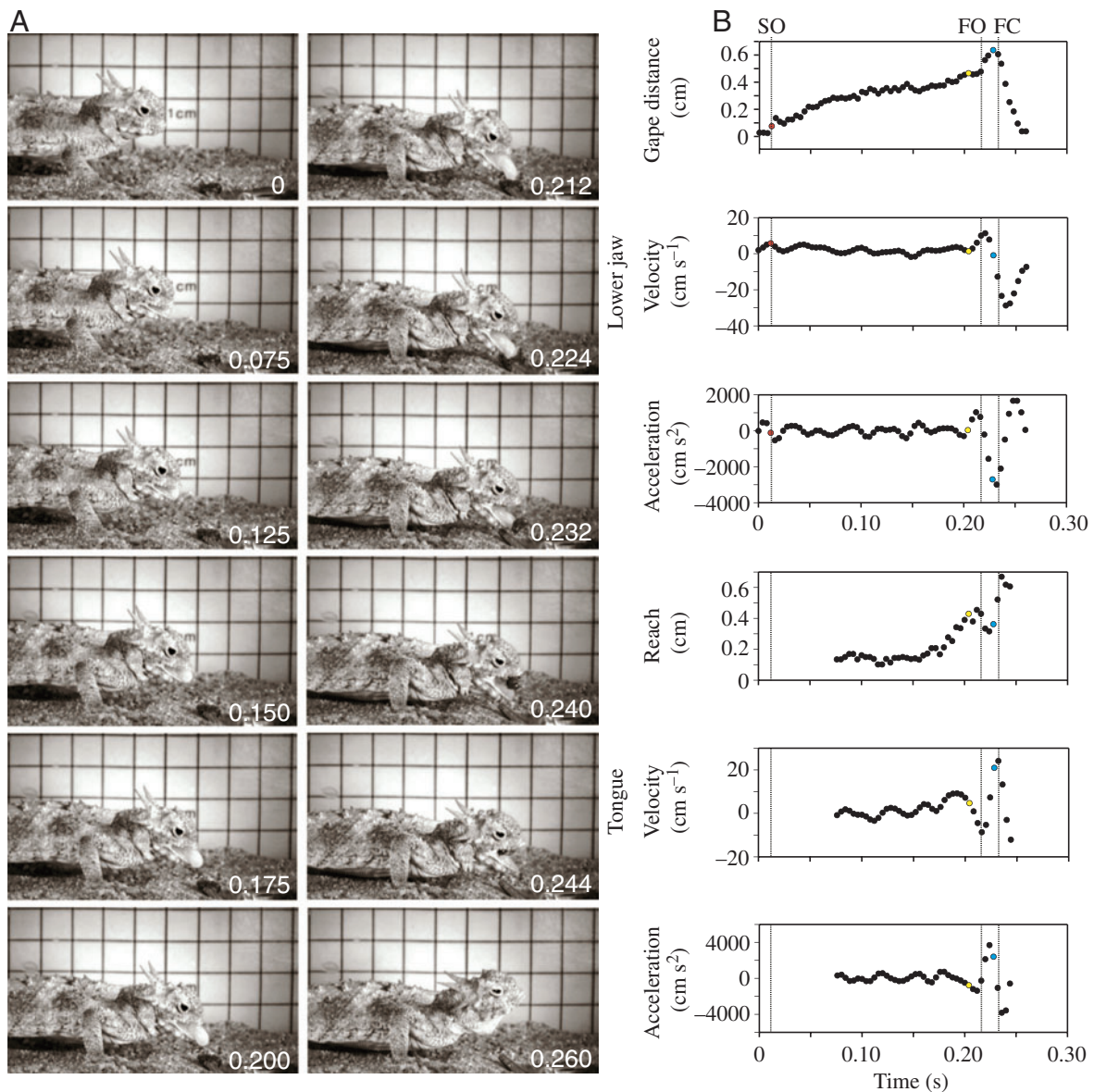

Fig. 5. Typical ant feeding event in *P. platyrhinos*. (A) *P. platyrhinos* capturing ant prey. Time (s) is given in the lower right of each frame. As in all iguanian feeding events, prey capture occurs using the tongue. Upon tongue retraction, the rotation of the dorsal papillae is visible as the prey is transported into the mouth. Note the characteristic shape of the tongue, which is very similar to *P. vitticeps* and *U. notata* but unlike *M. horridus*. (B) Selected kinematic profiles. The gape distance profile is typical of iguanians showing the slow open phase before prey contact. Colored dots denote onset of mouth opening (red), prey contact with the tongue (yellow) and maximum gape (blue). Onset of slow open (SO), fast open (FO) and fast close phases (FC) are denoted by dotted lines.
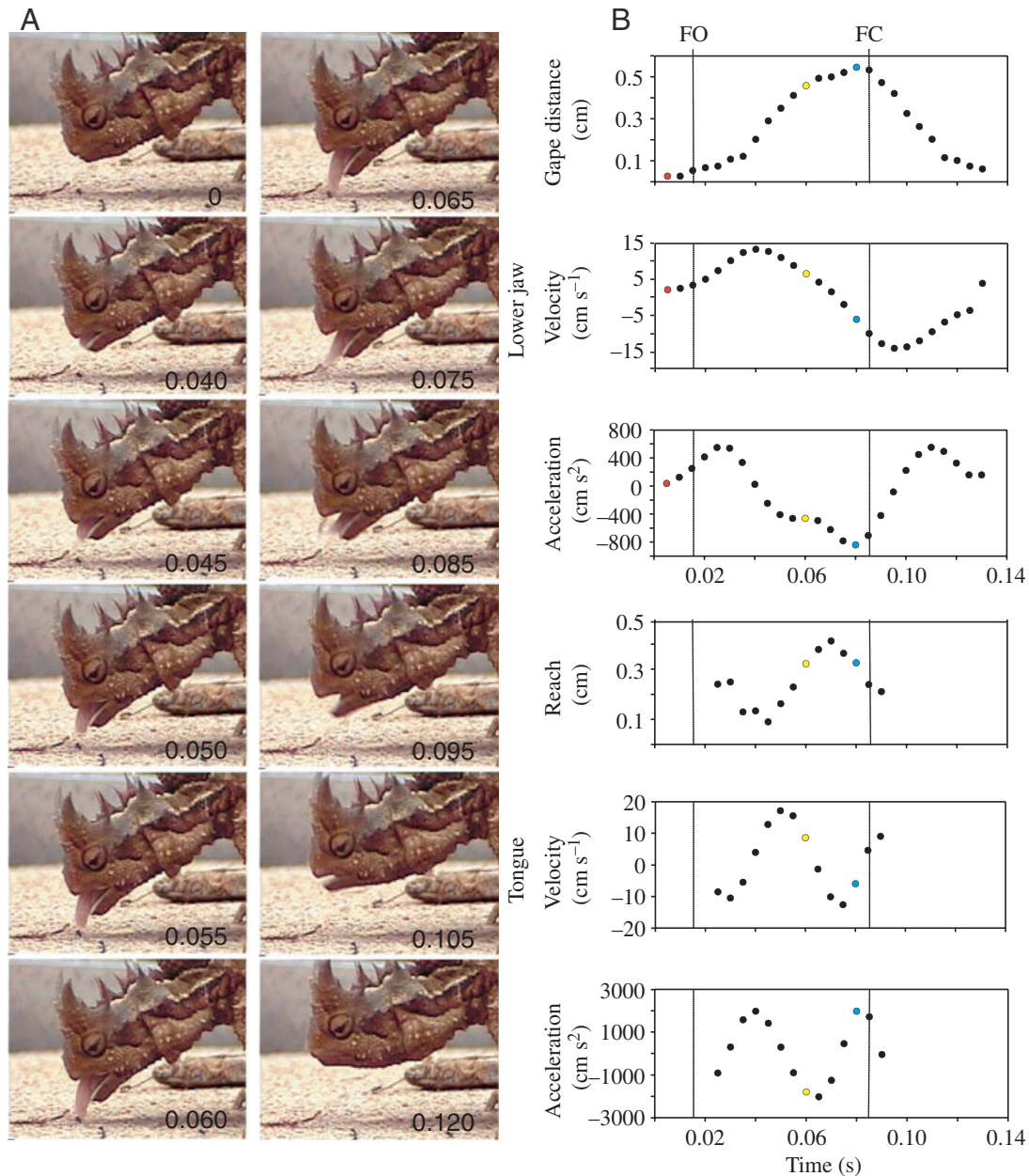
Fig. 6. Typical ant feeding event in *Moloch horridus*. (A) *M. horridus* capturing ant prey. Time (s) is given in the lower right of each frame. Note the pointy shape of the tongue at full extension, uncharacteristic of iguanians during prey capture but very similar to iguanians when tongue flicking. The entire capture event occurs in just over 100 ms. (B) Selected kinematic profiles, showing the abbreviated slow open phase (only 20% of the cylces contained a slow open phase) and the longer fast open and fast close phases. Colored dots denote the onset of mouth opening (red), prey contact with the tongue (yellow) and maximum gape (blue). Onset of fast open (FO) and fast close phases (FC) are denoted by dotted lines. Note the difference in time scale between Figs 2 and 3.

of the FO phase. Once the prey is moved into the buccal cavity, one or two rapid 'palatal crushing' movements typically occur before swallowing. As in *P. platyrhinos*, the lack of traditional prey processing reduces the overall duration of the feeding sequence in *M. horridus* compared to the two generalist species (see Table 1).

