

## Prey Capture Behavior in the Blue-tongued Skink, *Tiliqua scincoides*

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**ABSTRACT.**—Squamate prey capture evolved in two general directions; one toward an emphasis upon lingual prehension and the other toward an emphasis upon jaw prehension. In basal squamates (Iguania), lingual prehension characterizes prey capture. All other squamates (Scleroglossa) tend to use their jaws for prey prehension and the role of the tongue as a prehensile organ is reduced. However, within some scleroglossan lizards, lingual and jaw modes of prehension are present. Selection of a distinct prehension mode during a feeding bout in these lizards has been hypothesized to be related to prey size. To test for the presence of lingual prehension and correlation with prey size, we examined feeding behavior in the blue-tongued skink, *Tiliqua scincoides* using two prey types (mealworm and cricket). We confirmed that this skink uses both lingual and jaw modes of prehension with accompanying characteristic jaw kinematic profiles. With crickets, only jaw prehension was exhibited, but both modes were used when feeding on equivalently sized prey, mealworms. Consequently, prehension mode is not exclusively elicited by prey size. We, therefore, hypothesize that selection of prehension modes, lingual or jaws, in these basal scleroglossans also includes proximate factors related to prey behavior.

The tongue of iguanian lizards is used in prey capture (Throckmorton, 1976; Smith, 1984; Schwenk and Throckmorton, 1989; Bell, 1990; Bels and Goosse, 1990; Kraklau, 1991; Delheusy and Bels, 1992), an ancestral state for Squamata (Schwenk, 1988; Schwenk and Throckmorton, 1989). But within the more derived scleroglossans, there is a tendency for the tongue to become specialized for chemoreception (Burgardt, 1970; Schwenk, 1988, 1993), and its role in prey capture lost as the jaws assume the major role in prehension. Each feeding mode, lingual and jaw prehension, is accompanied by a characteristic kinematic profile (Fig. 1) (Bramble and Wake, 1985; Schwenk and Throckmorton, 1989; Goosse and Bels, 1992; Urbani and Bels, 1995; Bels and Kardong, unpubl. data). For iguanians, the kinematic pattern accompanying tongue prehension consists of four stages. Jaw opening begins with a slow open I (SOI), followed by a slower, slow open II stage (SOII), and ends with a fast open stage (FO) as the tongue projects from the mouth (Schwenk and Throckmorton, 1989; Bels et al., 1994). During closing, the jaws rapidly close (FC) (Fig. 1A). For some scleroglossans, the kinematic profile accompanying jaw prehension consists of a fast open (FO) and fast close stage (FC), and the tongue does not protrude from the mouth (Fig. 1B).

In general, lingual prehension characterizes the iguanian clade, and jaw prehension characterizes the scleroglossan clade, but there are ex-

ceptions. In herbivorous iguanians, the tongue may be used to draw the leaf or food to the mouth and crop it with the jaws. But occasionally the jaws are used to grasp and tear vegetation. In the sister group, *Sphenodon*, jaw prehension is used to secure large prey (Gorniak et al., 1982; Schwenk and Throckmorton, 1989). However, *Sphenodon* and all iguanians use lingual prehension for small prey (Schwenk and Throckmorton, 1989).

Exceptions to the general pattern of prehension by means of jaws also exist for scleroglossans. *Trachydosaurus rugosus* (Scincidae), feeding on snails, initially contact the prey with the tongue which drew the snail a short distance across the substrate until the jaws secured the prey (Gans et al., 1985). The snail is never lifted by the tongue and carried into the mouth, a behavior interpreted as kinematically distinct from that recorded in iguanians (Schwenk and Throckmorton, 1989). In another scleroglossan, *Zonosaurus laticaudatus* (Corydiylidae), jaws were used with large prey, but tongue use was used with small prey; it was concluded that the jaw kinematic profiles accompanying tongue use represented an ancestral prehension profile as observed in iguanian lizards (Urbani and Bels, 1995).

