

## KINEMATICS OF TONGUE PROJECTION IN *CHAMAELEO OUSTALETI*

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### Summary

The kinematics of prey capture by the chamaeleonid lizard *Chamaeleo oustaleti* were studied using high-speed cinematography. Three feeding sequences from each of two individuals were analyzed for strike distances of 20 and 35 cm, at 30°C. Ten distances and angles were measured from sequential frames beginning approximately 0.5 s prior to tongue projection and continuing for about 1.0 s. Sixteen additional variables, documenting maximum excursions and the timing of events, were calculated from the kinematic profiles. Quantified descriptions of head, hyoid and tongue movements are presented. Previously unrecognized rapid protraction of the hyobranchial skeleton simultaneously with the onset of tongue projection was documented and it is proposed that this assists the accelerator muscle in powering tongue projection. Acceleration of the tongue occurred in about 20 ms, reaching a maximum acceleration of 486 m s<sup>-2</sup> and maximum velocity of 5.8 m s<sup>-1</sup> in 35 cm strikes. Deceleration of the tongue usually began within 5 ms before prey contact and the direction of tongue movement was reversed within 10 ms of prey contact. Retraction of the tongue, caused by shortening of the retractor muscles, reached a maximum velocity of 2.99 m s<sup>-1</sup> and was complete 330 ms after prey contact. Projection distance influences many aspects of prey capture kinematics, particularly projection time, tongue retraction time and the extent of gape and head movements during tongue retraction, all of which are smaller in shorter feedings. Though several features of the chameleon strike have apparently been retained from lizards not capable of ballistic tongue projection, key differences are documented. Unlike members of a related family, the Agamidae, *C. oustaleti* uses no body lunge during prey capture, exhibits gape reduction during tongue projection and strongly depresses the head and jaws during tongue retraction.

### Introduction

Chamaeleonid lizards feed by projecting their tongues as much as an entire body

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length out of their mouth to capture prey. The extensibility of the chameleon tongue is thought to be unmatched among vertebrate muscular organs (Gnanamuthu, 1937; Rice, 1973; Kier and Smith, 1985) and the mechanistic basis of tongue projection has attracted attention from researchers since the last century (Houston, 1828; Duvernoy, 1836; Kathariner, 1894; Gnanamuthu, 1930; Zoond, 1933; Altevogt and Altevogt, 1954; Gans, 1967; Bels and Baltus, 1987; Bell, 1989, 1990). In spite of such long-standing interest in chameleon feeding, our understanding of the mechanism of tongue projection is incomplete (Altevogt and Altevogt, 1954; Gans, 1967; Bell, 1990) and few kinematic data have been brought to bear on current hypotheses of tongue function (Altevogt and Altevogt, 1954; Bell, 1990).

The primary purpose of this study is to provide a quantitative description of the kinematics of the chameleon strike and to interpret these data in the light of potential mechanisms of tongue function. We focused on movements of the head, hyobranchial structures and tongue during prey capture in the Malagasy chameleon *Chamaeleo oustaleti*. Three questions were of particular interest. (1) What is the role of the hyobranchial skeleton during tongue projection? (2) What are the velocity and acceleration profiles of the tongue during projection and retraction? (3) How does the distance to the prey influence strike kinematics? The results provide evidence in support of two previously proposed aspects of feeding behavior. First, movements of the hyobranchial apparatus play a central role during tongue projection. Second, projection distance influences many features of strike kinematics.

### Materials and methods

Two adult specimens (224 and 230 mm snout-vent length) of *Chamaeleo oustaleti* Mocquard were obtained commercially and housed indoors with water and food (crickets) provided daily. An incandescent light bulb provided a thermal gradient from which the animals could select body temperature. These specimens and two others (198 and 210 mm snout-vent length) were dissected and used for anatomical observations.

Ciné films were made of animals feeding while perched on a wooden dowel mounted in front of a 1 cm gridded background. Crickets were offered in a clip held a fixed distance (20 or 35 cm) from the animal's head at the same vertical height as the anterior margin of the jaws. In all feeding events the tongue trajectory was approximately horizontal and the camera view was lateral to the chameleon's head and perpendicular to the direction of tongue projection. Feeding events were filmed with a Redlake Locam camera operating at 200 frames<sup>-1</sup> using Kodak 4X reversal film and a shutter speed of 1/1200 s. A pair of 650 W flood lamps provided illumination. All filming was done in a temperature-controlled room set at 30°C into which animals were introduced up to an hour before filming commenced so that body temperature would adjust to ambient levels. At the end of each filming session body temperature was measured

cloacally. Films made of animals that were below 29°C or above 31°C were not analyzed.

For each chameleon three feeding events were analyzed for both distances, to give a total of 12 feedings. Feeding sequences were projected onto a digitizing tablet that provided an effective resolution of 0.003 mm with reference to the original subject, and a computer program assisted in measuring distances and angles from successive frames. We used the frame during which the tongue first contacted the prey as zero reference time. This point was chosen because it was the only unambiguously identifiable event that could be located consistently in every feeding sequence. From -400 ms to -75 ms, variables were measured from every fifth frame (=25 ms intervals). From -75 to +85 ms, every frame was analyzed (=5 ms intervals), and after this time, every third frame was analyzed (=15 ms intervals). Analysis of 20 cm feeding events continued until +500 ms, whereas 35 cm sequences were analyzed until +650 ms.

Ten variables were measured that quantified movements of the body, head, hyobranchial skeleton and tongue during the strike. These variables were chosen to facilitate comparisons with published data on other tetrapods and to capture the aspects of chameleon feeding that are unique. *Horizontal* and *vertical body position* were measured as the distance from a selected mid-dorsal body scale to reference lines on the background grid. Opening and closing of the mouth were documented both by measuring *gape distance*, the distance between the anterior tips of the upper and lower jaw, and by the relative contributions of lower and upper jaw movements. The *lower jaw angle* was measured as the angle between a line passing between the anterodorsal tip of the mandible and the axis of the jaws and a second line defined by the tips of two mid-dorsal body scales. *Head angle* was measured as the angle between a line passing between the anteroventral tip of the upper jaw and a selected spot on the posterior margin of the upper jaw and a second line defined by the same two body landmarks used to measure lower jaw angle. Lower jaw angle decreases as the lower jaw is depressed. Head angle decreases as the head is depressed ventrally.

Movements of the hyobranchial skeleton could be followed since key features of this apparatus bulged against the skin of the neck and throat. Movements of the posterior tip of the medial entoglossal process and the distal tip of the right ceratohyal were used to measure angular and linear excursions of these structures. The *hyoid distance* was measured as the distance between a selected mark near the vertex of the jaws and the posterior tip of the entoglossal process seen bulging ventrally. Thus, this variable decreases as the hyoid moves anteriorly. Similarly, the *ceratobranchial distance* was measured as the distance from the same selected spot near the vertex of the jaws to the distal tip of the ceratobranchial. The *hyoid angle*, the angle between the ceratobranchial and the entoglossal process, was measured as the angle defined by the distal tip of the ceratobranchial, the vertex of the posterior tip of the entoglossal process and a more anterior location on the entoglossal process. This variable increases as the hyobranchial apparatus unfolds.

Two variables were measured to describe the movements of the tongue during

the strike. *Horizontal tongue distance* was measured as the distance between the anterior-most tip of the tongue and a vertical line marked by the tip of the upper jaw. This variable increases as the tongue is projected out of the mouth. *Retractor muscle length* was measured as the distance along the dorsal margin of the retractor muscle from the anterior tip of the upper jaw to the posterior margin of the accelerator muscle where the two muscles join. Once the tongue is projected, the entoglossal process is protruded maximally so that the origin of the retractor muscle (at the base of the entoglossal process) is held near the margin of the gape.

Plots of each kinematic variable against time were used to calculate an additional 16 variables that quantified aspects of the timing and magnitude of movements during the strike. *Peak values* of gape distance, tongue distance, head angle, lower jaw angle and hyoid retraction were measured from each feeding. For each of these maxima the time from time zero (=prey contact) to the maximum was measured as the *time to maximum*. The *gape cycle time* was calculated as the time from minimum gape until the gape reached minimum again. The *duration of tongue projection* was measured from the first frame in which the tongue accelerated forward until prey contact. *Tongue retraction time* was measured from prey contact to the time at which the posterior margin of the accelerator muscle broke the margin of the gape.

The displacement records of tongue extension and retractor muscle length were used to calculate velocity and acceleration profiles for tongue projection and retraction. Velocity was calculated for each frame as the distance traveled between successive frames divided by the time elapsed. Acceleration was calculated as the change in velocity divided by the time elapsed. Velocities and accelerations are, therefore, averages across the time intervals between frames (5 ms) and are not instantaneous. *Maximum velocity* and *acceleration* were recorded for tongue projection and tongue retraction.

