

PREY TRANSPORT KINEMATICS IN *TUPINAMBIS TEGUIXIN* AND *VARANUS EXANTHEMATICUS*: CONSERVATION OF FEEDING BEHAVIOR IN ‘CHEMOSENSORY-TONGUED’ LIZARDS

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Summary

Although lizards have been predicted to show extensive intraoral prey-processing behaviors, quantitative analyses of the types of prey-processing behavior they demonstrate and of their kinematics have been limited. The more basal lizard lineages (Iguanians) have undergone some study, but the prey-processing repertoires of crown taxa have not been thoroughly examined and quantitative comparisons of behaviors within or among species have not been made. In this study, the prey transport behavior of the savannah monitor (*Varanus exanthematicus*) and gold tegu (*Tupinambis teguixin*) are described. Although these two lineages have independently evolved tongues that are highly specialized for chemoreception, we found that they

share the same three distinct types of transport behavior. These behavior patterns are (i) a purely inertial transport, (ii) an inertial transport with use of the tongue, and (iii) a non-inertial lingual transport. The tongue is used extensively in both the inertial and the purely lingual transport behaviors. More than 75% of all transport behaviors involved tongue movements. These species appear to exhibit a conservation of feeding kinematics compared with patterns known for basal lizards. A hypothesis for the evolution of inertial feeding is proposed.

Key words: feeding, kinematics, prey transport, functional morphology, lizard, *Varanus exanthematicus*, *Tupinambis teguixin*.

Introduction

Feeding in terrestrial vertebrates generally involves prey capture followed by varying amounts of prey processing before the food item is transported to the pharynx for swallowing. Although the tongue may or may not be used in prey capture, it plays a major role in prey-processing and transport behaviors (Throckmorton, 1976, 1980; Hiiemae, 1978; Gorniak et al., 1982; Smith, 1984; Gans et al., 1985; Schwenk and Throckmorton, 1989; Reilly and Lauder, 1990, 1991; Kraklau, 1991; Cleuren and De Vree, 1992; Delheusy and Bels, 1992; Herring, 1993). Primitive tetrapods (e.g. amphibians) consume intact active prey, and the efficient movement of prey from the jaws to the esophagus via a series of tongue-based prey transport movements is critical to swallowing and to the successful procurement of energy (Reilly and Lauder, 1990, 1991). In mammals, the feeding mechanism is not used simply to transport large whole prey to the esophagus, but to process prey in a variety of ways and to transport pieces of food using complex patterns of jaw and tongue movements (Hiiemae, 1978). One key to understanding the change from the simple transport behavior of primitive tetrapods to the complex repertoires of prey-processing behaviors in mammals lies in information on feeding behavior of phylogenetically intermediate taxa (e.g. lizards) that might contribute to an estimate of the ancestral condition for the amniotes.

Although lizards have been predicted to show extensive intraoral prey-processing behaviors (Bramble and Wake, 1985; Reilly and Lauder, 1990), quantitative analyses of types of prey-processing behaviors and their kinematics have been limited. Lizards are believed to employ lingual transport behaviors involving movements generally described as intermediate between those of salamanders and mammals (Throckmorton, 1976; Smith, 1984; Schwenk and Throckmorton, 1989). Although the kinematic patterns of basal lizard taxa (Iguania) have been described (Bels and Baltus, 1988; Bels, 1990; Bels and Goosse, 1990; Kraklau, 1991; So et al., 1992; Wainwright and Bennett, 1992; Herrel et al., 1996, 1997, 1999; Herrel and De Vree, 1999), few studies have examined higher lizard taxa (Scincomorpha and Anguimorpha; Smith, 1982, 1984, 1986; Urbani and Bels, 1995; Herrel et al., 1999; Goosse and Bels, 1992). The higher taxa have been shown to possess highly protrusible tongues specialized for chemoreception and to exhibit inertial prey transport behaviors not found in other lizards (Fig. 1A; Smith, 1982, 1984; Schwenk and Throckmorton, 1989; Cooper, 1994). The extent of prey-processing behaviors and their kinematics have not been quantified in these chemosensory-tongued lizards.

In the present study, we describe and compare prey transport behavior in the savannah monitor (*Varanus exanthematicus*,

Varanidae) and gold tegu (*Tupinambis teguixin*, Teiidae) lizards, focusing on three questions. First, what prey transport behaviors are used by these taxa? Tegus are known to use both lingual and inertial transport movements during feeding (Smith, 1984), and our initial observations revealed tongue use in monitors as well. Second, are the prey transport behaviors and kinematics similar in these taxa that share specialized chemosensory tongues? Third, how do the prey transport behaviors and kinematics of these taxa compare with general patterns known from the Iguania? The results of this comparative analysis will expand our understanding of the range of prey-processing behavior and kinematics in lizards and contribute to inferences about the evolution of complex feeding behaviors in other tetrapods.

Materials and methods

Behavioral and kinematic data were collected from four individuals each of *Varanus exanthematicus* (Bosc) ('monitor lizards') (snout-vent length, SVL=150, 200, 250 and 375 mm) and *Tupinambis teguixin* L. ('tegus') (SVL=300, 318, 341 and 353 mm). 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 background grid of 12 mm squares was used for scale, and a heat lamp was mounted above the aquarium to maintain an air temperature of at least 27 °C and no more than 30 °C. Freshly killed mice were presented to each lizard a few centimeters in front of the tips of the jaws using forceps, and the entire feeding bout was filmed from the strike to the completion of ingestion. From initial observations of monitor lizards, we found that the prey transport behaviors we wished to quantify were often not used on prey smaller than half the head length, as observed by Smith (1982). Therefore, we standardized prey size to roughly match lizard head size, which varied among individuals (SVL, tegus 45–50 cm; monitors 15–40 cm).

General patterns of feeding behavior

Seventy-one complete feeding sequences ($N=42$ for tegus, $N=29$ for monitors, including multiple sequences from each of the four individuals per species) were used to describe general patterns of feeding behavior. Feeding involved the strike and several variable biting and positioning movements before a series of three different 'transport' movements positioned the prey for swallowing. The occurrence of the three different transport behaviors was quantified by recording the number of times each individual utilized a purely inertial transport (I), an inertial transport with tongue usage (I_t) or a non-inertial lingual transport (T) and calculating the mean percentage occurrence of each behavior across individuals for each species.