While jaw prehension is the sole mode of capture in derived scleroglossans, even with very small prey (Smith, 1982, 1986; Schwenk and Throckmorton, 1989), there is evidence that tongue use is present in some groups of basal scleroglossan lizards and choice of feeding mode is related to size of the prey (Urbani and

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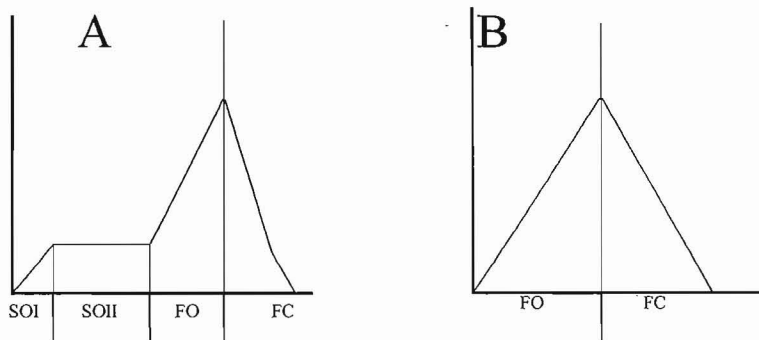


FIG. 1. Characteristic kinematic profile (modified from Bramble and Wake, 1985). (A.) The kinematic pattern accompanying lingual prehension consists of four stages. Jaw opening begins with a slow open I (SOI) followed by a slower, slow open II stage (SOII), and ends with a fast open stage (FO) as the tongue projects from the mouth. During closing, the jaws rapidly close (FC). (B.) The kinematic profile accompanying jaw prehension consists of a fast open (FO) and fast close stage (FC), and the tongue does not project from the mouth.

Bels, 1995). It has been hypothesized that when lingual prehension is present in a species, a switch in prehension mode is mediated by the size ratio of predator to prey, a consequence of changing surface area of the tongue relative to the prey size (Bramble and Wake, 1985; Schwenk and Throckmorton, 1989; Urbani and Bels, 1995). Consequently, the prehension mode is largely determined by the wet adhesive properties of the tongue relative to prey size, such that, as the prey becomes larger the tongue loses its effectiveness and the lizard must capture prey using jaw prehension (Bramble and Wake, 1985; Schwenk and Throckmorton, 1989). The significance of lingual prehension in some species of scleroglossans is disputed as whether it represents an isolated occurrence, or characterizes these species as functional intermediates between ancestral iguanian lizards and more derived scleroglossans (Schwenk and Throckmorton, 1989).

To characterize the relationships between prey type and prehension mode, we examined feeding behavior in a scleroglossan species, the blue-tongued skink, *Tiliqua scincoides*, which we found to use both lingual and jaw prehension. We determined prehension mode when presented with two prey types (mealworms and crickets) and examined whether or not the prehension modes were correlated with prey size alone.

#### MATERIALS AND METHODS

*Tiliqua scincoides* is a scleroglossan lizard placed within the Scincidae (Estes et al., 1988). We adopted the squamate classification presented by Estes et al. (1988) because it is most complete and consistent with squamate monophyly. This phylogeny recognizes two major clades, the iguana and the scleroglossa.

*Lizards.*—Data were gathered from four, cap-

tive bred blue-tongued skinks, *Tiliqua scincoides*, obtained from a commercial dealer. All had been in captivity over six months before feeding trials were initiated. Each lizard was isolated in a terrarium (100cm × 50cm × 50cm) before filming. An incandescent bulb and two True-Lite tubes provided the animal with a temperature of 21 C (night) and 29 C (d). The relative humidity was maintained near 70%. Animals were conditioned to feed on the cage floor in front of a reference grid (10 × 10 mm). In filming trials the prey consisted of equivalently sized mealworm larvae (mean size: 23 ± 11 mm) and crickets (mean size: 31 ± 8mm).

*Feeding Trials.*—For high-speed cinematography, four adult blue-tongued skinks, *Tiliqua scincoides* (SVL: 27.11 ± 8.0cm) were filmed at 100 frames/sec using Eastman Ektachrome high-speed 7250 tungsten 16 mm film, using a photosonic 1 PL camera under two 1000w tungsten photoflood lights. At the initiation of a mealworm feeding trial, a preweighed and measured mealworm was placed in front of the lizard using long forceps. The camera was started and the ensuing predatory behavior filmed. For a cricket feeding trial, one preweighed and measured cricket was tied to the end of a line and placed on the surface in front of the lizard. A total of 44 mealworm feeding trials were filmed. Of these, 21 trials were of feeding in which the head of the skink did not turn and remained at right angles to the camera. These favorable views were used for quantitative analysis. A total of 16 cricket feeding trials were filmed, of which seven trials were true lateral and the cricket was captured from the substrate. Frame by frame quantitative analysis of these film sequences was performed using a Pony-cam 16mm cine projector.