Variation in feeding kinematics

Prey capture occurs most quickly in *M. horridus*, with the total prey capture cycle completed in less than 115 ms, but taking up to 2.5 times longer in the other species (Table 1). The SO phase is highly variable in duration and is the predominant reason for variation in prey capture duration. It may comprise anywhere between 50% and 89% of the total prey capture sequence in *P. vitticeps*, *U. notata* and *P. platyrhinos*. However, in *M. horridus* prey capture duration is shortened by the lack, or shortening, of the SO phase. In the few cases in which an SO phase is present in *M. horridus*, it occurs at a

Table 2. *Kinematic phases (SO, FO, FC) during prey capture*

Phase	*Moloch horridus*		*Pogona vitticeps*		*Phrynosoma platyrhinos*		*Uma notata*	
	Time (s)	%	Time (s)	%	Time (s)	%	Time (s)	%
Slow open (SO)	0.055±0.018	38	0.230±0.066	75	0.202±0.124	72	0.119±0.028	56
Fast open (FO)	0.057±0.009	35	0.034±0.013	12	0.033±0.014	14	0.069±0.017	32
Fast close (FC)	0.043±0.008	27	0.039±0.005	13	0.032±0.004	14	0.025±0.007	13
Duration of prey capture (s)	0.151±0.029		0.277±0.095		0.244±0.107		0.203±0.040	
Slow open (SO)	0	0						
Fast open (FO)	0.065±0.006	61						
Fast close (FC)	0.043±0.006	39						
Duration of prey capture (s)	0.104±0.013							

Values are means ± S.D. The number of individuals (number of sequences digitized) for all individuals are 3 (8) for *P. vitticeps*, 3 (9) for *P. platyrhinos* and 2 (10) for *U. notata*.

For *M. horridus*, values of profiles exhibiting a SO phase (4 trials) and those without a slow open phase (16 trials) are given.

lower gape and proceeds more rapidly than in the other species, representing only 38% of the prey capture sequence (Table 2).

The FO phase of prey capture typically commences after prey contact, but the timing of the FO phase varies considerably among species. In *P. vitticeps*, prey contact always occurs before the FO phase (Fig. 3B), whereas in *U. notata* and *P. platyrhinos* the timing of prey contact and the FO phase are more variable (Figs 4B, 5B). In *M. horridus*, prey contact always occurs near the end of the FO phase (Fig. 6B). The lack of an SO phase in *M. horridus* seems to have resulted in a somewhat longer FO phase, comprising 55% of the cycle, compared to only 12–32% in other species (Table 2). Mean duration of the FO phase in *M. horridus* is 63 ms, which is similar to *U. notata* but almost twice as long as that of the other two species. The end of FO and start of FC occur as tongue retraction ends and the animal reaches maximum gape. The FC phase exhibits the least variation within and among all species and appears to be more 'stereotyped' than the opening phases (Tables 2, 3). A SC phase was not noticeable in most sequences and may not be characteristic of prey capture events associated with small prey.

For many of the timing variables, *M. horridus* exhibits shorter durations than the other three species. Yet, surprisingly the shorter timing events do not appear to be the result of more rapid feeding movements. While mouth opening duration was shorter in *M. horridus*, maximum mouth opening speeds were not different among species (Table 1). Tongue protraction occurs more quickly in *M. horridus* (16.20 cm s^{-1}) than any of the other species, *P. platyrhinos* (10.00 cm s^{-1}), *U. notata* (9.23 cm s^{-1}) and *P. vitticeps* (9.39 cm s^{-1}). However, tongue retraction and mouth closing velocities and accelerations either did not differ between species or were generally faster in *P. platyrhinos* (28.57 cm s^{-1}) and *P. vitticeps* (29.28 cm s^{-1}).

Although prey capture in *U. notata* is faster than that of all other species except *M. horridus*, the processing movements and duration of prey processing result in a feeding event that is three times longer than either of the ant specialists. Processing in *P. vitticeps* is even slower, requiring nearly eight times longer than *M. horridus* to process prey (Table 1). The

duration of prey processing appears to separate the ant specialist from the generalist lizard species. On average, *M. horridus* takes only 257 ms to process prey after capture. *P. platyrhinos* is even faster, taking only 164 ms to process and transport prey. In contrast, both of the generalist species take more than 1000 ms. The lack of this rapid processing behavior significantly reduces the duration of the entire feeding sequence and makes the total duration of a feeding attempt in *P. platyrhinos* (416 ms) similar to *M. horridus* (350 ms). The primary differences in processing times are due to a complete lack of prey crushing and a decrease in the number of processing/transport cycles in both *M. horridus* and *P. platyrhinos* (only 0–3 cycles in the ant specialists). Unlike the ant specialist species, *P. vitticeps* and *U. notata* crush the ants extensively before transporting them into the posterior buccal cavity for swallowing (processing and transport can take 7–11 cycles).