Transport kinematics

Quantitative analyses of transport kinematics focused on the two tongue-based transport behaviors (I_t and T) because these clearly dominate the transport movements in these lizards, because they provide data for comparisons with similar tongue-based transport behaviors in other vertebrates and because the

inertial behaviors had been described previously (Smith, 1982, 1984, 1986). A subset of the feeding sequences that had clear lateral views of the landmarks during prey transport and similar durations of transport behaviors were selected for analysis. Five sequences per behavior (I_t and T) for each individual ($N=4$) for each species were analyzed, giving a total of 80 prey transport gape cycles used in the quantitative kinematic analysis. Images for each transport sequence were downloaded to a PC, and two-dimensional coordinates for landmarks were digitized using MeasurementTV (MTV: Updegraff, 1990). Time zero of a gape cycle was defined as the frame before tongue protraction began (which was coincident with the onset of mouth opening). During the relatively inactive period following time zero, images were sampled every 8–20 frames (40–100 ms), and during the more active period (fast open to close) images were sampled every 1–2 frames (5–10 ms) depending on the duration of the behavior.

Kinematic analyses

Jaw angle was computed for each frame throughout the gape cycle (Fig. 1) from two-dimensional coordinates for the tips of the upper and lower jaws and the ventral-most aspect of the tympanum (vertex). Jaw angle, which is not zero at time zero because the prey is in the jaws, was normalized by subtracting the angle at time zero from all values throughout the gape cycle.

To assess differences between behaviors and species quantitatively, a series of angular, distance and timing variables was measured from each gape cycle to describe and to compare statistically the movements of the jaws and tongue. Maximum tongue protraction distance was calculated from the anterior tip of the tongue at maximum protraction to a line through the tips of the jaws. This distance was scaled to upper jaw length (measured from the same images to ensure proper scaling) for each individual. The tongue is initially projected to the point at which we measured its maximum protraction, but it remains extended after this time (see Results). From the gape profile of each transport, a series of angular and timing variables were measured. Gape angle was measured at the onset of fast opening, at peak gape and at closing. The time of onset of fast opening was measured at the obvious rapid change in gape angle, observed in every gape cycle, that indicates the end of the slow opening phase. Time to peak gape, time to peak tongue protraction and gape cycle time were also measured. The timing variables were expressed both in milliseconds and as a fraction of gape cycle duration.

Statistical analyses

To illustrate and compare transport movement patterns, mean kinematic profiles for inertial transports with tongue use and normal transports were generated for one individual from each species. Mean gape angles for five cycles of each behavior were plotted from time zero, with mean profiles expressed as a fraction of gape cycle duration and times to peak tongue protraction indicated.

To compare kinematic variables, we used a three-way analysis of variance (ANOVA) with behavior [testing the differences in behaviors (I_t versus T)] and species (testing differences between

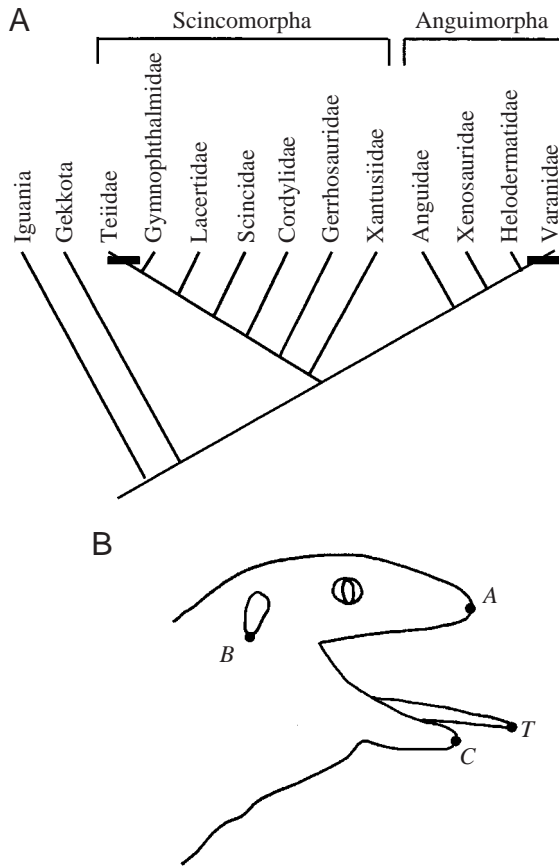


Fig. 1. (A) Phylogeny of lizards indicating the position of the study species (savannah monitor *Varanus exanthematicus*, Varanidae; gold tegu *Tupinambis teguixin*, Teiidae). Black bars indicate the presence of derived chemosensory tongue morphology and of inertial-based transport behaviors. (B) Kinematic landmarks used to quantify prey transport behavior in chemosensory-tongued lizards. Gape angle (angle ABC) was calculated for a series of images from each transport sequence from two-dimensional coordinates digitized in lateral view for the tips of the jaws (landmarks A and C) and the ventral-most edge of the tympanum (landmark B, used as a proxy for the angle of the jaw). During transport behaviors, the tongue was initially projected anteriorly and then moved around variably until beginning to retract at the onset of fast opening. The amount of tongue protraction during the initial anterior movement was measured as the distance between the tip of the tongue (landmark T) and a line through the tips of the jaws (line AC).

tegus and monitor lizards) treated as independent factors crossed with the four subjects as the individual effect. Because all individuals serve in all four species-by-behavior treatment combinations, this analysis employs a pure within-subjects (repeated-measures) design (Zolman, 1993, p. 59). This repeated-measures design (performed using Systat version 6.0) has the advantage of testing differences in the main effects after variation among individuals, within individuals within behaviors, and residual error have been extracted. The *a priori* choice to use the same individuals in all the treatment combinations was made to control for the problem of interindividual variation and because the within-subjects design provides more conservative tests for significance than standard

analysis of variance tests (Zolman, 1993). The *F*-ratios for the main effects and their interaction are calculated by dividing the mean square for these effects by the appropriate interaction mean square rather than the error mean square. Given the more conservative design, we were confident that $P < 0.05$ was sufficient to indicate statistical significance in the tests of main effects and in *post-hoc* tests even with multiple univariate comparisons. In addition, eight kinematic variables (see Table 3, the real-time values of gape cycle components were excluded) were used in a principal components analysis (PCA) to visualize species and behavioral differences in multivariate space. Because variables differed in units (angles and times), a correlation matrix was used to generate the eigenvalues.