Recently Harper and Blake (1989*a,b*) have emphasized the difficulties inherent in differentiating kinematic data from films to calculate accelerations. To avoid most pitfalls they recommend the use of small accelerometers (<0.5 g) that can be attached to the objects under study. While these devices have many advantages, their usefulness is limited in cases where the objects being studied are small. Accelerometers even as small as 0.5 g were impractical, given that the mass of the chameleon tongues we studied averaged less than 4.0 g. Webb (1977) recommended the use of a five-point moving regression developed by Lanczos (1956) to reduce the effects of some measurement errors that occur during film analysis. The moving regression method (Lanczos, 1956) was developed for engineering applications and assumes that forces and accelerations are relatively constant during the event being analyzed. This assumption is probably not valid in most biological situations (e.g. Calow and Alexander, 1973; Harper and Blake, 1988) and we feel that it is unreasonable for tongue projection in chameleons.

To estimate the error rate inherent in our film analysis, one feeding sequence was selected and the tongue distance data were measured from that sequence 10 times by the same investigator. Each of these 10 data sets was then used to

calculate velocity and acceleration profiles by differentiating the distance data once or twice with respect to time. For the period encompassing tongue projection and prey contact the coefficient of variation (CV) for tongue distance varied from 0.3% to 0.7%. During this time the CV for tongue velocity varied between 1.6% and 6.6%, with the CV for the frame at which maximum velocity occurred being 2.4%. The CV for maximum acceleration was 7.6%, though it was as high as 46.9% when acceleration reached zero. Thus, our film analysis protocol provides an acceptable level of measurement error for our measures of maximal velocity and acceleration. Inaccuracies in film speed and naturally rapid fluctuations in acceleration may make our estimates of maximum acceleration smaller than those actually realized by the chameleon tongue (Harper and Blake, 1989b).

Two analyses were carried out to explore the possibility that *C. oustaleti* can modulate prey capture kinematics in response to the distance the tongue must be projected to capture the prey. By 'modulate' we refer to the ability of the animal to alter kinematics in response to experimentally controlled differences in projection distance. In the first analysis, the 16 derived variables were analyzed with a two-way analysis of variance (ANOVA), individuals crossed with projection distance ( $N=3$  in each cell of this  $2 \times 2$  experimental design). Because the individual effect is random and the projection distance is a fixed effect, the  $F$ -ratios that tested projection distance were constructed with the mean squares of the projection distance effect in the numerator and the mean squares for the interaction term in the denominator (Sokal and Rohlf, 1981). In an exploratory procedure, a principal component analysis (PCA) was performed on the correlation matrix of the data set of 15 of the 16 derived kinematic variables. Maximum projection distance was omitted from this analysis because it was controlled in the experiment. The PCA was used to reduce the dimensionality of the data set so that overall comparisons between 20 cm and 35 cm feeding events could be made with only a few statistically independent variables.

## Results

The anatomy of the chameleon head, hyoid apparatus and tongue have been described and discussed by numerous authors (Mivart, 1870; Gnanamuthu, 1930, 1937; Zoond, 1933; Altevogt and Altevogt, 1954; Gans, 1967; Tanner and Avery, 1982; Bell, 1989; So *et al.* 1991). The reader is referred to these works for detailed descriptions of anatomy. Here we provide a brief anatomical description and provide more detailed comments within the context of the discussion of prey capture kinematics.

The feeding apparatus of *Chamaeleo oustaleti* (Fig. 1) and other chameleons has three major components; the skull, the hyobranchial apparatus and the tongue. The hyobranchial skeleton is composed of a large medial entoglossal process and paired, bony ceratobranchials articulated to the base of the entoglossal process. Paired ceratohyals are present as reduced cartilaginous forms anterior to the ceratobranchials. The hyobranchial skeleton is suspended within the throat region

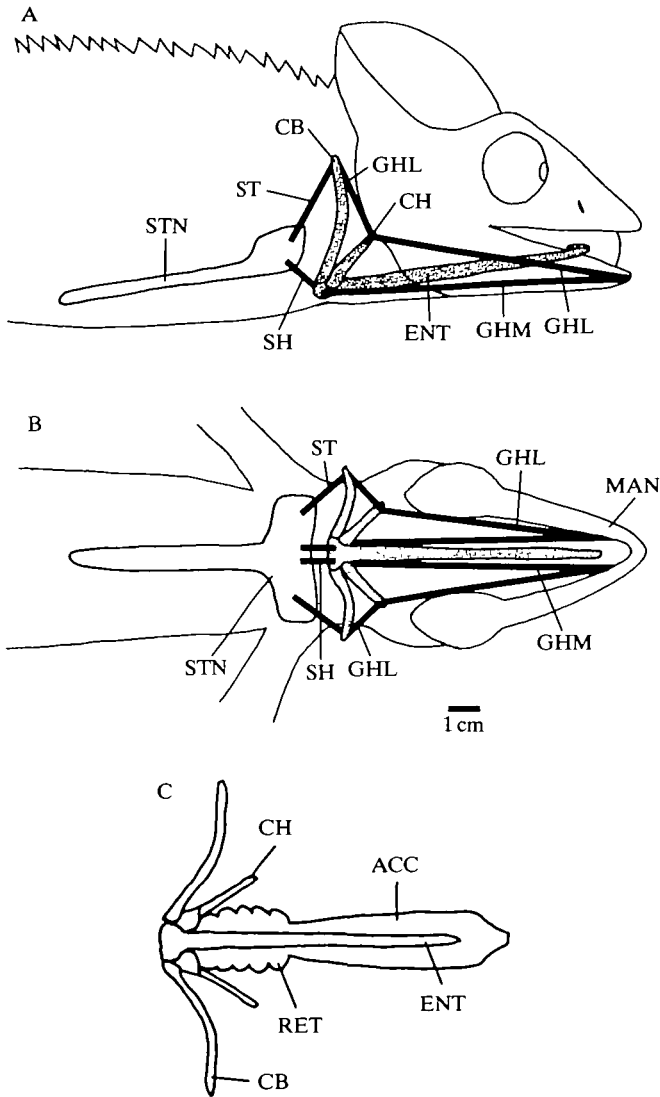


Fig. 1. Lateral (A) and ventral (B) schematic views of the head and hyobranchial structures of *Chamaeleo oustaleti*. Thick black lines indicate the attachments of the primary muscles. The intrinsic tongue muscles are illustrated in C in a retracted state. ACC, accelerator muscle; CB, ceratobranchial; CH, ceratohyal; ENT, entoglossal process; GHL, geniohyoideus lateralis muscle; GHM, geniohyoideus medialis muscle; MAN, mandible; RET, retractor muscle; SH, sternohyoideus muscle; ST, sternothyroideus muscle; STN, sternum.

with muscular connections to the anterior margin of the lower jaw, posteriorly to the sternum and dorsally to the pectoral girdle. The tongue is attached to the base of the entoglossal process by the paired retractor muscles (hyoglossi muscles). These muscles attach to the posterior margin of the large 'tongue knob' that is

formed by the large accelerator muscle and a fleshy tongue pad that forms the anterodorsal-most part of the tongue. The retractor muscles are able to extend to over 17 times their contracted length (Rice, 1973) and accommodate the extreme projection of the tongue knob that is characteristic of the chameleon strike. The accelerator muscle is a powerful sphincter with a central lumen into which the entoglossal process fits when the tongue is at rest in the chameleon's mouth.

#### *Kinematics of the strike*

Figs 2, 3 and 4 show film frames of the major events that occur during prey capture by *C. oustaleti*. Fig. 5 shows the means and standard errors of seven variables measured from the films of the six 20 cm feeding events. Additional variables are shown for the period of tongue projection in Fig. 6. Below we focus our description of tongue projection on the 20 cm feeding events and follow this with a discussion of the effect of projection distance on strike kinematics.