*Qualitative and Quantitative Analysis.*—Kine-

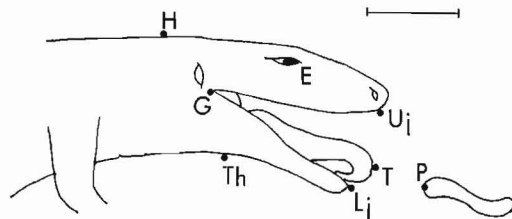


FIG. 2. Digitized points, using natural and distinct markings on the lizard's body: UJ—Upper Jaw, LJ—Lower Jaw, G—Gape, TH—Throat, E—Eye, H—Head, T—Tongue, and P—Prey. Reference bar 2 cm.

matic profiles of each feeding mode were determined as described elsewhere (Delheusy and Bels, 1992). From the lateral images, vertical y- and horizontal x- coordinates of selected points were recorded, using natural and distinct markings on the lizard's body (Fig. 2). Points at the anterior tips of the upper and lower jaw ( $U_j$  and  $L_j$ ) the corner of the mouth, gape (G), and the eye (E) were digitized. The head (H) was represented by a point immediately posterior to the cervical region, the throat (TH) was digitized as natural marking at the middle of the throat for each individual lizard, and a point on the tongue (T) was selected and followed throughout the feeding episode as the portion of the tongue first leaving the buccal cavity. The prey (P), mealworm or cricket, was digitized at the anterior-most point on each individual. Projected images were digitized using a Summagraphics MM 1201 digitizing tablet and analyzed using Lotus 123 and Statmost (DataMost Corp) software packages. All x- and y- coordinates plotted as graphs were corrected to avoid the effects of vertical rotation of the head. For each trial, the fixed grid, divided into 10 mm square units and placed immediately behind the lizard, was used as the inertial reference frame.

**Statistical Variables.**—The prey capture behavior was scored as lingual if the foretongue moved anteriorly from the mouth and protruded outside the buccal cavity. Capture was scored as jaw prehension if the tongue remained within the buccal cavity during prey capture. The following accompanying kinematic variables for capture cycles were scored for the two modes of prehension: *Maximum gape angle* (MGA), maximum gape angle, calculated from the points  $U_j$ , G, and  $L_j$ , during the prey capture trial; *time-to-peak gape* (TPG) time when jaws first begin to part to maximum gape angle;

*time-to-close* (TC), time from peak gape angle to jaw tips closed; and *gape cycle time* (GCT), time when jaws first begin to part to jaws tips closed. *Maximum head rotation* (MHR), the tilting of the snout downward, as measured from the horizontal substrate, was analyzed for missed versus successful prey capture trials. These data were not entirely independent, because we analyzed several feeding trials from one animal. Due to the opportunistic design of the study, resulting in uneven sample sizes, any suitable nonparametric test resulted in the loss of informative data. As a result, each trial was treated as an independent sample and two-tailed student t-tests were used to compare statistical variables between prehension modes. In addition, a chi-square test was used for measuring the correlation between the mode of capture and the prey item. Of the four animals used, no single individual accounted for more than 30% of the data.