Results

General feeding behavior

Both species exhibited a similar general sequence of behaviors during feeding (Fig. 2) involving the strike when the prey item was seized, followed by biting and positioning movements, before a series of transport behaviors moved the prey to the rear of the mouth for swallowing. During the strike, the body lunged forwards while the jaws rapidly opened and then closed on the prey, often pinning the prey against the substratum. The prey was usually held for several to many seconds (while it was often dragged against the floor and walls of the aquarium) before being dropped and inspected by the lizard with numerous tongue flicks. A series of biting and positioning movements followed. The prey item was deliberately and slowly bitten to dispatch, soften and moisten it before transport began. Biting occurred all along the body of the prey, with the prey either lying on or being pushed against the substratum, or with several inertial movements to move the prey from side to side in the jaws for biting. The prey was then positioned longitudinally in the jaws (usually in a head-first manner) either using inertial movements or by grasping it directly from the substratum. The tongue remained retracted

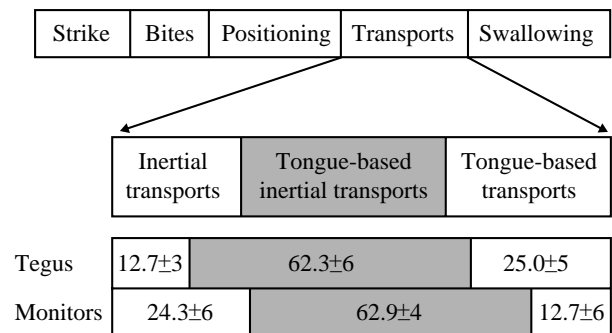


Fig. 2. General feeding repertoire (top) and percentage occurrence (± S.E.M.) of transport behaviors (bottom) observed in tegus and monitor lizards feeding on mice. After the prey capture (the strike) and a series of biting and positioning movements, the prey was transported using three distinct behavior patterns (described in the text) before swallowing. Note that tongue-based transports dominate prey transport behaviors. Mean values are based on pooling multiple feeding sequences from each of the four individuals from each species ($N=42$ for tegus, $N=29$ for monitors).

during the strike and during subsequent biting and positioning movements.

Once the prey had been positioned longitudinally, a series of transport sequences occurred during which it was moved posteriorly in the jaws and eventually swallowed. An initial review of feeding sequences revealed that both species were using three distinct transport behaviors in sequence. The first behavior used was a purely inertial transport (termed I). Inertial transports involve tossing the prey upwards while propelling the jaws forwards around the prey. In both species, I patterns were used early in the transport sequence to move the prey from the tips of the jaws into the mouth cavity. These purely initial transports were followed by the two tongue-based transport behaviors illustrated in Figs 3 and 4. Once the prey had been positioned well within the jaws, the lizards used a series of inertial transports in which the tongue was extended and then retracted during the gape cycle (termed I_t ; Figs 3, 4, left-hand panels). After the prey had reached a more posterior position in the mouth, it was transported using a series of 'normal' tongue-based transports (termed T) in which the tongue was extended and retracted during the gape cycle, with little or no inertial movement of the head (Figs 3, 4, right-hand panels). These T patterns are considered to be homologous to the primitive transport behavior for tetrapods because they are kinematically similar to the general static transport behavior seen in basal lizards and salamanders (S. M. Reilly and L. D. McBrayer,

unpublished data). Jaw movements in both types of inertial transport appeared, in general, to match previous descriptions of inertial transports (Gans, 1961; Smith, 1982, 1984, 1986) except for the extensive use of the tongue in I_t patterns (see below).

Prey transport in both species involved the sequential use of these three behavior patterns. A typical feeding sequence involved 1–4 purely inertial transports (I) to move the prey from the tips of the jaws into the mouth, followed by 7–8 I_t patterns, and then 1–4 T patterns moving the prey further into the throat in preparation for swallowing. The species differed somewhat in the relative use of I and T patterns, with monitors using I patterns twice as often as tegus, and tegus using T patterns twice as often as monitors (Fig. 2). I_t patterns were the predominant transport behavior used (averaging 62% of the transport behaviors), and percentage occurrence was the same in both species. Combining I_t and T patterns shows that transport involving the use of the tongue made up 76% of transport behaviors in monitors and 87% in tegus.

After the final T pattern, the mouth closed, the head was tilted upwards, presumably to facilitate the movement of the prey into the esophagus for swallowing, and the lizards often used undulations of the neck to aid swallowing.

Tongue-based transports

Gape cycle components

Mean profiles for jaw and tongue movements show that in

Table 1. *Jaw and tongue kinematics for tegus and monitor lizards during normal transport and inertial feeding behavior*

Variable	<i>Tupinambis teguixin</i>		<i>Varanus exanthematicus</i>	
	Transport, T	Inertial feeding, I_t	Transport, T	Inertial feeding, I_t
Gape angle at onset of FO (degrees)	2±0	5±0	3±0	3±0
Time to onset of FO (ms)	225±29	388±22	236±22	222±23
Time to onset of FO (fraction of GCYT)	0.36±0.03	0.78±0.01	0.50±0.02	0.63±0.01
Peak tongue protraction	0.24±0.02	0.20±0.02	0.72±0.05	0.64±0.05
Time to peak tongue protraction (ms)	188±24	203±15	144±11	156±11
Time to peak tongue protraction (fraction of GCYT)	0.30±0.03	0.41±0.02	0.33±0.02	0.47±0.01
Peak gape angle (degrees)	16±1	22±1	15±2	18±1
Time to peak gape (ms)	434±41	424±24	350±34	255±25
Time to peak gape (fraction of GCYT)	0.72±0.02	0.85±0.01	0.71±0.02	0.73±0.01
Gape angle at close (degrees)	-0.27±0.40	-0.41±0.58	-3.82±0.92	-5.62±0.69
Gape cycle time (ms)	586±39	498±26	478±41	346±32

Values are means ± s.e.m. pooled for four individuals ($N=5$ cycles per individual per behavior; thus $N=20$ for each mean).