Prey capture by chameleons has previously been divided into five phases (Altevogt and Altevogt, 1954; Bell, 1990): fixation, tongue protrusion, tongue

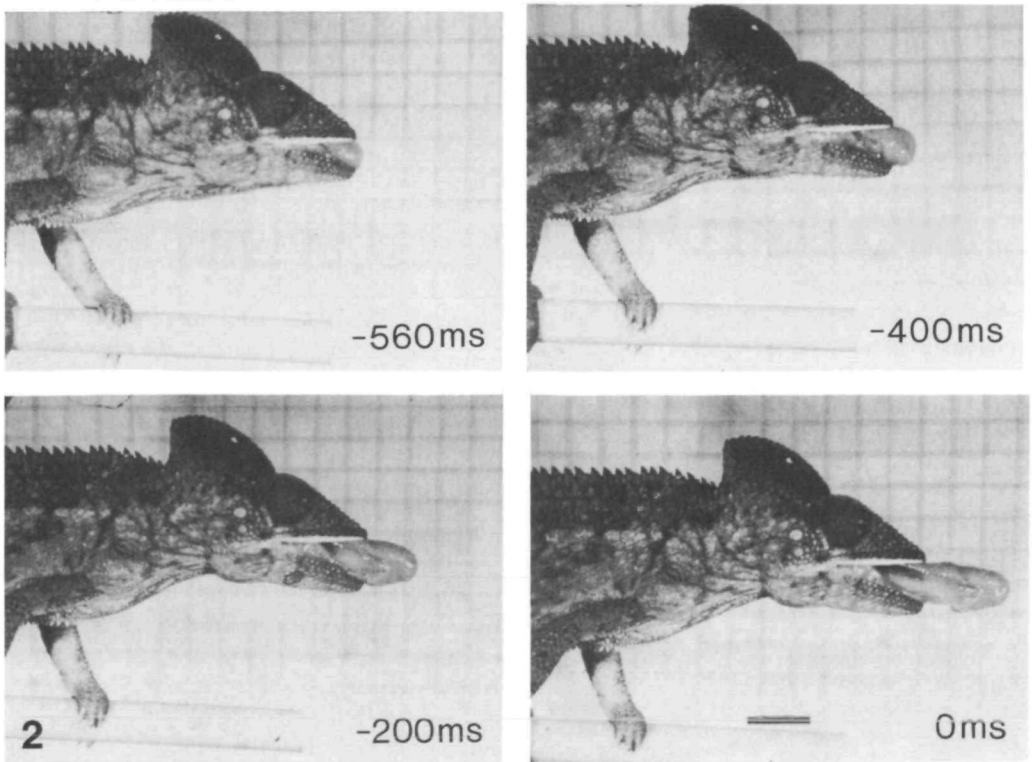


Fig. 2. Four film frames of *Chamaeleo oustaleti* during the tongue protraction stage of prey capture that occurs prior to tongue projection. Times are measured relative to the frame immediately prior to the onset of tongue projection. Scale bar, 2.0 cm. Note the gradual increase in gape and lack of whole-body movements as the tongue is protruded beyond the gape.

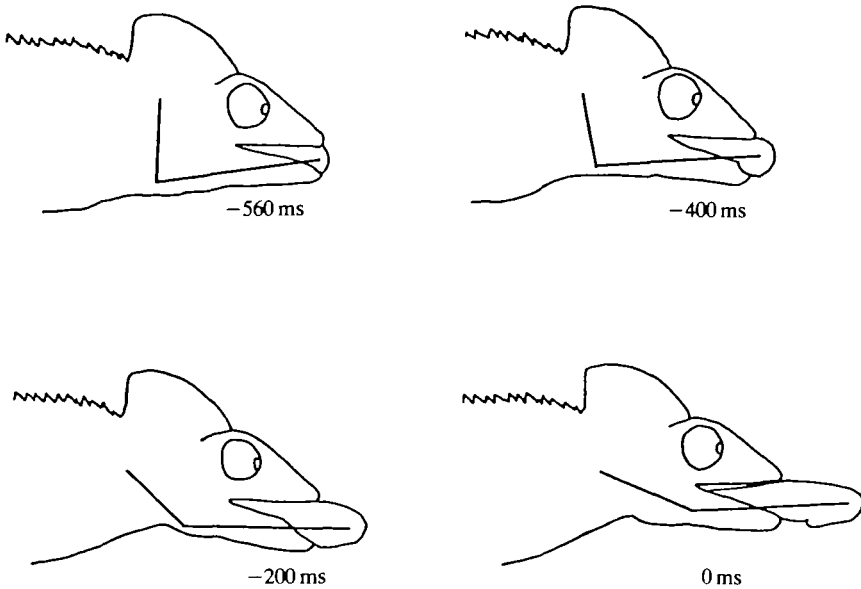


Fig. 3. Tracings of the four film frames shown in Fig. 2 with the position of the hyobranchial bones in the throat as this structure is unfolded during tongue protrusion. Ceratobranchial and entoglossal process positions were visible as the tip of the ceratobranchial and the vertex of this bone and the entoglossal process could be seen bulging through the skin. The anterior tip of the entoglossal process was assumed to be immediately behind the visible tip of the tongue.

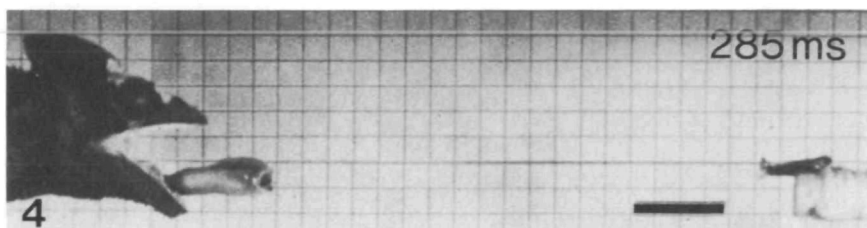
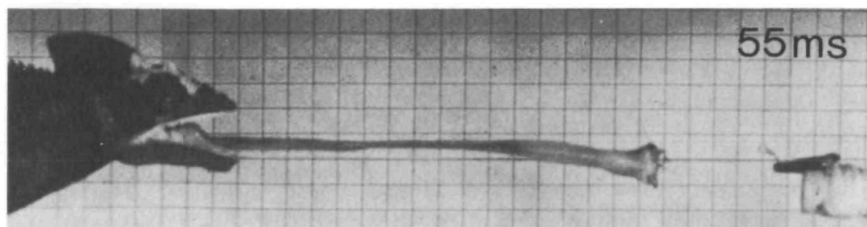
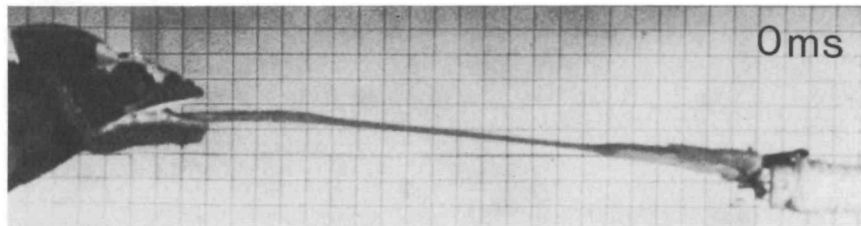
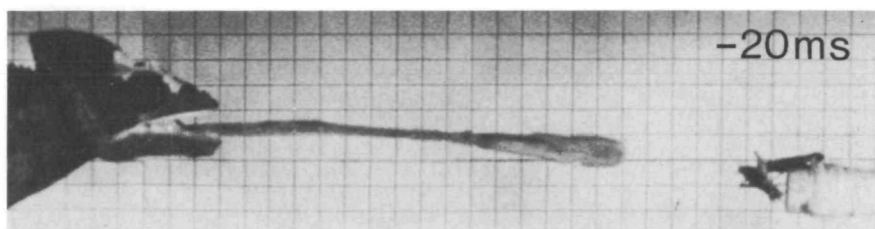
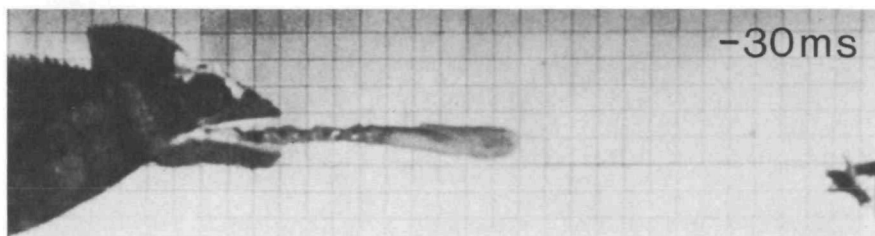
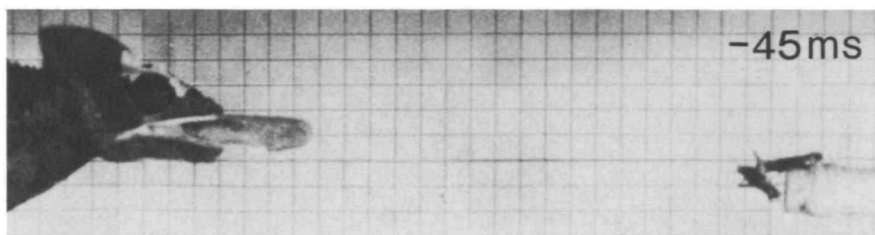
projection, tongue retraction and hyoid retraction. During fixation both eyes are directed at the prey and the animal positions its entire body in preparation for the strike (e.g. Harkness, 1977; Flanders, 1985). Fixation is followed by tongue protrusion, during which the hyobranchial apparatus undergoes complex changes as it moves dorsally and anteriorly to protrude the tongue out of the mouth. The duration of tongue protrusion in our observations of *C. oustaleti* was highly variable, being as short as about 2 s in some feeding events and longer than 2 min in others. Our film analysis does not include fixation and begins with the last 0.5 s of protrusion. A strike may be aborted at any time during fixation or protrusion. Tongue projection is rapid, lasting about 45 ms. Following prey contact, the tongue is retracted by a shortening of the retractor muscles, a process that requires about 250 ms. Once the tongue has been returned to its position on the entoglossal process, hyoid retraction begins and the unfolding of the branchial skeleton that occurs during protrusion is reversed. This phase lasts 300–500 ms.