While all species capture prey using the tongue, there are distinct differences in the part of the tongue that contacts the prey. Of the four species, only *M. horridus* appears to be lacking the robust, fleshy tongue characteristic of iguanian lizards. During normal tongue protrusion, the dorsal surface of the tongue rotates forward, such that the dorsal tongue pad and not the anatomical tongue tip contacts the prey. Rotation of the tongue pad is easy to see during tongue retraction, when the prey rotates posteriorly on the dorsal surface of the tongue and is transported into the mouth (see Figs 3A, 4A, 5A). *M. horridus* exhibits a strikingly different tongue prehension behavior. First, the shape of the tongue during protrusion is different in *M. horridus*, appearing more slender and pointed. In addition, the tongue pad does not appear to rotate, and instead, the prey is flicked back into the mouth using the tongue tip (Fig. 6A). Observations of *M. horridus* trying to capture ants held lightly by forceps suggest limited adhesive properties of the tongue.

Quantitative analysis

A principal components analysis on the kinematic data revealed three significant factors which explained 71% of the

variation in feeding kinematics (Fig. 7). The first factor explains 45% of the variation and separates the ant specialist from the dietary generalists. This factor is mainly composed of duration events, but also includes gape distance and mouth opening/closing speeds (Table 4). The other two axes, while also significant, are defined by lower factor loadings that consist of mouth closing and tongue retraction events. Results of a MANOVA on the factor scores revealed highly significant species effects (Wilks' Lambda $F=83.74$, $P<0.0001$). Bonferroni *post-hoc* tests revealed significant differences among ant specialists and between the specialist and generalist

species for factor 1 ($P<0.0001$), yet the generalist species did not differ from one another ($P=1.00$). The other two factors appear to separate the species phylogenetically with all species comparisons being different ($P<0.006$) except for the agamids *P. vitticeps* and *M. horridus* on factor 2 ($P=0.078$) and the phrynosomatids *U. notata* and *P. platyrhinos* on factor 3 ($P=0.496$).

The results of our phylogenetic ANOVAs comparing the feeding duration variables of ant-eating and non ant-eating lizards are summarized in Table 5. *F*-statistics from the traditional analysis were compared to the empirical null

Table 3. *Summary of the duration of each kinematic phase during prey capture, prey capture duration, total feeding duration, prehension mode and prey type for feeding studies of lizards*

	Duration (ms)							
	Kinematic phase (%)						Prey	
Species	SO	FO	FC	Capture	Feeding	PM	type	Reference
Rhyncocephalia								
Sphenodon punctatus	280 (39)	200 (28)	150 (21)	720		T	?	Schwenk, 2000
Iguania								
Agamidae								
Agama agama	460 (85)	40 (7)	45 (8)	545		T	cr	Kraklau, 1991
Agama stellio	265 (71)	38 (10)	32 (9)	373		T	cr	Herrel et al., 1995
Pogona vitticeps	230 (75)	34 (12)	39 (13)	277	2100	T	ant	This study
					6500	T	cr	J. J. Meyers and A. Herrel unpublished data
Pseudotrapelus sinaitus	333 (84)	33 (8)	33 (8)	399	2400	T	cr	Meyers and Nishikawa, 2000
Moloch horridus		65 (61)	43 (39)	108	350	T	ant	This study
Phrynocephalus helioscopus	155 (64)	40 (16)	50 (20)	245		T	mw	Schwenk and Throckmorton, 1989
Chamaeleontidae								
Chamaeleo jacksonii	1000 (84)	92 (8)	100 (8)	1192	10990	T	cr	Meyers and Nishikawa, 2000
Crotaphtyidae								
Crotaphytus collaris	117 (59)	50 (25)	33 (16)	200	2200	T	cr	A. Herrel, unpublished data
Iguanidae								
Dipsosaurus dorsalis	290 (80)	45 (12)	30 (8)	365		T	ww	Schwenk and Throckmorton, 1989
	317 (68)	83 (18)	67 (14)	467	18500	T	cr	A. Herrel, unpublished data
Phrynosomatidae								
Phrynosoma cornutum	115 (62)	30 (16)	40 (22)	185	410	T	cr	Schwenk, 2000
Phrynosoma platyrhinos	202 (72)	33 (14)	32 (14)	244	416	T	ant	This study
Sceloporus undulatus	167 (67)	33 (13)	50 (20)	250	3570	T	cr	Meyers et al., 2002
Uma notata	119 (56)	69 (32)	25 (13)	203	1353	T	ant	This study
Urosaurus ornatus	233 (74)	33 (10)	50 (16)	317	8900	T	cr	A. Herrel, unpublished data
Polychrotidae								
Anolis equestris	150 (46)	70 (22)	105 (32)	325		T	gh	Bels, 1990
Anolis carolinensis	220 (65)	80 (24)	40 (11)	340		J?	m	Bels and Goosse, 1990
					17200	T	cr	Herrel unpublished data
Anolis sagrei	350 (84)	33 (8)	33 (8)	416	6330	T	cr	A. Herrel, unpublished data
Opluridae								
Oplurus cuvieri	370 (82)	40 (9)	40 (9)	450		T	cr	Delheusy and Bels, 1992