Underlining indicates the results of pairwise *post-hoc* tests for significance among means and comparisons that are not significantly different at the $P<0.05$ level.

FO, fast opening; GCYT, gape cycle time

Tongue protraction distance is scaled to upper jaw length for each individual.

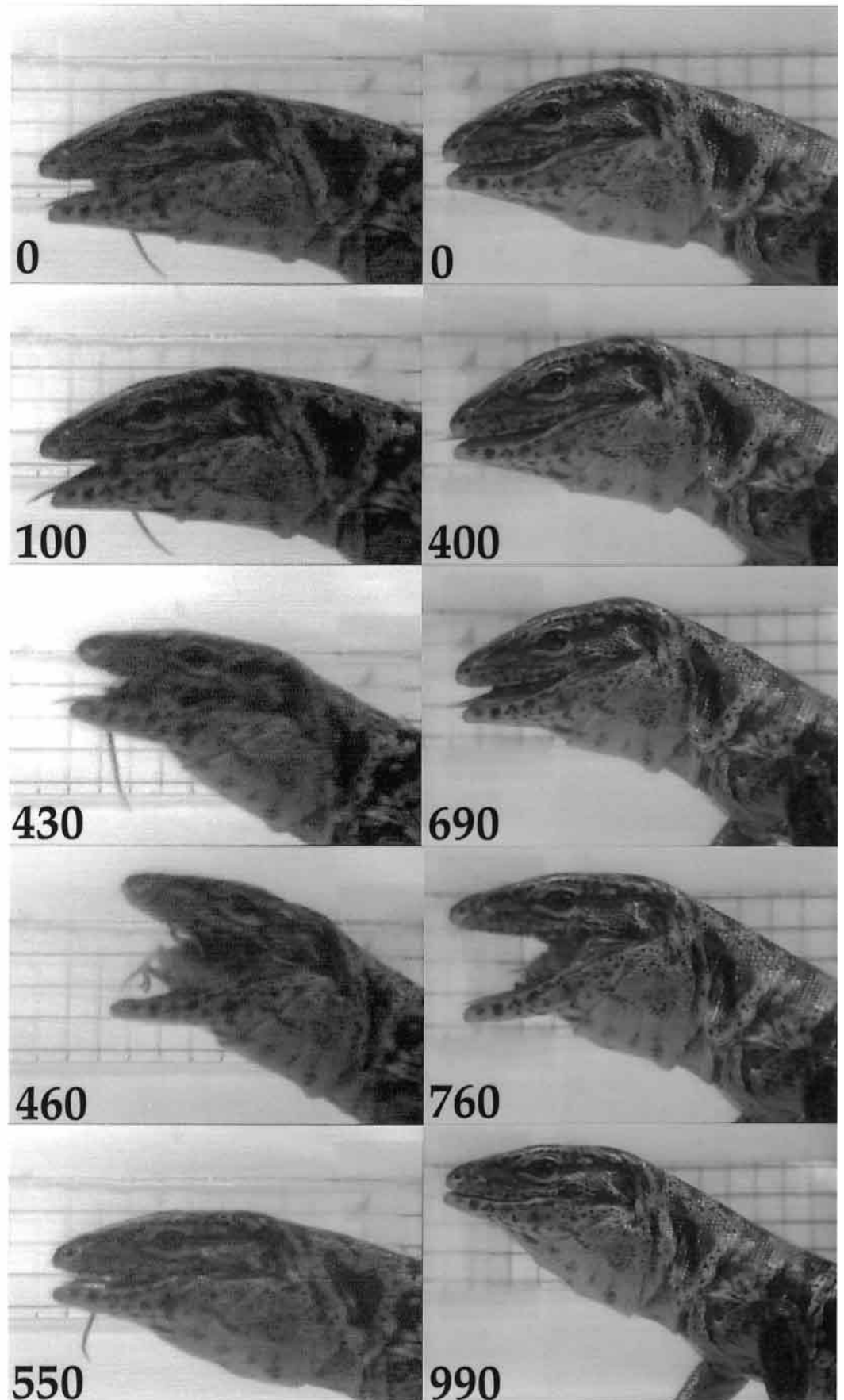


Fig. 3. Lateral images from high-speed video recordings illustrating normal transport (T, right-hand panel) and inertial tongue-based transport (I_t, left-hand panel) in the gold tegu *Tupinambis teguixin*. Time is indicated on each frame in milliseconds from the frame before the onset of tongue protraction (time zero), which is coincident with the frame before the mouth begins to open. Note the extensive use of the tongue in both behaviors and the inertial head movements in the left-hand panel.