During the last 0.5 s of protrusion, the tongue was extended from about 1 cm to

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Fig. 4. Six frames of *Chamaeleo oustaleti* during tongue projection, prey contact and tongue retraction. Time zero is the time of prey contact. Frame  $-45$  ms is the frame immediately prior to the onset of tongue projection. 15 ms later the tongue is traveling at over  $3\text{ ms}^{-1}$ . Tongue retraction takes longer than projection, requiring almost 300 ms. Note the slight elevation of the head and decrease in the gape during tongue projection. Scale bar, 3.0 cm.





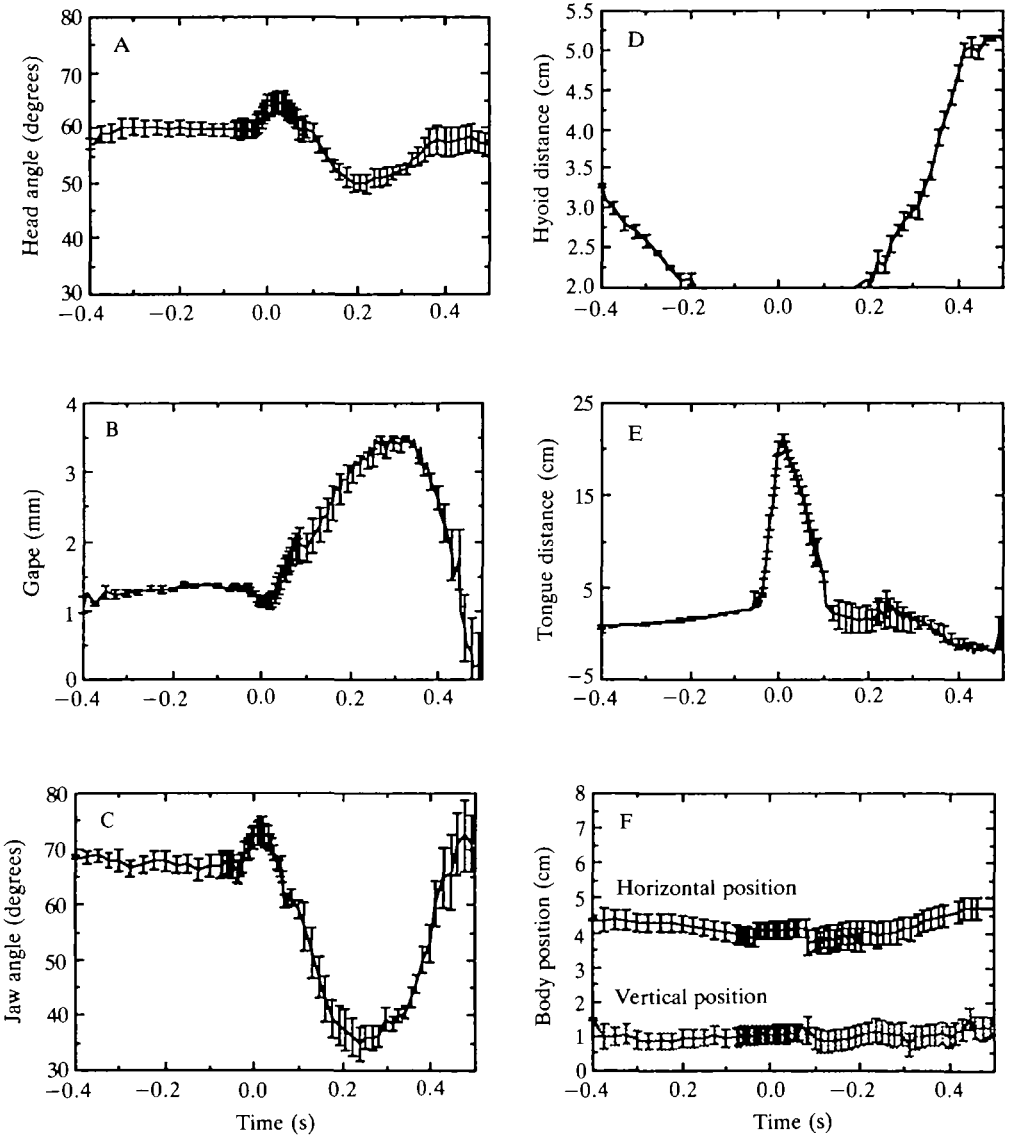


Fig. 5. Average kinematic profiles of seven variables measured from films of two *Chamaeleo oustaleti* feeding on crickets held 20 cm in front of the animal's head. Plotted points are mean  $\pm 1$  standard error for the variables measured from three feeding events from each of two individuals for a total of six feeding events. Time zero is the time of tongue contact with the prey. (F) Body position variables are horizontal body position on top and vertical body position in the lower plot. Variables are defined in the text.

about 3 cm beyond the margin of the gape (Figs 2, 3 and 5E). This protrusion is caused by movements of the hyobranchial skeleton that bears the tongue on its entoglossal process (Fig. 3). As the tongue was protruded, the angle between the

ceratobranchial and the entoglossal process increased until it reaches about  $160^\circ$  (Figs 2, 3 and 6F). After this time the angle could not be measured in our films because the posterior base of the entoglossal process slid anteriorly behind the vertex of the jaws and could no longer be seen bulging through the skin of the throat (Fig. 6F). As the tongue slowly protruded from the mouth the gape increased to accommodate the depth of the tongue. Beginning about 150 ms prior to tongue projection, the gape did not increase, and often decreased slightly (Fig. 5B). Slight movement of the body in the direction of the prey occurred during protrusion, as the animal extended towards the prey (Fig. 5F).

During projection, the tongue was accelerated off the entoglossal process towards the prey (Fig. 4). Immediately following the onset of tongue projection, the head and lower jaw angles began to rise and continued to increase until about 30 ms after prey contact (Figs 4 and 5). Peak head and jaw elevations of about  $15^\circ$  occurred during this phase (Fig. 5A,C). Thus, the head was tilted back sharply while the tongue was moving towards the prey. As this movement occurred after the onset of tongue projection, no upward vector was imparted to tongue projection. Following the onset of tongue projection, and while the head was tilting back, the gape decreased by about 3 mm, and it continued to decrease through the time of prey contact. Increases in gape then began 10–20 ms following prey contact. Tongue projection was rapid, requiring an average of 43 ms from its onset until the prey was contacted 20 cm away from the animal's jaws (Fig. 4; Table 1). Initially, the tongue accelerates for about 20 ms, reaching average peak accelerations of  $393 \text{ m s}^{-2}$  and average maximum velocities of  $4.9 \text{ m s}^{-1}$  (e.g. Fig. 6B,C). Velocity of the tongue then reached a plateau that continued until just before prey contact. In seven of our twelve feedings the tongue did not show any signs of deceleration until the frame during which prey contact occurred (e.g. Fig. 6C). In the other five sequences deceleration was evident in the frame prior to prey contact. Thus, deceleration began less than 10 ms prior to prey contact, and often less than 5 ms prior to prey contact. Once the tongue contacted the prey, it continued forward for a short distance before stopping and beginning retraction. In seven of our sequences peak projection distance occurred in the frame following prey contact and in the other five sequences it occurred in the second frame after prey contact. The time that is required for deceleration from unimpeded projection to maximum extension was therefore less than 20 ms.

Forward acceleration of the hyobranchial skeleton occurred simultaneously with tongue projection (Fig. 6A,D). During the first few frames of tongue projection, we were able to follow the posterior tip of the ceratobranchial as it slid anteriorly until it moved behind the vertex of the jaws and could no longer be seen. Movements of the ceratobranchial tip matched those of the tongue during this period (Fig. 6). Average maximum protraction velocity of the ceratobranchial was  $0.69 \text{ m s}^{-1}$  (Table 1).