Percent of capture duration is noted in parentheses.
Durations of kinematic profiles are taken from generalized feeding sequences in the cited studies. In addition, from our own studies, we have provided feeding durations of other lizards.
Prehension mode (PM) refers to (J) jaw or (T) tongue prehension.
Prey types are cricket (cr), waxworm (ww), mealworm (mw), grasshopper (gh) and ant.
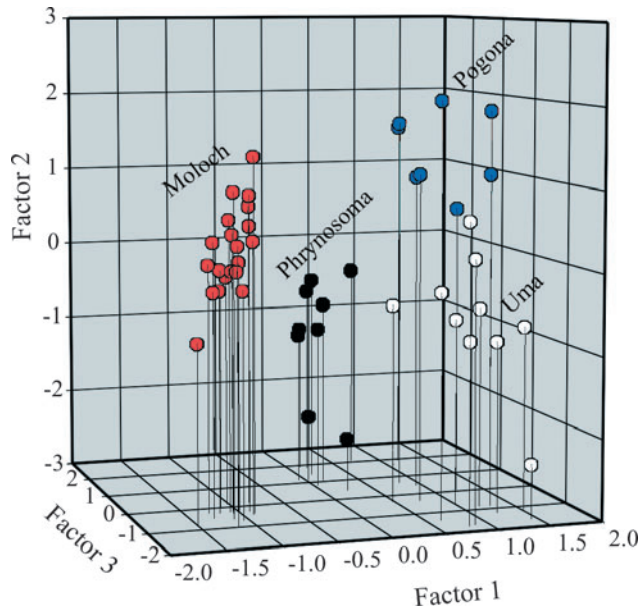
Fig. 7. Plot of the three significant axes from the factor analysis showing the position of the different species in kinematic space. The ant-eating species (*Moloch* and *Phrynosoma*) are significantly different than the generalists (*Pogona* and *Uma*) on axis 1. The other two axes appear to separate the species phylogenetically, with all species comparisons being different except for the agamids *P. vitticeps* and *M. horridus* on axis 2 and the phrynosomatids *U. notata* and *P. platyrhinos* on axis 3.

distributions obtained from the 1000 simulations of character evolution along the phylogenetic tree (Fig. 2). The analyses revealed significant differences between ant-eaters and other lizards for the duration of mouth opening and total feeding duration. In ant-eaters, the mean duration of mouth opening and total feeding duration (149 and 392 ms) are much shorter than for non ant-eating lizards (361 and 7354 ms). Although not quite significant ($P=0.051$), prey capture duration also appeared to differ, being more than twice as fast in ant-eaters (181 ms) *versus* non ant-eaters (408 ms). The phylogenetic analysis thus confirms the results of our multivariate analysis and suggests that ant-eating lizards exhibit divergent feeding behaviors associated with their diet.

Discussion

Our results indicate that the feeding behavior of *M. horridus* differs strikingly from *P. vitticeps*, *U. notata* and *P. platyrhinos* feeding on ant prey. While the latter species exhibit the typical kinematic phases that are characteristic of iguanian lizards, *M. horridus* is capable of significant modulation, resulting in the absence of the SO phase in most cycles. By eliminating the SO phase during capture, *M. horridus* substantially shortens the overall time needed to capture ant prey. Although kinematically different in their capture profile, both ant-eating species exhibit similarities in prey processing behaviors. Neither species crushes the prey, but instead transports it to the back of the oral cavity in as few as two cycles.

Table 4. *Eigenvalues, percentage of the variation explained and component loadings of the three significant factors based on a principal components analysis of the kinematic data*

	Factor		
	1	2	3
Eigenvalue	9.075	3.024	2.218
% variation explained	45.373	15.119	11.088
Duration of mouth opening	0.871	0.329	–0.045
Duration of tongue protraction	0.832	0.435	0.050
Duration of tongue retraction	0.030	0.371	0.661
Duration of mouth closing	–0.633	0.194	0.507
Duration of prey capture	0.817	0.379	0.058
Maximum gape angle	–0.742	0.519	–0.136
Absolute gape	0.602	0.497	0.044
Maximum tongue reach	0.427	0.246	0.203
Distance to prey	0.818	–0.191	–0.209
Mouth opening velocity	–0.655	0.225	–0.017
Mouth opening acceleration	–0.204	0.136	–0.374
Tongue protraction velocity	–0.883	–0.013	0.036
Tongue protraction accleration	–0.926	–0.156	–0.072
Tongue retraction velocity	–0.342	0.609	0.523
Tongue retraction acceleration	–0.501	0.545	0.392
Mouth closing velocity	0.712	0.489	–0.291
Mouth closing acceleration	0.389	0.562	–0.507
Duration of prey processing	0.733	–0.387	0.419
Duration of feeding sequence	0.872	–0.195	0.320
Number of processing/transport movements	0.599	–0.537	0.465