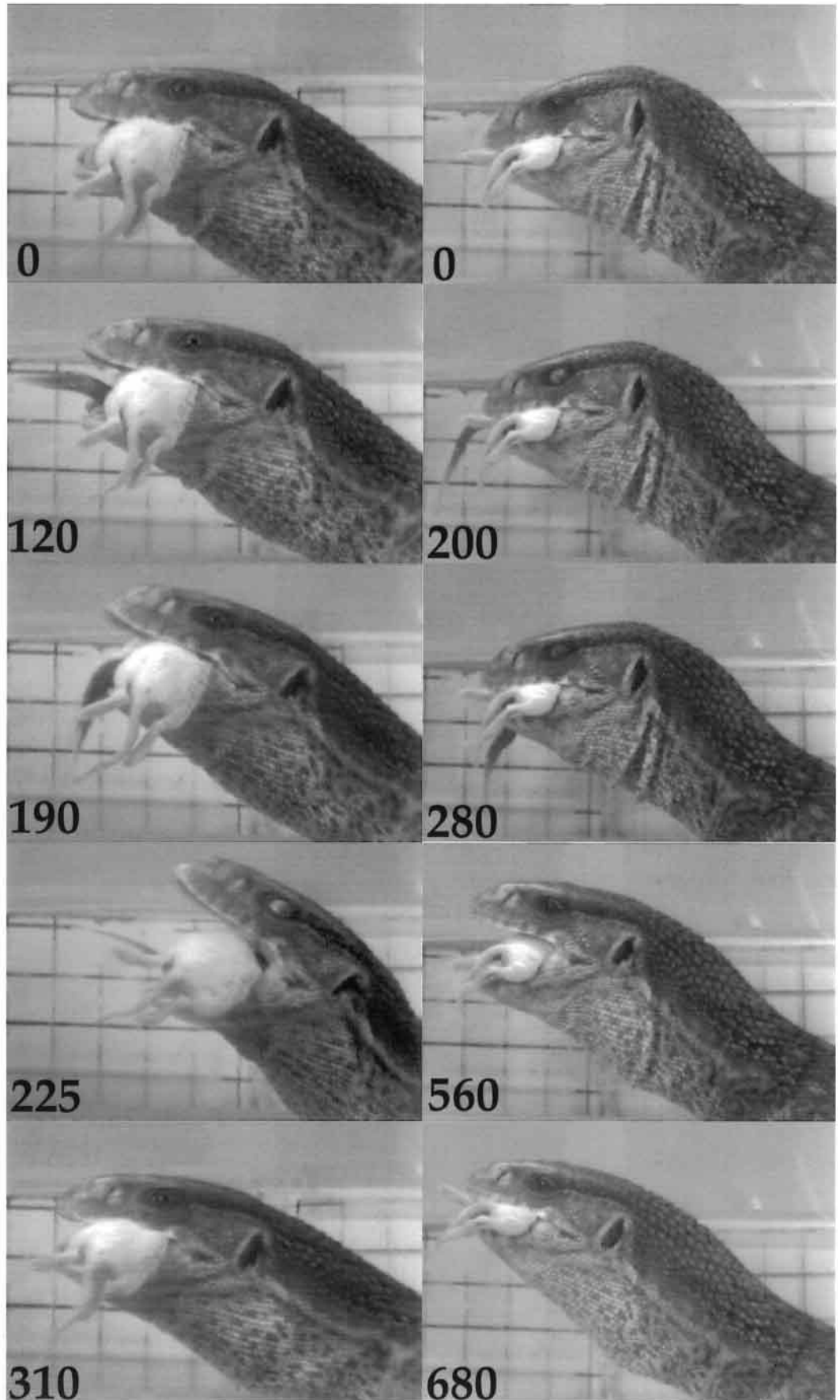


Fig. 4. Lateral images from high-speed video recordings illustrating normal transport (T, right-hand panel) and inertial tongue-based transport (I_t , left-hand panel) in the savannah monitor lizard *Varanus exanthematicus*. Time is indicated on each frame in milliseconds from the frame before the onset of tongue protraction (time zero), which is coincident with the frame before the mouth begins to open. Note the extensive use of the tongue in both behaviors and the inertial head movements in the left-hand panel.

Table 2. Repeated-measures ANOVA results for the effects of species (tegus versus monitor lizards) and behavior (normal transports versus inertial tongue-based transport) on the timing and movements of the jaw and tongue based on variation among four individuals per species

Variable	Behavior (d.f.=1,3)		Species (d.f.=1,3)		Interaction (d.f.=1,3)	
	F	P	F	P	F	P
Gape angle at onset of FO	13.304	0.036*	0.083	0.792	4.138	0.135
Time to onset of FO in ms	44.25	0.007*	0.381	0.581	5.181	0.107
Time to onset of FO/GCYT	136.18	0.001*	0.004	0.955	11.977	0.041*
Peak tongue protraction	1.863	0.266	53.295	0.005*	1.474	0.312
Time to peak tongue protraction in ms	0.403	0.570	0.626	0.487	0.02	0.896
Time to peak tongue protraction/GCYT	10.211	0.050	2.833	0.191	0.216	0.674
Peak gape angle	11.273	0.044*	0.981	0.395	1.496	0.309
Time to peak gape in ms	1.531	0.304	1.038	0.383	0.902	0.412
Time to peak gape/GCYT	3.982	0.140	0.478	0.539	3.1	0.177
Gape angle at close	1.165	0.359	14.691	0.031*	1.324	0.333
Gape cycle time	6.864	0.079	1.073	0.376	0.064	0.817

FO, fast opening; GCYT, gape cycle time.

* $P < 0.05$.

both species both behaviors exhibited the same basic gape cycle components (Fig. 5; Table 1). The jaws, which were closed on the prey item prior to the onset of a transport movement, began to open, and gape angle slowly increased to between 2 and 5° over 36% to 78% of the gape cycle duration, depending on the behavior (Figs 3, 4; top three frames). This consistent slow opening phase was seen in the mean plots (Fig. 5) and in each individual gape profile. The end of slow opening was easily identified by an obvious increase in the gape angle between frames. The gape angle then rapidly opened to a peak of 16–22° (Figs 3, 4; third and fourth frames). This fast opening phase was followed by a rapid closing phase during which the jaws closed on the prey again (Figs 3, 4; bottom two frames).

Tongue use during transports

Tongue protraction in both I_t and T patterns began with the onset of jaw opening, and the tongue moved anteriorly out of the mouth (Figs 3, 4; top two frames) and then, while remaining extended, it moved around variably (Figs 3, 4; second and third frames) before it was retracted during the fast opening and closing phases. The initial protraction phase involved 30–47% of the gape cycle (Table 1) and 52–83% of the slow opening phase and was consistently present in both species (time to peak tongue protraction and maximum tongue protraction distance were therefore measured at the end of this straight protraction phase). The 'variable' portion of the tongue protraction phase differed between the species, with the monitor lizards exhibiting three times more tongue protraction (20–24% versus 64–72% of upper jaw length, Table 1) and much more extensive tongue bending (Figs 3, 4; third frame). The contribution of the tongue to prey transport also differed. In monitors, the sheathed tongue could not contact the prey once retracted into the mouth, whereas in tegus, the scaly tongue adhered to the prey item. In addition, in the T patterns immediately preceding swallowing, tegus often wrinkled up the

thick, posterior portion of the tongue longitudinally to form a bulge that appeared to aid in transporting the prey (see Fig. 7). The tongue-wrinkling behavior was also observed during intermediate I_t patterns. The anterior chemosensory forks of the tongues rarely contacted the prey during transport in either species.