Retraction of the tongue occurred more slowly than projection (Figs 5 and 6). Maximum velocity of tongue retraction was  $2.01 \text{ m s}^{-1}$  (Table 1) and was achieved at about 60–70 % of peak tongue extension. Typically, the tongue swung below the

Table 1. Summary statistics and F-ratios from two-way ANOVA results for 16 variables measured from kinematic profiles of two tongue distances in *Chamaeleo oustaleti*

Variable	20 cm (N=6)		35 cm (N=6)		ANOVA factors (degrees of freedom)		
	Mean	S.E.	Mean	S.E.	Distance (1, 1)	Individual (1, 8)	Interaction (1, 8)
	Maximum gape distance (cm)	3.12	0.075	3.46	0.052	5588.70*	3.13
Maximum head angle (degrees)	-11.87	2.038	-25.57	4.658	21525.08*	1.53	0.00
Maximum lower jaw angle (degrees)	-37.40	3.635	-53.58	2.710	11373.87*	3.02	0.01
Maximum hyoid retraction distance (cm)	5.22	0.056	5.23	0.078	0.03	0.05	1.15
Maximum tongue projection distance (cm)	20.23	0.638	34.87	0.842	484.11*	0.01	0.06
Time to onset of projection (s)	-0.043	0.002	-0.071	0.078	75.25	7.69*	1.23
Time to maximum gape (s)	0.323	0.014	0.389	0.039	1.11	24.39*	10.12*
Time to maximum head angle (s)	0.246	0.024	0.263	0.044	0.10	7.88*	2.03
Time to maximum lower jaw angle (s)	0.258	0.016	0.284	0.034	1.32	6.53*	0.53
Time to maximum hyoid retraction (s)	0.464	0.024	0.523	0.034	1.36	7.54*	0.09
Time to tongue retraction (s)	0.251	0.008	0.328	0.022	346.00*	1.11	0.03
Gape cycle time (s)	0.469	0.022	0.610	0.021	23.32	2.01	1.03
Maximum tongue projection velocity (ms <sup>-1</sup> )	4.897	0.205	5.825	0.112	2.80	8.02*	20.75*
Maximum tongue projection acceleration (ms <sup>-2</sup> )	392.767	17.357	486.000	16.08	2.42	0.01	14.29*
Maximum tongue retraction velocity (ms <sup>-1</sup> )	2.01	0.084	2.99	0.235	4.98	1.19	11.94*
Maximum hyoid protraction velocity (ms <sup>-1</sup> )	0.685	0.249	0.771	0.192	0.86	0.04	0.34

Sample sizes are three feedings at each distance from each of two individuals for a total of 12 sequences.

See text for definitions of the variables.

\*  $P < 0.05$ .

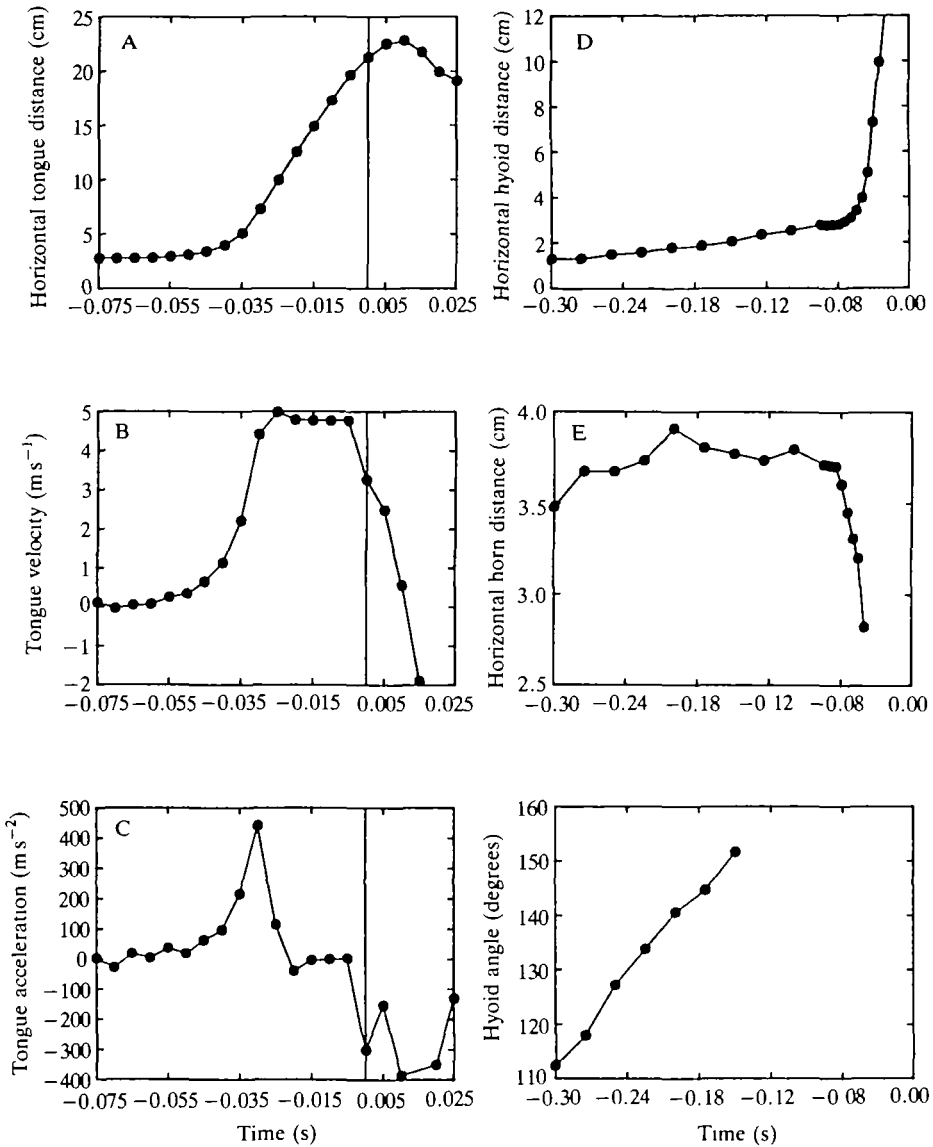


Fig. 6. Sample kinematic plots from one feeding event from *Chamaeleo oustaleti* feeding on a cricket held 20 cm in front of the animal. (A) The original displacement data for the tongue; (B,C) the derived velocity and acceleration values obtained by differentiating the distance data once and twice. Note that the time scales for the plots in the two columns are different. Horizontal horn distance (E) is the distance from the distal tip of the ceratobranchial to the vertex of the jaws. As the ceratobranchial is protracted this variable decreases. Note that the ceratobranchial is rapidly protracted at the onset of tongue projection. Time zero (vertical line in A–C) is the time of first contact of the tongue on the prey.

animal's head back towards the body, sometimes actually contacting the body, before it could be retracted into the mouth (Fig. 5E). The rate of tongue retraction did not change drastically until the tongue had swung behind the animal's head (Fig. 5E), indicating that the retractor muscle is being steadily shortened throughout most of the tongue retraction process. The average time required to retract the tongue back into the mouth was 251 ms (Table 1). Beginning 5–10 ms after the onset of tongue retraction, the gape increased continuously until it reached a maximum average value of 3.12 cm, an average of 323 ms following prey contact (Fig. 5B; Table 1). The gape then remained relatively constant for about 150 ms until it began to close as the tongue was pulled within the margin of the jaws. This opening of the gape that occurred during tongue retraction was accompanied by strong depression of both the head and the lower jaw (Fig. 5A,C). The peak change in head angle was  $-11.9^\circ$  and occurred 246 ms after prey contact (Table 1). Peak depression in lower jaw angle was  $-37.4^\circ$  occurring 258 ms after prey contact. Thus, peak gape occurred simultaneously with tongue retraction and about 80 ms after the head and lower jaw were maximally depressed.

As the tongue was retracted back onto the entoglossal process, the hyobranchial apparatus began to retract back into the mouth. Hyoid retraction began to be visible about 200 ms following prey contact (about 50 ms prior to peak gape and tongue retraction) and continued throughout the period of gape closing until an average maximum retraction of 5.22 cm was reached at an average of 464 ms after prey contact (Fig. 5; Table 1). As the hyoid was retracted, the ceratobranchial was returned to its near vertical position immediately behind the jaws. Typically, the prey item was not pulled all the way into the mouth but was immediately gripped in the closing jaws.

#### *Effects of projection distance on kinematics*

Summary statistics for the two projection distances and the results of two-way ANOVAs comparing them are listed in Table 1, and plots of the average kinematic profiles for five variables are presented in Fig. 7. Several of the 16 kinematic variable means reported in Table 1 revealed noteworthy differences between the 20 and 35 cm feeding events. However, only five variables showed significant differences between projection distances (Table 1).

The magnitudes of head and jaw movements were smaller in 20 cm feedings (Fig. 7). Maximum gape, maximum head angle and maximum lower jaw angle were all significantly larger in the 35 cm strikes (Table 1). The peak head and jaw angles that occur during tongue retraction were about  $14^\circ$  and  $16^\circ$ , respectively, larger in the longer feedings. In contrast, maximum hyoid retraction distance was nearly identical for the two distances.