Table 5. *Results of phylogenetic analysis comparing the kinematic feeding durations of ant-eating lizards and lizards that are dietary generalists*

Variable	F_{trad}	P_{trad}	F_{phyl}	P_{phyl}
Mouth opening duration*	5.31	0.042	5.01	~0.039
Mouth closing duration	0.59	0.459	4.80	~0.426
Prey capture duration	4.79	0.051	5.20	<0.051
Feeding duration	20.68	<0.001	4.80	<0.001

F_{trad} and P_{trad} are the results of traditional ANOVAs on the original data. F_{phyl} is the F-value at $\alpha=0.05$ from the empirical F-distribution obtained from the simulation analysis. P_{phyl} is calculated from the empirical F-distribution using the F_{trad}-value. Variables are significantly different if the traditional ANOVA values (F_{trad}) are higher than F-values from the simulation analysis (F_{phyl}).

*Combined SO and FO durations.

Variation from the feeding model

Studies of lizard feeding behavior have documented similarities in jaw and tongue movements among groups, revealing a basic dichotomy in prey capture behavior that appears to have a phylogenetic basis (Schwenk and Throckmorton, 1989; Schwenk, 2000). Whereas all iguanian lizards use the tongue to capture prey, most scleroglossans do not (Schwenk, 2000). In addition, all iguanians studied to date show gape profiles during capture that are composed of all the phases defined in the Bramble and Wake (1985) model (SO, FO, FC). Scleroglossans, on the other hand, appear to have lost the SO phases of the gape profile during capture (Bels and Goosse, 1990; Delheusy and Bels, 1992, 1999; Goosse and Bels, 1992; Delheusy et al., 1995; Urbani and Bels, 1995). Interestingly, while the presence of the phases is rather static, the duration of the SO phase appears to vary dramatically within and among species (Table 3).

Our results suggest that among the species studied most of the variation in the duration of prey capture is due to variation in the duration of the SO phase. Although the SO phases of *P. vitticeps*, *U. notata* and *P. platyrhinos* (Table 2) are roughly comparable to those of other iguanian species (Table 3), a phylogenetic ANOVA showed significant differences in the duration of the entire opening phase (SO and FO combined) when comparing ant-eaters with other iguanian lizards (Table 5). There appears to be significant modulation of the SO phase, however, with the generalist *U. notata* exhibiting a much faster SO phase than the specialized *P. platyrhinos*. When the SO phase is present in *M. horridus*, the duration of a single prey capture event is similar to the fastest events recorded for *P. platyrhinos* and *U. notata*. However, when *M. horridus* eliminates the SO phase, the prey capture event as a whole becomes more than 30% faster than that in *P. platyrhinos* and at least twice as fast as any other iguanian (Table 3). Because scleroglossans lack an SO phase, the duration of prey capture (using the jaws) tends to be faster than that of most iguanians and is generally comparable to that of *M. horridus*. However, when using tongue prehension, prey

capture in scleroglossans is remarkably slower (75%) than when using jaw prehension alone (Urbani and Bels, 1995).

The longer duration of tongue prehension cycles in scleroglossans makes the prey capture event in *M. horridus* all the more interesting. In the absence of a SO phase, the time in which to protract the tongue during mouth opening is significantly reduced. Indeed, the longer durations exhibited by scleroglossans attempting tongue prehension (Urbani and Bels, 1995) suggest that it may be difficult to coordinate fast tongue and jaw movements. It is possible that the rapid tongue protraction exhibited by *M. horridus* is necessary to accommodate rapid mouth opening (Table 1). However, tongue retraction and mouth closing velocities are both slower in *M. horridus* than in the other species examined here. The observed reduction in the speed of tongue retraction and mouth closing may be responses to the timing of prey contact. If tongue retraction is only initiated near the onset of mouth closing, as in *M. horridus*, then it may indeed be more advantageous to close the mouth more slowly to reduce the risk of dislodging the prey, especially considering the apparent limited adhesive capacity of the tongue of *M. horridus*.