Species effects

The monitor lizards exhibited significantly greater maximum tongue protraction (Table 2), which averaged three times the distance observed in tegus (Table 1). Monitors also exhibited significantly greater mouth closing than tegus (gape angle at close; Tables 1, 2) closing their jaws on the prey to a position approximately 4–6° less than that at the beginning of a transport behavior, whereas in tegus the jaws returned to approximately the point at which they started. The second principal component of the PCA analysis (PC2, Fig. 6) separated the species on the basis of peak tongue protraction and gape angle at close (Table 3). In addition, the PCA indicated that time to peak tongue protraction (scaled to gape cycle duration) and the gape cycle time (variables tending to

Table 3. Correlations of kinematic feeding variables with principal components (PC) 1 and 2

Variable	PC1	PC2
Gape angle at onset of FO	0.714	-0.142
Time to onset of FO/GCYT	0.826	-0.255
Peak tongue protraction	-0.364	-0.531
Time to peak tongue protraction/GCYT	0.0465	-0.559
Peak gape angle	0.691	0.081
Time to peak gape/GCYT	0.702	0.359
Gape angle at close	0.205	0.721
Gape cycle time	-0.108	0.712

FO, fast opening; GCYT, gape cycle time.

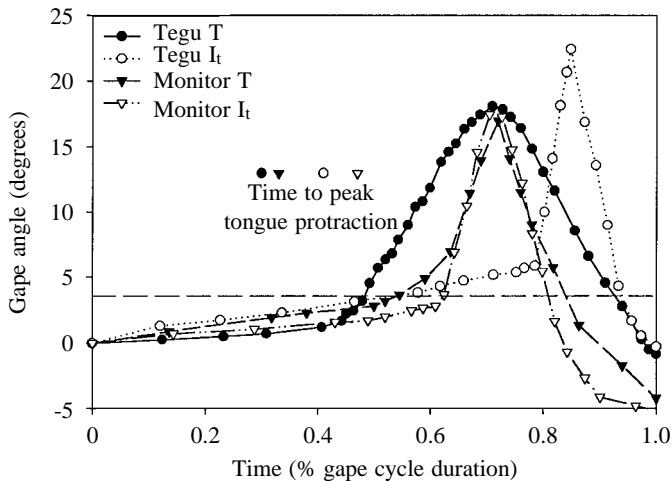


Fig. 5. Mean gape profiles (in degrees) for *Tupinambis teguixin* (circles) and *Varanus exanthematicus* (triangles) for normal tongue-based transport (T pattern; filled symbols) and inertial tongue-based transport (I_t pattern; open symbols). Two-dimensional angular means are shown for five cycles each from one individual of each species performing both behaviors. The x-axis indicates time as a percentage of gape cycle duration beginning at the frame before the tongue emerges from the mouth (time zero) and ending when the mouth closes on the prey again. Free-floating symbols indicate the time of peak tongue protraction. Significant differences between species and behaviors are based on the results of *post-hoc* tests (Table 1) from a repeated-measures analysis of variance (Table 2). Note the obvious differences in the profile for the tegu I_t behavior.

vary but not significantly different in the ANOVA) contributed to separating the species on PC2.

Behavioral effects

ANOVA of the main effects revealed four significant behavior effects (Table 2) but the *post-hoc* pairwise tests revealed these were a result of the significantly different kinematics of the tegu I_t patterns compared with the other three patterns. In tegu I_t patterns, the time to onset of fast opening (in real time and scaled to gape cycle duration), the gape angle at the onset of fast opening, maximum gape angle and the time to maximum gape scaled to gape cycle duration were significantly greater (Table 1). The strikingly different kinematic patterns of the tegu I_t patterns were also evident in the gape profiles (Fig. 5) and on PC1 (Fig. 6). The other three behaviors (tegu T patterns and monitor I_t and T patterns) were not significantly different in time to onset of fast opening (in real time), gape angle at the onset of fast opening, time to peak tongue protraction (in real time), peak gape angle or time to peak gape angle (in real time and scaled). They were different in that the time to onset of fast (scaled) opening was significantly different in all three behaviors, peak tongue protraction was smaller in tegu T patterns and time to peak gape (in real time) was significantly shorter in monitor I_t patterns (Table 1).

Significant behavioral effects within each species were observed in increases in time to onset of fast opening and

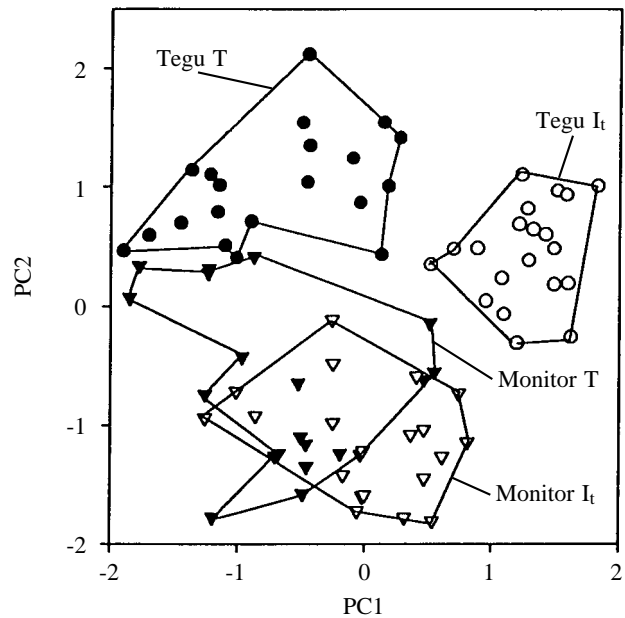


Fig. 6. Principal components analysis of gape and tongue kinematics for *Tupinambis teguixin* (circles) and *Varanus exanthematicus* (triangles) during normal transport (T patterns; filled symbols) and tongue-based inertial (I_t patterns; open symbols) transport behaviors. Principal component 1 (PC1; 32.1% of variance) separates the tegu I_t pattern from the other three behaviors on the basis of gape components, while the species are separated on PC2 (23.5% of variance) by the two tongue variables and gape cycle time.

scaled time to peak tongue protraction in I_t patterns. The single significant interaction (Table 2) is again an effect of the major difference in the tegus, which results in a difference in the direction of change in scaled time to fast opening across behaviors within species, but all four species \times behavior treatments were significantly different for this variable. In the principal components analysis, PC1 revealed an overlap of tegu T patterns with both monitor I_t and T patterns. The tegu I_t patterns were clearly different in terms of the timing and extent of jaw movements at the end of the slow opening phase and at peak gape.