All of the timing variable means were longer for the 35 cm feedings but none showed a significant distance effect in the ANOVAs except for the time to tongue retraction, which was longer in the longer strikes (Table 1). The time between the

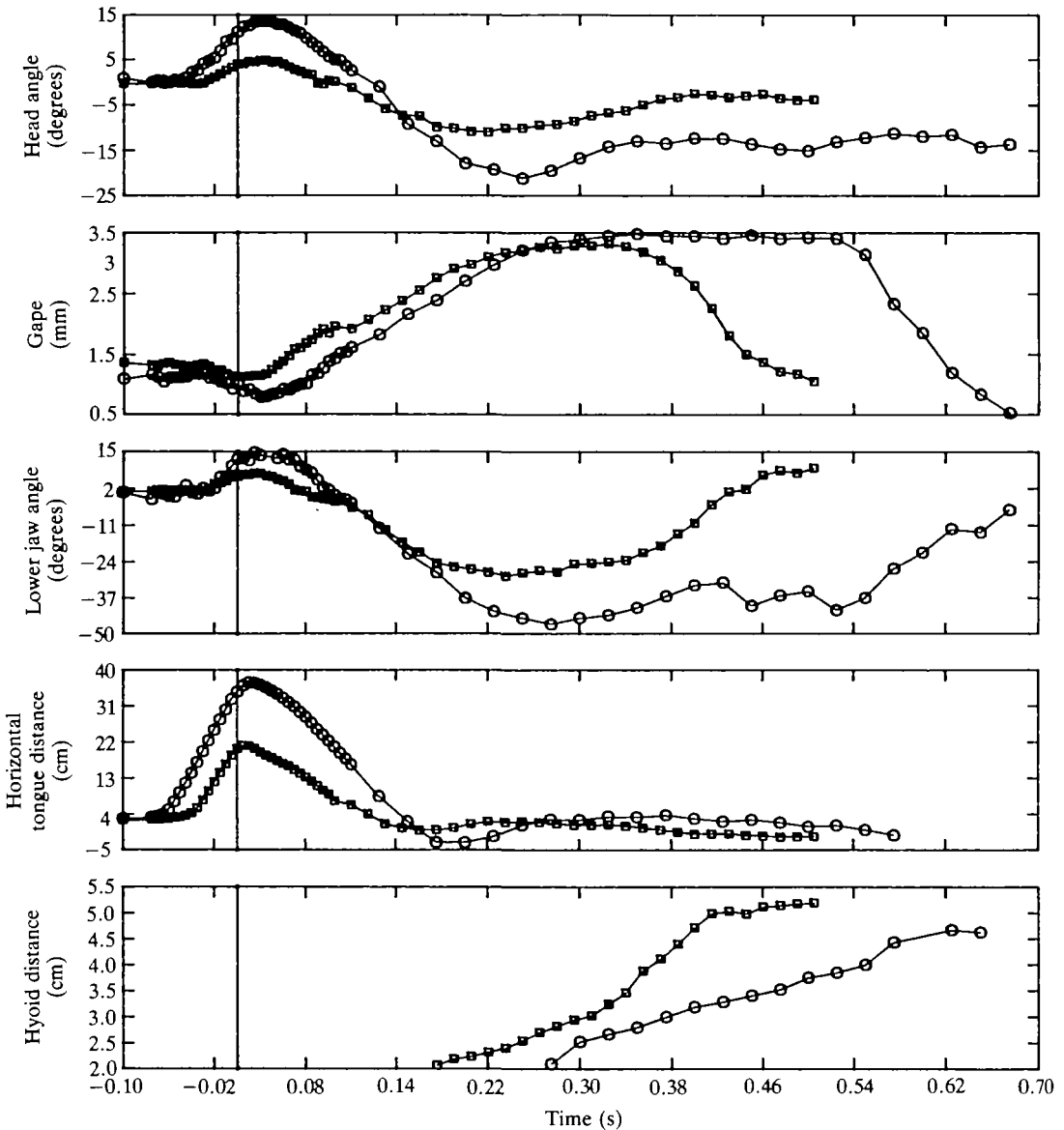


Fig. 7. Comparative plots of average values of five kinematic variables measured from two individual *Chamaeleo oustaleti* feeding on crickets from 20 cm ( $\square$ ) and 35 cm ( $\circ$ ). Plotted points are means for each time for three feeding events from each of two individuals for a total of six feeding events per point. Variables are defined in the text.

onset of tongue projection and prey contact was 43 ms for 20 cm strikes and 71 ms for 35 cm strikes, with no overlap in this variable for the two distance data sets. Average times to maximum head and lower jaw angle were similar for the two distances but time to peak gape was over 60 ms longer in the longer feedings. The

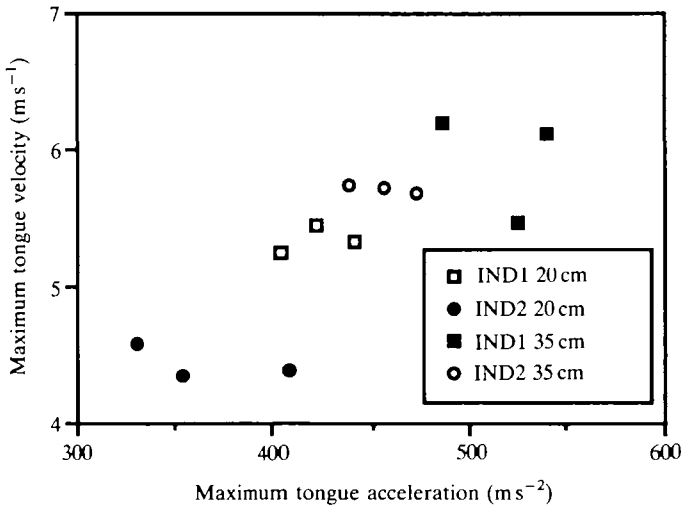


Fig. 8. Plot of maximum tongue projection velocity against maximum tongue acceleration for the 12 feeding events analyzed in this study. The correlation between the two variables is 0.81. Although 20 cm feedings tended to have lower velocity and acceleration than 35 cm feedings there was considerable individual variation and some overlap.

mean time to peak hyoid retraction was about 80 ms longer during the longer strikes.

Movements of the tongue were more rapid for the 35 cm feedings (Figs 7 and 8), though none of the velocity and acceleration variables showed significant distance effects in the ANOVAs. Average peak tongue projection velocity was  $5.8 \text{ m s}^{-1}$  in the 35 cm strikes and  $4.9 \text{ m s}^{-1}$  in the 20 cm strikes, suggesting that a real difference may exist. Maximum acceleration was  $486 \text{ m s}^{-2}$  for the longer distance and  $393 \text{ m s}^{-2}$  for the shorter distance. A plot of maximum projection velocity against maximum tongue acceleration for the 12 feedings events (Fig. 8) shows (1) that all of the 20 cm sequences were accomplished with lower velocity and all but one with lower acceleration than in 35 cm feeding, and (2) that there was a close relationship between these two variables (correlation=0.81). Retraction velocity was less than projection velocity for both distances but was higher ( $2.99 \text{ m s}^{-1}$ ) for the 35 cm strikes than for the 20 cm strikes ( $2.01 \text{ m s}^{-1}$ ). Average peak hyoid protraction velocity was slightly higher for the 35 cm strikes:  $0.77 \text{ m s}^{-1}$  vs  $0.69 \text{ m s}^{-1}$  for the 20 cm strike.

Six of the 16 kinematic variables showed significant variation between individuals and four variables exhibited significant interaction terms (Table 1). All of the 'time to maximum' variables varied between the two chameleons, as did maximum tongue projection velocity. A significant interaction term indicates that the effect of projection distance was not the same on the two individuals for that variable. This was the case for time to peak gape, and maximum tongue projection velocity and acceleration. Interestingly, the two individuals did not adjust



Table 2. Correlations of 15 kinematic variables with the first two principal components of a principal component analysis (PCA) conducted on the correlation matrix of these variables measured on 12 feedings

Variable	PC(1)	PC(2)
Time to tongue retraction	0.74	0.48
Maximum tongue projection velocity	0.78	0.33
Maximum tongue projection acceleration	0.92	0.06
Time to onset of projection	-0.92	-0.13
Maximum gape distance	0.65	0.58
Maximum head angle	0.48	0.76
Maximum lower jaw angle	0.61	0.68
Maximum hyoid protraction velocity	0.38	0.15
Maximum hyoid retraction distance	0.19	-0.11
Time to maximum head angle	0.40	-0.71
Time to maximum lower jaw angle	0.48	-0.78
Time to maximum gape	0.77	-0.60
Time to maximum hyoid retraction	0.39	-0.75
Gape cycle time	0.93	-0.64
Maximum tongue retraction velocity	0.84	-0.33
Variance explained (%)	40.6	30.0

See text for definitions of variables.

maximum velocity and acceleration of the tongue similarly in response to the distance that the tongue was projected (e.g. Fig. 8).