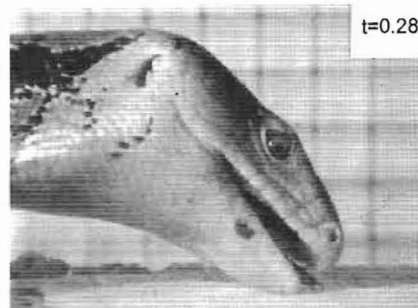
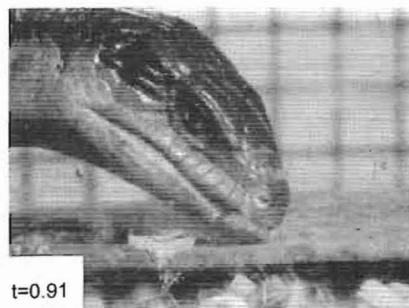
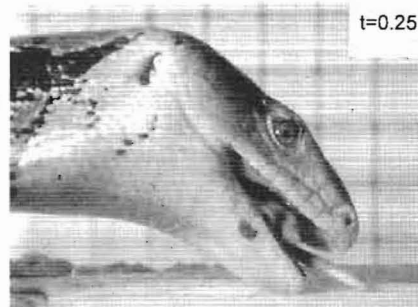
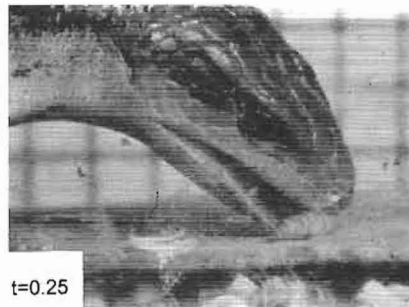
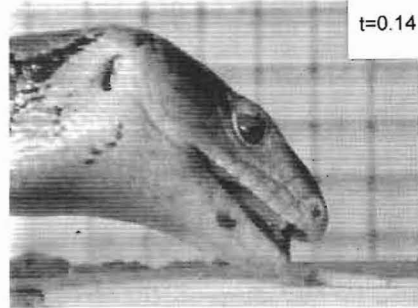
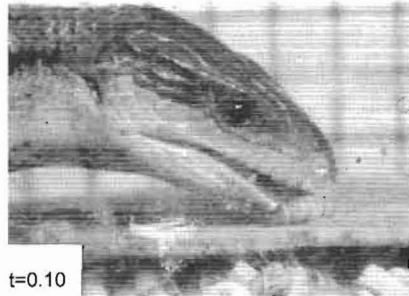
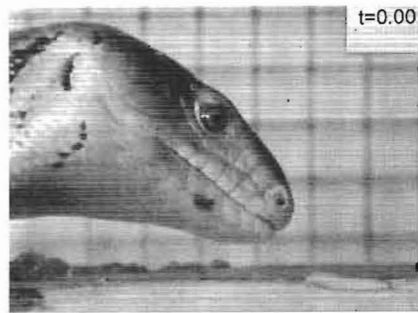
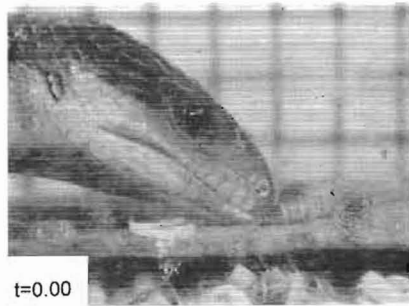
## RESULTS

**General Patterns.**—The blue-tongued skink, *Tiliqua scincoides* when presented with individual, equivalently sized mealworms, used both jaw and lingual modes of prehension in capturing the prey (Fig. 3). When presented with crickets, only jaw prehension was used. The mode of prehension, jaw or lingual, was accompanied by a characteristic kinematic pattern.

Approach and capture stages of a feeding trial often consisted of several tries, lingual or jaws, preceding successful prey capture. Capture success was similar, 32.3% (21/65) and 34.4% (11/32), for mealworm versus cricket (Fig. 4A). In none of the 21 mealworm trials was a missed lingual attempt followed immediately by a jaw prehension attempt. However, in many ( $N = 15$ ) mealworm trials, a missed jaw capture attempt was followed by successful lingual capture. While the tongue and jaws were used equally during missed attempts, the tongue was used more frequently during a success (Fig. 4B).

After a missed attempt(s), the lizard made behavioral modifications, changing head and body positioning. This included tilting the snout downward at a more direct angle to the prey, lifting the body at the shoulders, or head rotation about the long axis of the skull thereby presenting one side of the jaws to the prey. Often these head rotations and postural changes were used in combination (Fig. 5). A missed attempt, either lingual or jaw, was characterized by less

FIG. 3. Prey capture. Jaw prehension (left). Lingual prehension (right). Elapsed time shown in corner of frames.