Relative timing of gape components

The tegu I_t patterns were noticeably different in the relative timing of the gape phases. In the monitor I_t and T patterns and tegu T patterns, however, the scaled time to peak gape was essentially identical, indicating that scaled closing duration is similar in these three behaviors. Given that the scaled time to fast opening (the duration of slow opening) varied significantly across all behaviors and that the scaled time to peak gape did not then, by subtraction, the duration of fast opening varied as well. This indicates that the durations of both slow and fast opening differ among these three behaviors.

Discussion

The most striking finding of this study is the extensive use

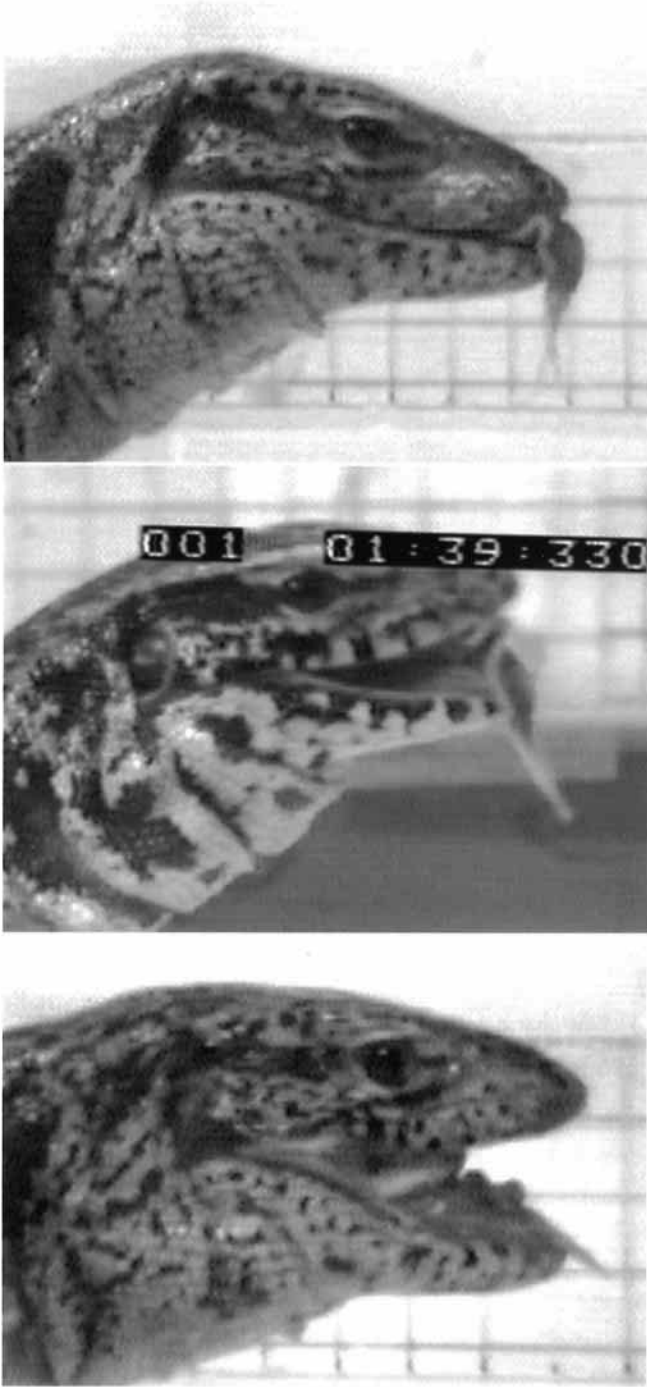


Fig. 7. Anterior tongue 'wrinkling' in tegus. During some of the later tongue-based transports (T patterns), tegus were observed to wrinkle up the anterior portion of the fleshy posterior part of the tongue to form a cog that aided directly in prey adhesion.

of the tongue in these lizards. Tegus and monitor lizards possess independently evolved deeply incised, chemosensory tongues (Cooper, 1994). They are modified in form to have a forked tip and a slender shape, and are used extensively to find and taste prey (McDowell, 1972; Cooper, 1994, 1995). In tegus, the posterior half of the tongue is similar in form (wide, thick, muscular, attached to the posterior floor of the oral

cavity) to non-chemosensory tongues in other lizards (Smith, 1984), but the anterior half is narrow and apparently more suited to chemosensory function. Scales are found on the surface of the tegu tongue, the anterior three-quarters of the tongue is not attached to the floor of the oral cavity, and the base of the tongue is supported by the hyobranchial elements. On the basis of morphology, tegus effectively have a two-part tongue, with a posterior part like that of basal lizards that could function in moving prey and an anterior part specialized for chemosensory function (Smith, 1984). Monitors have a more extreme tongue that is similar to that of snakes, being very narrow throughout its length, with no scales, and the entire tongue is withdrawn into a sheath that opens to the oral cavity at approximately one-quarter of the head length posterior to the tips of the jaws (Smith, 1986). On the basis of morphology, the monitor tongue is fully chemosensory in function, and its retraction into a sheath under the oral surfaces limits its use in transporting prey (especially in the posterior three-quarters of the oral cavity behind the opening to the sheath). Studies of inertial feeding do not report tongue use monitors; in fact, it is stated that the tongue is not used in feeding (Smith, 1982, 1986). Our data show that non-tongue-based inertial transports (I patterns) constitute only 13% of transport behaviors in tegus and 24% in monitors. However, we found that the tongue is used not only in normal transports (T patterns) but also in 72–83% of inertial transports (Fig. 2: $I+I_t$ patterns). Given that these two species belong to genera for which inertial transports are common and that the tongue is specialized for chemoreception, it may be that the non-tongue-based inertial transports (I patterns) appeared as a novel transport behavior to accommodate the decreased prey transport function of their derived chemosensory tongues.