In most studies of prey capture in iguanians, the fast mouth opening phase coincides with tongue retraction and transport of prey into the mouth (Herrel et al., 1995; Schwenk, 2000). The timing of FO and tongue retraction is important because rapid mouth opening will allow larger prey items to clear the jaw margins as the tongue is retracted, reducing the risk of dislodging the prey as it is transported into the mouth. Indeed, *P. vitticeps* always initiates the FO phase just after prey contact, but the timing varies considerably in *P. platyrhinos* and *U. notata*. In *M. horridus*, tongue retraction is initiated near the end of the FO phase. Based on our data, we suggest that the timing of prey contact and FO are likely to reflect prey type and more generally diet. The diet of the generalist *P. vitticeps* and *U. notata* includes a diversity of prey (Greer, 1989; Cogger, 2000; Turner, 1998), whereas the diet of *M. horridus* consists of only relatively small prey (Pianka and Pianka, 1970; Withers and Dickman, 1995), requiring a minimal gape to be safely transported past the mandible tips. While predominately an ant eater, *P. platyrhinos* also includes other prey its diet (Pianka and Parker, 1975), and modulation of prey contact and the timing of jaw closure may be a strategy to accommodate larger prey (e.g. coleopterans, lepidopteran larvae).

Tongue function during capture

The tongue serves an important function in prey capture among iguanians, providing a protrusible, adhesive surface with which to apprehend prey. During typical iguanian tongue protrusion, the sticky dorsal surface of the tongue is rolled forward to contact the prey. Thus, the tongue is positioned so that the 'adhesive' area of high papillary density is in contact with the prey item (Schwenk, 2000). Unlike in the other species, which exhibit the typical iguanian pattern, the tongue of *M. horridus* is extended straight with the anatomical tip, instead of the dorsal surface, contacting the prey. Not only does

this tongue shape resemble a 'tasting' tongue flick of iguanian lizards, but the kinematic profile also shares similarities. Kinematically, prey capture in *M. horridus* and the tongue flick in *Uromastix acanthinurus* and *Plocederma stellio* (Herrel et al., 1998) are similar in that both behaviors exhibit only two kinematic phases. However, it should be noted that while the duration of the gape cycle during tongue flicking is considerably longer, the duration of the actual tongue displacement is similar to that seen during prey capture. These similarities in tongue shape and kinematic profile are suggestive of the use of a different mechanism of tongue protrusion in *M. horridus*.

It is widely thought that tongue flicking is accomplished using predominately a muscular hydrostatic mechanism rather than being mainly the result of hyobranchial protraction (e.g. Herrel et al., 1998; Schwenk, 2000; De Groot et al., 2004). Because muscles maintain a constant volume as they change shape (Kier and Smith, 1985), shortening of intrinsic muscle fibers must be directed into either lateral expansion or forward elongation of the tongue, or both. The long, pointy shape and the apparent lack of anterior attachment of the tongue in *M. horridus* (Fig. 6A) are suggestive of a muscular hydrostatic mechanism.

Why use a muscular hydrostatic mechanism for tongue protrusion? One possibility is that this mechanism may require less total movement of the hyobranchial system. The SO phase of iguanian prey capture is typified by hyobranchial protraction associated with intrinsic movement of the tongue as it is shaped and positioned for lingual prehension. However, the lack of an SO phase in *M. horridus* precludes these preparatory movements, and its fast tongue movements may require rapid protrusion with limited hyobranchial movement. In addition, muscular hydrostats are defined by finely controlled movements that may facilitate more coordinated movements and overall accuracy (Ritter and Nishikawa, 1995; Nishikawa et al., 1999). While this protrusion mechanism may allow more rapid and accurate tongue protrusion, it may come as a trade-off. Prey contact with the tongue tip instead of the tongue's dorsal surface significantly reduces the area contacting the prey, and hence tongue prehensibility. In fact, we observed that *M. horridus* is incapable of prehending ant prey held lightly with forceps. Thus, it appears that although a hydrostatic mechanism of protrusion may facilitate the rapid feeding behavior of *M. horridus*, it may also reduce the area of prey contact and in effect reduce dietary breadth to small, lightweight prey.

Rapid tongue protrusion may be facilitated by another unique characteristic of the feeding behavior of *M. horridus*. In general, lizards tend to lunge while capturing prey, rotating forward over the forelimbs to bring the tongue or jaws in contact with the prey item. However, in *M. horridus* there is a distinct lack of the lunge behavior and the initial prey distance is accounted for as the animal positions itself near a column of ants (Withers and Dickman, 1995; Pianka et al., 1998). Once in close proximity to the ants the animal remains relatively stationary and, instead of lunging toward each ant, swivels its head within range using the long, mobile neck. The neck of *M. horridus* is 3–10 times longer than either *P. vitticeps* or *P. platyrhinos*, respectively (neck length is approximately 35% of body length in *M. horridus*, 3% in *P. platyrhinos*, 10% in *U. notata* 11% and *P. vitticeps*, compare Figs 3A–6A). The loss of the forward lunge may beneficial for several reasons; the rapid tongue flick could be accommodated by the significantly more mobile head, which could track rapidly moving prey; it may decrease the amount of movement invested in each prey capture event; and it would allow the animal to remain relatively cryptic during a feeding bout.