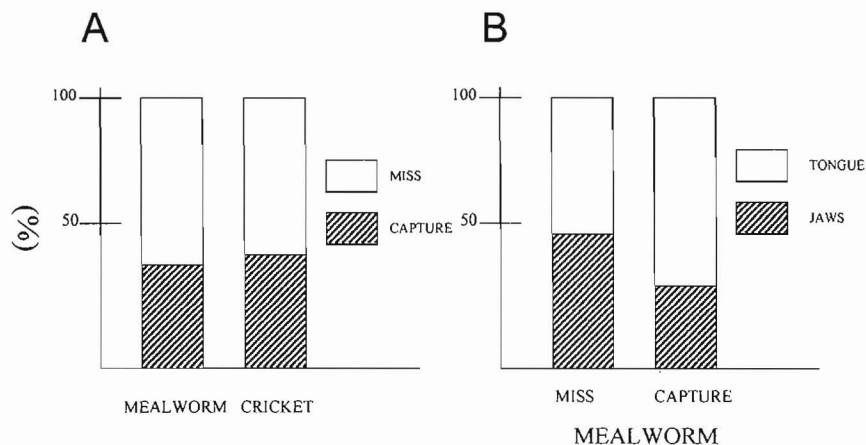


FIG. 4. Prey Capture Success (percentage %). (A.) A feeding trial often consisted of several missed attempts, mealworm or cricket, preceding successful prey capture. (B.) While the tongue and jaws were used equally during missed attempts on mealworms, the tongue was used more frequently during a success.

head rotation than in a successful capture sequence (36.14 vs. 46.7 degrees) (Table 1). In many of these missed attempts, the head tended to be held horizontal to the substrate. This appeared to produce an unfavorable orientation of the jaw tips to the prey. The lizard tended to either push the prey away with the forward-moving lower jaw or it did not gain a firm grasp on the prey between the jaw tips.

Statistical variables for capture cycles were compared for the two modes of prehension, lingual versus jaw (Table 1). The time to peak gape (0.25 vs. 0.15s,  $t = 3.87$ ,  $P < 0.01$ ) and gape cycle time (0.37 vs. 0.27s,  $t = 2.61$ ,  $P < 0.05$ ) were significantly faster during jaw prehension. Neither maximum gape angle (23.26 vs. 17.70 degrees,  $t = 2.03$ ,  $P > 0.05$ ), or time-to-close (0.11 vs. 0.13,  $t = -1.11$ ,  $P > 0.05$ ) were significantly different between lingual and jaw modes of prehension. A chi-square test shows a significant association between prey type and mode of prehension ( $\chi^2 = 14.3$ ;  $df = 1$ ;  $P < 0.01$ ).

*Lingual Prehension.*—Of the 21 mealworm tri-

als, 11 involved lingual prehension. With the presentation of an individual mealworm, the lizard positioned its head close to and in front of the prey during the approach stage. In most, 72.7% (8/11) the lower jaw made contact with the substrate followed by tongue protraction. The tongue protracted toward the mealworm and curled so that the tongue tips curved ventrally and caudally, exposing the wider dorsal surface of the tongue to the prey (Fig. 3).

In the majority, 81.8% (9/11), of lingual prehension trials, the lower jaw exhibited no forward displacement while the tongue retracted. In the remaining tongue prehension trials, 18.2% (2/11), the rate of tongue retraction equaled the rate of forward movement of the head. In these trials, jaw advancement was not impeded by contact with the substrate or contact with substrate indirectly via tongue-pinning. In a characteristic capture bout, the retracting tongue carried the prey well back into the mouth behind the mid-region of the buccal cavity.

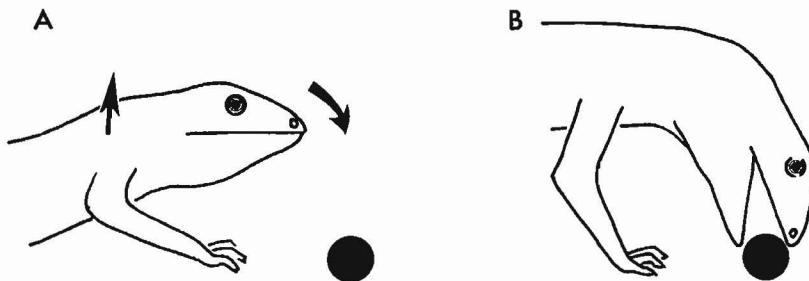


FIG. 5. After a missed attempt(s), the lizard made behavioral modifications, changing head and body positioning. Rotation included tilting the snout downward at a more direct angle to the prey and lifting the body at the shoulders (A) thereby presenting the jaws to the prey (B).