Iguanian lizards and salamanders clearly use their wide, muscular tongues (with surfaces and secretions used to adhere to the prey) to transport prey through the whole range of prey positions from the tips of the jaws (after initial capture), further into the jaws and to the rear of the mouth using a series of normal tongue-based transport sequences (Throckmorton, 1980; Gans et al., 1985; Schwenk and Throckmorton, 1989; Herrel et al., 1997). In tegus and monitors, non-tongue-based inertial movements (I) were used to position the prey and to begin to transport it. Inertial transports involving the tongue (I_t) were used to bring the prey further into the jaws, followed by tongue-based transports (T) (that we hypothesize to be homologous to those of basal lizards; S. M. Reilly and L. D. McBrayer, unpublished data), which were used when the prey was well into the mouth. Thus, the behavior pattern changed with prey position. Initial transports in which the narrow chemosensory tongues could have little effect were purely inertial. Once the prey were half-way into the mouth, inertial movements and tongue-based movements (which would add the utility of hyoid retraction to prey movement) were used. This demonstrates that these lizards have a complex behavioral repertoire for prey transport.

The correlation between prey position and the phasing out of inertial movements while tongue movements are phased in

suggests that non-tongued-based inertial transports may not have arisen *de novo*. We hypothesize that tongue-based inertial transports first arose by the addition of inertial head movements to the normal transport behavior involving the normal use of the tongue. Such behavior has been reported anecdotally in other lizards (*Sphenodon punctatu*, Gorniak et al., 1982; *Ctenosaura similis*, Smith, 1984) and salamanders (Reilly and Lauder, 1990). Subsequently, we suggest that pure inertial transports became possible by decoupling the protraction of the tongue from the behavior. This functional progression is seen in reverse in tegus, in which the jaws alone, together with inertial head movements, transport the prey first (I patterns), then the rear part of the tongue (and presumably the hyobranchial apparatus) begins to move prey with the aid of inertial movements (I_t patterns), then normal tongue- and hyoid-based transport ensues (T patterns) using both the posterior part of the tongue and the wrinkled up anterior portion. The two-part tongue in tegus may explain why tegu tongue-based inertial transports were so different. The significantly longer and more extensive slow opening phase in tegus may indicate that the tongue is being projected further and for relatively longer, perhaps to facilitate the use of the posterior part of the tongue in inertial transports in which the prey is in the middle position in the jaws. The faster fast opening/closing phases in tegu I_t pattern indicate that they use faster inertial movements. It appears that the I and I_t patterns are associated with the loss of tongue transport function anteriorly in the chemosensory-tongued lizards and that tegus have retained a dual functionality of their tongues and can use the anterior portion of the fleshy portion to aid in transporting prey (Fig. 7). Surprisingly, monitor lizards exhibit equally extensive tongue movements even though there appears to be little the tongue can actually contribute to moving the prey at any position in the mouth. Thus, monitors appear to have lost the transport function of the tongue but appear to retain primitive tongue movements nonetheless. Tegus and monitor lizards exhibit conservation of tongue behavior even though these lizards possess independently evolved chemosensory modifications of their tongues that limit their use in feeding. A similar conservation of transport behavior is seen in chameleons (So et al., 1992).

Comparisons with other vertebrates

The characteristic gape cycle in both I_t and T patterns involved a long slow opening phase during which the tongue was protracted, followed by fast opening and closing phases during which the tongue was retracted. This pattern was consistent within and across individuals and species and matches transport kinematics seen in other lizard species (Throckmorton, 1980; Urbani and Bels, 1995; Herrel et al., 1997). The slow opening phase fits the generalized gape profile predicted for lizards (slow opening I, Bramble and Wake, 1985; slow opening, Reilly and Lauder, 1990). During the slow opening phase, the gape gradually increases while the tongue slides under the prey. The tongue is then retracted during fast opening and closing. It has been proposed that lizards have a

'slow opening II phase' in which the gape profile levels off between slow opening and fast opening (Bramble and Wake, 1985). However, we found no evidence of a plateau in the gape profiles during which the jaws remain at a constant angle after slow opening. In fact, it was easy to ascertain the point at which fast opening began, and there was a slow consistent increase in gape prior to that point. No study to date (including crown and basal taxa) has shown a consistent plateau in the gape profile of lizards during prey transport or other behaviors (Goosse and Bels, 1992), and it seems, therefore, that a slow opening II phase is absent in lizards. Further analyses of phylogenetically intermediate lizard taxa are needed to corroborate this hypothesis.

One conspicuous difference between the species was in the kinematics of the jaws at the end of the closing phase. The monitors had a significantly greater gape angle at closing than the tegus, and the rate of gape closing tended to decrease at the end of closing (Fig. 5). Greater closing on the prey and a decreased rate of closing at the end of the closing phase appear to be evidence of the 'slow close-power stroke' that has been proposed for lizards (Bramble and Wake, 1985) in which increased jaw force is thought to be delivered to the prey during feeding. These characteristics in monitors were more pronounced in I_t than in T patterns when the prey would be in a better position for biting with opposing teeth. They are clearly not present in tegus and most other lizards for which we have kinematic data (L. D. McBrayer, unpublished data), but it seems that the monitors may employ such patterns.

Finally, although lizards are predicted to possess extensive intraoral food-processing behaviors (Bramble and Wake, 1985; Reilly and Lauder, 1990), the range of feeding behaviors of lizards is not well understood. While general strike (Bels and Baltus, 1988; Bels, 1990; Bels and Goosse, 1990; Kraklau, 1991; Delheusy and Bels, 1992; Herrel et al., 1995) and transport (Throckmorton, 1980; Urbani and Bels, 1995; Herrel et al., 1996, 1999) kinematics have been studied in other species and the presence of inertial feeding in lizards has been described (Gans et al., 1978; Smith, 1984, 1986; present study), this is the first study to quantify the relative use of individual patterns within the range of behaviors (i.e. the repertoire) used by a given species. Many similar analyses of specific feeding behaviors, their kinematics and their relative occurrence are needed to test predictions about the complexity and evolution of feeding in squamates and tetrapods.

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