Evolutionary considerations

Although more different than similar, the feeding behavior of the two ant-specialized lizards exhibits several convergent aspects. First, prey processing has diverged drastically from the primitive condition found in *Sphenodon* and most iguanian lizards, where prey are reduced extensively before swallowing (Throckmorton, 1976; Gorniak et al., 1982; Smith, 1984; Bels and Baltus, 1988, 1989; Schwenk and Throckmorton, 1989; Kraklau, 1991; Herrel et al., 1996; So et al., 1992). Whereas the generalist species studied here (*P. vitticeps* and *U. notata*) exhibit the typical feeding pattern by processing the prey before swallowing, neither *M. horridus* nor *P. platyrhinos* appear to perform any puncture crushing bites using the mandibles. Schwenk (2000) noted a lack of processing in another species of horned lizard (*Phrynosoma cornutum*) and suggested that this may be a general aspect of lizards feeding on small prey. It is possible that a behavioral repertoire including prey processing is absent in some dietary specialists (as appears to be the case for *P. platyrhinos* feeding on multiple prey types; J. J. Meyers, personal observation), especially if the predominant diet consists of prey that require minimal reduction.

While there is a distinct lack of puncture crushing bites in *M. horridus*, there appears to be a fast 'chewing' movement that occurs after ingestion. McBrayer and Reilly (2002a) described a processing behavior they termed palatal crushing, during which the prey is thought to be crushed between the tongue and the palate. While it is possible that *M. horridus* may use a type of palatal crushing as a method of immobilizing ant prey, we cannot confirm this behavior. To adequately describe these intra-oral movements it will be necessary to record feeding behavior using high-speed cineradiography. It is unclear if and how *P. platyrhinos* immobilizes prey upon ingestion, since the prey is transported directly into the posterior buccal cavity (Fig. 5A). Sherbrooke (2003) suggested that lizards of the genus *Phrynosoma* immobilize prey by coating them with a thick mucous secreted in the buccal cavity. While adequate for ants, mucosal secretions may not immobilize larger potentially dangerous prey (Sherbrooke, 2002) and the lack of processing may represent a costly trade-off. Both palatal crushing and mucous secretions are possible mechanisms of disabling potentially dangerous prey items such as ants and both should be investigated more thoroughly.

As a result of a reduction in prey processing, ant specialists

have achieved significantly shorter feeding events than generalists (Table 5). If we compare the duration of a feeding event in *P. platyrhinos* and *M. horridus*, we see that on average *P. platyrhinos* takes only 50 ms longer (Table 1). This result may seem unexpected given the more rapid capture phase of *M. horridus*. However, *M. horridus* and *P. platyrhinos* employ different strategies to reduce the feeding duration. While *M. horridus* is routinely faster at the capture stage, it performs 'processing'-like behaviors that increase the duration of the feeding event. In contrast, the slower capture phase of *P. platyrhinos* is overcome by the complete lack of prey processing and the immediate swallowing of prey upon ingestion.

The capture of a prey item is generally the fastest stage of a feeding event, and the majority of the feeding event in generalized lizards is composed of processing and transport of the prey. While modulation of the capture phase can decrease the duration of a feeding event, as it does in *M. horridus* and many scleroglossans, reducing the processing and transport phases appears to have a more significant effect on feeding duration. This is exemplified by a comparison of feeding durations in various lizards (Table 3), which revealed that the fastest feeding event (*M. horridus*) occurred 52 times faster than the slowest. That is, a feeding event in a specialist can occur in less than half a second, while it can take up to 18 s in generalist lizards (see Table 3). Prey size clearly influences the duration of a feeding event and we might expect lizards to feed more rapidly when feeding on small prey. Our observations support this assertion; *P. vitticeps* is nearly three times faster when feeding on ants *versus* crickets (Table 3). Yet, *P. vitticeps* is still 4–6 times slower than both *P. platyrhinos* and *M. horridus* feeding on ants, suggesting significant modification of the overall feeding behavior in these ant specialists.

Our data clearly show that ant specialists have undergone significant phenotypic evolution associated with novel feeding behaviors and diverging function of the hyobranchial system. While *M. horridus* is decidedly divergent both behaviorally and kinematically from the other species, the ant-specialized species exhibit convergent behaviors that minimize feeding movements and reduce overall feeding time. It appears that, like herbivorous lizards (Herrel et al., 1999), myrmecophagous lizards do not exhibit a universal solution to dietary specialization, but instead have evolved a variety of strategies. Since most myrmecophagous lizards do not show the extreme morphological modifications exhibited by *Moloch* and *Phrynosoma*, it will be interesting to document their behavioral strategies when feeding on ants. In particular, will scleroglossan lizards use tongue or jaw prehension when feeding on ants? Based on our observations, we would predict that like *M. horridus* and *P. platyrhinos*, other myrmecophagous lizards will exhibit behaviors that reduce the amount of time invested in each feeding event.

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