TABLE 1. Statistical variables during head rotation and comparison between the two modes of prehension, lingual versus jaw for capture cycles (student t-test \*  $P < .05$ , \*\*  $P < .01$ ).

Variables	Miss			Capture			t-test
	N	Mean	SE	N	Mean	SE	
Maximum Head Rotation (MHR) (Degrees)	22	36.14	2.059	13	46.70	3.436	$P < 0.0020^{**}$
	Lingual prehension			Jaw prehension			t-test
	N	Mean	SE	N	Mean	SE	
Maximum Gape Angle (MGA) (Degrees)	9	23.2609	2.1569	8	17.7018	1.6788	$P < 0.0770$
Time to Peak Gape (TPG) (Seconds)	9	0.2467	0.0163	8	0.1525	0.0185	$P < 0.0061^{**}$
Time of Close (TC) (Seconds)	9	0.1178	0.0097	8	0.1350	0.0073	$P < 0.3052$
Gape Cycle Time (GCT) (Seconds)	9	0.3689	0.0238	8	0.2657	0.0275	$P < 0.0398^*$

The kinematic profile accompanying lingual prehension resembled the general iguanian kinematic profile consisting of four stages: a short initial slow open (SOI) stage, followed by a slower, slow open (SOII), a fast open (FO) stage, and completed in a fast close (FC) stage (Figure 6A). In the two trials where there was no jaw contact with the substrate, a well-defined SOII stage was missing. These two trials were analyzed kinematically independently of the other lingual prehension trials.

*Jaw Prehension.*—In many, 42.9% (9/21), mealworm trials and in all, 100% (16/16), cricket trials the jaws were used during capture. When using the jaws for capturing, the lizard commonly lunged in the direction of the prey and, as with tongue-use, the depressed lower jaw made contact with the substrate. Initially, the prey was grasped just inside the tips of the jaws. The tongue was employed during the subsequent gape cycle to transport the prey intraorally (Fig. 3).

The kinematic profile accompanying jaw prehension resembled the generalized scleroglossan profile: gape angle increased and decreased at a constant rate, with fast open (FO) and fast close (FC) stages, respectively (Fig. 6B).

#### DISCUSSION

For the blue-tongued skink *Tiliqua scincoides*, two modes of prehension, lingual and jaw, are present during independent feeding trials. Each mode is associated with a characteristic kinematic profile, and these profiles are similar to those of prehension reported in other lizard groups. Although lingual prehension in *Tiliqua* is kinematically similar to lingual prehension in iguanians, the phylogenetic position of skinks within Scleroglossa strongly suggests that lin-

gual feeding in *Tiliqua* is a reversal, i.e. secondarily re-evolved from a jaw-feeding ancestor within Scleroglossa.

Our results also differ from reports of tongue use in lizards with specialized diets. In *Trachydosaurus rugosus*, the tongue is not used to lift the prey (snail) and transport it to the buccal cavity (Gans et al., 1985; Schwenk and Throckmorton, 1989). However, in some of our trials with *T. scincoides*, the tongue was presented in a similar position (curled) as seen in iguanians and used to actually transport the mealworm into the mouth. In addition, unlike the distinctive kinematic profile of *T. rugosus*, the kinematic profile of tongue prehension in the blue-tongued skink was similar to the general feeding pattern (Bramble and Wake, 1985).

Unlike iguanians feeding on small prey, which are obligate tongue-feeders, and the vast majority of scleroglossans, which are obligate jaw-feeders, *Tiliqua* is capable of switching its prehension mode. The proximate basis for selecting prehension mode in this skink species is consequently of special interest. On theoretical (Bramble and Wake, 1985) and empirical grounds (Schwenk and Throckmorton, 1989; Urbani and Bels, 1995), increasing prey size is hypothesized to favor jaw prehension; small prey lingual prehension. Certainly our data are consistent with this hypothesis. The jaws were used exclusively on crickets (large) compared to mealworms (small). However, our data suggest that other proximate factors might be involved as well.