The principal component analysis factored the 15-variable correlation matrix and produced two factors that explained 70.6 % of the original variance (Table 2). Subsequent factors each explained less than 10 % of the original variance and are not discussed here. A plot of the factor scores for the 12 feeding events on the first two principal components reveals that complete separation between the two strike distances was achieved along the first principal component (Fig. 9). Most variables correlated highly and positively with the first principal component (40.6 % of the original variance; Table 2). This principal component clearly polarizes the feeding events for the two distances (Fig. 9) and the strong correlations among most of the variables indicate that this component contrasts feeding events that have high values for most variables with those that have low values. As discussed above, examination of the means for each distance shows that the 35 cm strikes generally have higher values for all variables than do the 20 cm strikes. The second principal component (30 % of the original variance) loadings show a contrast between feedings with high maximum gape, head angle and lower jaw angle and low times to peak gape, peak head angle, peak lower jaw angle, peak hyoid retraction and gape cycle time. Fig. 9 shows that this component does not distinguish the two distances, but rather that it separates the two individuals. At both distances one animal tended to have higher gape and jaw excursions and lower times to maximum values than did the second animal.

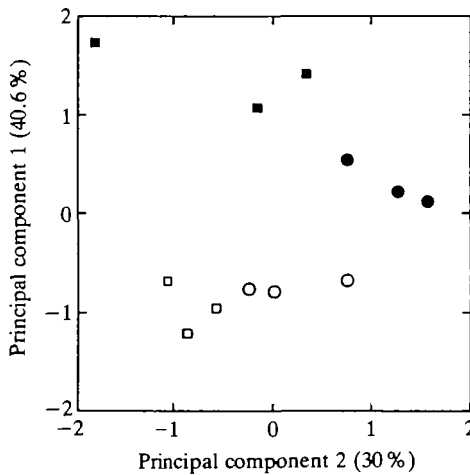


Fig. 9. Plot of factor scores of 12 feeding events on the first two principal components of a principal components analysis performed on the correlation matrix of 15 kinematic variables. Filled symbols are 35 cm feedings, open symbols are 20 cm feedings. Circles and squares indicate the different individuals. The first principal component completely separates the feeding events for the two distances, whereas the second principal component tends to distinguish between the two individuals.

### Discussion

In addition to providing a detailed, quantitative description of the kinematics of ballistic tongue projection in *C. oustaleti*, our analysis has produced three key results that have important implications for models of the mechanism of chameleon tongue projection. These results are (1) the hyoid accelerates forward simultaneously with the onset of tongue projection, (2) deceleration of the tongue from over  $5 \text{ m s}^{-1}$  to  $0 \text{ m s}^{-1}$  occurs in less than 15 ms, and (3) projection distance influences several aspects of strike kinematics. Below we discuss each of these results and their implications for understanding chameleon tongue function.

#### *Role of the hyoid during tongue projection*

Previously published data on strike kinematics in chameleons have focused mostly on movements of the jaws and tongue (Altevogt and Altevogt, 1954; Bell, 1990), though some data are available for hyobranchial movements (Bels and Baltus, 1987). The role of the hyoid during tongue projection has been much debated in the literature with some models suggesting that movements of the hyoid alone power acceleration of the tongue (Duvernoy, 1836; Kathariner, 1894), and other authors speculating that rapid anterior movements of the hyobranchial apparatus were not involved in launching the tongue (Gnanamuthu, 1930; Gans, 1967). Zoond (1933) demonstrated the primary role of the accelerator muscle in generating propulsive forces, and Brücke (1852), Zoond (1933) and Altevogt and Altevogt (1954) have all proposed that anterior movements of the hyoid *assist* the

accelerator muscle in facilitating tongue projection, though none was able to provide data in support of this hypothesis.

Our observations on the movements of the posterior tip of the ceratobranchial show clearly that rapid hyobranchial protraction accompanies the onset of tongue projection (Fig. 6). Thus, the tongue is projected from an already moving platform that may impart its momentum to the tongue as the accelerator forces the tongue off the entoglossal process. The added acceleration and velocity that could be provided by this mechanism are considerable. Our measures of peak hyoid protraction velocity exceeded  $0.75 \text{ m s}^{-1}$ , compared to the average peak tongue velocity of  $5.8 \text{ m s}^{-1}$ . Further, our measures of hyoid velocity may underestimate actual maximum values. In our films the ceratobranchial bulged laterally through the skin of the throat region and could be followed only until it slid anteriorly behind the vertex of the jaws. As the hyoid was accelerating when it slid behind the jaws, it is likely that our estimates of maximum hyoid protraction velocity actually underestimate peak values.

The most likely agents of hyoid protraction are the paired medial and lateral geniohyoideus muscles that attach the anterior region of the lower jaws to the base of the entoglossal process and the ceratobranchials (Fig. 1). The role of these muscles during hyoid protraction could be tested with electromyographic recordings made during tongue projection.

The only previously published data on hyobranchial movements during chameleon feeding are for *C. dilepis* (Bels and Baltus, 1987; Fig. 2a). These authors describe *retraction* of the hyoid beginning with the onset of tongue projection and continuing throughout tongue projection and retraction until it is fully retracted shortly after the onset of gape closing. This observation is strikingly different from the pattern we observed in which the hyoid is *protracted* rapidly during early tongue projection (Fig. 6E). We were unable to follow the hyoid during the period of prey contact and initial hyoid retraction, but beginning about 150 ms before return of the tongue to the mouth, the hyoid reappears behind the jaw vertex and rapidly retracts, not reaching peak retraction until 464 ms after prey contact, just before the gape is closed (Fig. 5). Further, we have recorded high-speed videos ( $200 \text{ fields s}^{-1}$ ) of tongue projection in *C. dilepis* and several other species (*C. jacksonii*, *C. parsoni* and *C. schubotzi*) and have noted rapid hyoid protraction at the time of tongue projection in all species. We have not seen the pattern described by Bels and Baltus (1987). We therefore propose that simultaneous hyoid protraction and tongue projection is a general feature of the chameleon feeding mechanism.

#### *Control of projection distance*

Previous work has shown an effect of projection distance on maximum projection velocity of the tongue (Bell, 1990). Bell found that the maximum velocity in two *C. zeylanicus* was positively related to projection distance, but that values of maximum velocity varied by a factor of 2 at any given projection distance. Similarly, we found that the average maximum velocity and maximum

acceleration of the tongue at 20 cm were less than those at 35 cm (Fig. 8), though these differences were not significant in the ANOVAs (see below for a discussion of ANOVA results), suggesting that *C. oustaleti* can alter the force that is used to power tongue projection in response to the distance to the prey. Modulation of activity in the accelerator muscle or possibly the geniohyoideus muscles could be used to control tongue acceleration and velocity. If this is the case, then one would expect electromyographic recordings to reveal a positive correlation between electrical activity in the accelerator muscle and projection distance.

In our films, once the tongue reached maximum velocity, there was little change in velocity until immediately prior to prey contact (Fig. 6B). In the 20 cm feeding events the tongue changed from near its peak forward velocity of  $4.9 \text{ m s}^{-1}$  to the beginning of retractor shortening in less than 15 ms. We concur with Bell (1990) that this rapid deceleration and reversal of the direction of tongue movement is probably due to contraction of the retractor muscles. It is important to emphasize that the tongue was not stopped by the prey item, as the crickets in our experiments were held lightly in a clip and offered minimal resistance to the approaching tongue. Also, analyses of events in which the tongue missed the prey (Bell, 1990) have shown that the same pattern of tongue deceleration occurs regardless of whether prey contact occurs. These observations imply that chameleons use visual cues to judge distance to the prey and implement temporal control of contraction of the retractor muscles, a hypothesis that has been supported by experimental manipulations of the apparent distance to the prey (Harkness, 1977). The proposed role of the retractor muscles during tongue deceleration could be tested by recording electrical signals from these muscles during the strike in conjunction with an analysis of the muscle's contractile properties during lengthening.

In summary, our results are generally in agreement with Bell (1990) in finding that the distance of tongue projection is primarily controlled by the apparent timing of hyoglossi muscle activity. In all instances, the tongue is brought very sharply to a stop, and clearly does not gradually slow as it approaches the prey (Figs 5 and 6). Harkness (1977) has shown that distance is judged visually. Chameleons may also alter projection velocity and acceleration in response to the distance to the prey, though this relationship is not precise in *C. oustaleti* (Fig. 8) or in *C. zeylanicus* (see Fig. 6 in Bell, 1990) and may be strongly influenced by factors such as motivation, satiation and body temperature.