When presenting skinks with the same sized prey (mealworms), we expect that the same prey capture mode would be used. This did not happen. The lizards used both prehension modes, not just lingual prehension. Although

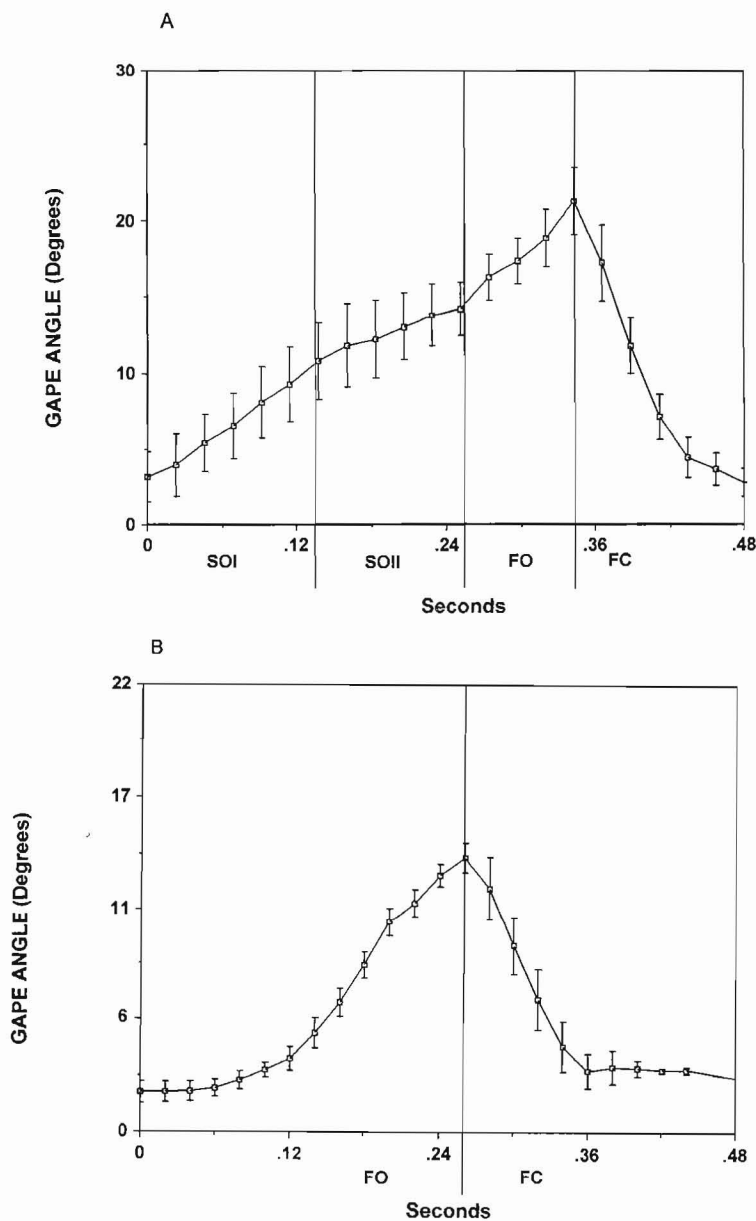


FIG. 6. (A.) The kinematic profile accompanying lingual prehension displayed as the mean gape angle with error (standard error) bars. (B.) The kinematic profile accompanying jaw prehension displayed as the mean gape angle with error (standard error) bars.

not quantified, we noted that the activity of a mealworm changed in several ways during the approach of the lizard. The mealworm might be motionless or moving. If moving it might be traveling away from the lizard or in one of the other possible directions (toward, across). Such "evasive" action by the mealworm increases the chance the lizard will lose the prey. We did determine that jaw prehension was significantly faster, to peak gape, than lingual prehension. A

rapid means of prey capture (jaw) would therefore be likely when the prey is active and the risk of escape great. This would suggest jaw prehension with mealworms was induced by prey-activity, not prey size, per se. This would also suggest why with a very active prey, crickets, jaw prehension was predominant.

Thus the selection of feeding modes is likely related to factors in addition to prey size (length). Other factors may include prey move-

ment, orientation of prey presentation, height of prey above the substrate, as well as factors related to size, such as the diameter silhouette of the prey and the prey's actual mass.

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