#### *Effects of projection distance on kinematics*

Though most kinematic variables conformed to a trend of less extensive movements and shorter times to maximum values in the shorter 20 cm strikes, only five of the 16 variables showed a significant distance effect in the ANOVAs. In our two-way ANOVAs the significance tests for the distance effect had 1, 1 degrees of freedom. Such low degrees of freedom are partly due to the presence of the mean square for the interaction term in the denominator of the F-ratio and indicate that this is not a powerful experimental design for testing distance effects. Because of

this difficulty in interpreting the ANOVA results, we do not rely entirely on them for testing distance effects, but prefer to view the ANOVA results in combination with the PCA when determining trends.

Our analysis suggests that most kinematic features of the strike in *C. oustaleti* are affected by projection distance. *C. oustaleti* modulates the kinematics of prey capture in response to the distance that the tongue must be projected to capture the prey. A distinct trend was found in which the 20 cm feeding events were more rapid and generally involved less extensive movements than the longer 35 cm strikes (Table 1; Fig. 7). This interpretation is supported by the principal component analysis, which revealed complete separation of the two distances along the first principal component (Fig. 9). Most variables were highly correlated with the first principal component, indicating that this factor contrasts those feeding events with high values for most variables with those that had low values.

All phases of the strike covered in our analysis conform to this trend. Tongue projection took an average of 71 ms in the 35 cm feeding events and 43 ms in the 20 cm feeding events, and, although the ANOVA showed no significant difference between the two distances ( $F$ -ratio=72.25), the values of this variable were completely non-overlapping in the six 20 cm and six 35 cm strikes. Tongue retraction time and time to maximum hyoid retraction tended to be shorter in the 20 cm feeding events, though there was considerable variation in both (Table 1). Velocity and acceleration of the tongue were higher in the longer strikes (Fig. 8).

During tongue retraction the tongue swings below and behind the head and during this time peak gape is reached. Following the longer strikes the tongue tended to exhibit greater movements, requiring the head and jaws to be more greatly depressed and the gape to be wider. The more extensive movements of the head and jaws during retraction in the longer strikes were the most distinct effects of projection distance (Table 1).

As noted above, previous work has shown that *C. zeylanicus* modulates tongue projection velocity in response to the distance to the prey (Bell, 1990). Our results confirm this result for *C. oustaleti* and further demonstrate the ability of this species to modulate the kinematics of other stages of prey capture when feeding on prey held at a variable distance. This is the first quantitative demonstration of modulation of prey capture kinematics in a lizard in response to the position of the prey.

Several recent studies have found that individual animals often vary significantly in the kinematics of prey capture (Shaffer and Lauder, 1985a; Kraklau, 1990; Reilly and Lauder, 1990) or in the motor pattern used during prey capture (Shaffer and Lauder, 1985b; Sanderson, 1988; Reilly and Lauder, 1989, 1991; Wainwright *et al.* 1989). In our analysis, significant differences were found among individuals in six of the 16 kinematic variables (Table 1). In the PCA most of these variables were strongly correlated with the second principal component, which almost completely separated the feeding events from the two individuals (Fig. 9). Increasingly, it appears that significant differences among individuals in the kinematics and motor patterns of prey capture and processing is a general feature

of vertebrate feeding mechanisms. Such intraspecific variation could underlie differences in feeding performance and, ultimately, the fitness of animals. However, no attempt has yet been made to relate individual variation in functional variables of the type reported here to feeding performance, nor have the repeatability or heritability of these differences been demonstrated. Such work will be necessary in attempts to determine the consequences of individual variation in patterns of feeding behavior, like that reported here, for individual fitness (Arnold, 1983; Emerson and Arnold, 1989).

#### *Comparative prey capture kinematics*

Published kinematic profiles and descriptions of two other chameleon species (Bels and Baltus, 1987; Bell, 1990) show gape and tongue profiles that are very similar to our findings for *C. oustaleti*. Details such as (1) the slight closing of the gape immediately following the onset of tongue projection, (2) the swinging of the tongue behind the head during tongue retraction, and (3) the occurrence of peak gape immediately prior to the return of the tongue into the mouth have been described in *C. zeylanicus* (Bell, 1990) and *C. dilepis* (Bels and Baltus, 1987). The only discrepancy between our results and those available for other chameleon species concerns the movements of the hyobranchial structures reported by Bels and Baltus (1987) and discussed above.

Interest in the evolutionary origins of the chameleon feeding mechanism has led several authors to note the similarities in anatomy and general kinematics of feeding between chameleons and agamid lizards (Gnanamuthu, 1930; Schwenk and Bell, 1988; Smith, 1988; Schwenk and Throckmorton, 1989). Together with the Iguanidae, the Chamaeleonidae and Agamidae constitute the monophyletic Iguania (Estes *et al.* 1988; Schwenk, 1988). The agamids are believed to be the sister group to Chamaeleonidae (Estes *et al.* 1988), making the condition of the feeding mechanism in this group the most likely representative of the more generalized condition from which the highly specialized chameleon feeding apparatus evolved. Only recently, however, have enough kinematic data on chameleons and agamid species become available to make comparisons based on more rigorous analyses. Gape, tongue and head movements were documented in the agamids *Uromastix aegyptius* and *Phrynocephalus helioscopus* (Schwenk and Throckmorton, 1989) and these and several other variables have been measured in *Agama agama* (Kraklau, 1990).

Several noteworthy similarities and differences exist between the kinematic profiles of the chameleon strike and those of the three agamid species. Like *C. oustaleti*, all three agamids exhibit a prolonged period of gradual jaw opening that ends with a period of tongue protraction. In all three agamids and the chameleon, prey are contacted and apprehended by the tongue at peak tongue protraction, prior to peak gape. Also, complete retraction of the tongue back into the mouth occurs shortly after peak gape, though it may occur longer after peak gape in *C. oustaleti* than in the agamids. Thus, as noted by Schwenk and Bell (1988) and Bell (1990), tongue protrusion and prey contact occur at a similar stage

of the feeding cycle, the latter part of what has been termed 'slow opening' (Bramble and Wake, 1985), or that time immediately prior to fast opening of the gape. It is clear that *C. oustaleti* and these agamids share many key features of the gape and tongue profiles during the strike.

The key difference between the strike in *C. oustaleti* and that in the agamids is the mechanism used to move the tongue tip the last few centimeters before prey contact. In *C. oustaleti* this movement is accomplished by ballistic tongue projection. Agamids lack the ability to project the tongue completely off the hyobranchial apparatus and instead rely on lunging with the body to move the tongue tip towards the prey (Schwenk and Throckmorton, 1989; Kraklau, 1990). The advantage gained by tongue projection in *C. oustaleti* is that the tongue can be moved 35 cm in just over 71 ms, while *Agama agama* may cover only 3 cm in about 50 ms. Hence, not only will the velocity of the tongue approaching the prey be greater in the chameleon but the distance covered during the strike is greater as well.

In addition to the novel mechanism of tongue projection, *C. oustaleti* also exhibits modifications of the gape cycle during and after tongue projection. Agamids show no evidence of the distinct decrease in gape seen during tongue projection in *C. oustaleti* (Figs 5 and 6); instead, the gape is stationary or slowly increases during the lunge (Schwenk and Throckmorton, 1989; Kraklau, 1990). During tongue retraction the head and jaws of *C. oustaleti* are strongly depressed as the tongue swings below and behind the head. In contrast, the head is elevated during tongue retraction in the three agamid taxa as the animal recovers from its anteroventral lunge. Additional details that may differ between chameleons and agamids, but for which there are no comparative data, are the movements of the hyobranchial skeleton. The unfolding during tongue protraction and rapid protraction at the onset of projection in *C. oustaleti* may be novel features of the chameleon strike not shared by agamids. In summary, though numerous features of strike kinematics are shared by the agamids and *C. oustaleti*, there are also several aspects unique to the chameleon.

Although chameleons are the only lizards known to exhibit ballistic tongue projection, this behavior has evolved independently in plethodontid salamanders (Lombard and Wake, 1976; Bramble and Wake, 1985). The functional mechanism of tongue projection in plethodontids is quite different from that in chameleons (Lombard and Wake, 1976, 1977), but recently published kinematic data permit qualitative comparisons of the gape and tongue profiles of *C. oustaleti* with results obtained for *Bolitoglossa occidentalis* (Larsen *et al.* 1989).

As described above for *C. oustaleti* and the three agamid taxa, the strike of *B. occidentalis* involves an initial period of jaw opening, followed by more rapid jaw opening and jaw closing (Larsen *et al.* 1989). At the end of the initial period of jaw opening the tongue is projected towards and contacts the prey. As in *C. oustaleti*, no body lunge occurs and prey contact is followed by tongue retraction and peak gape. Also as in *C. oustaleti*, the tongue is fully retracted well before peak gape is achieved. Differences between this salamander and the

chameleon are the lack of gape decrease during tongue projection and strong head and jaw depression during tongue retraction. Overall, the strike kinematics of *B. occidentalis* are more similar to those described for the three agamids, with the primary difference being the replacement of a body lunge in the salamander with projection of the tongue up to one head length beyond the gape.

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