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FEEDING KINEMATICS OF PHYLLOMEDUSINE TREE FROGS

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Summary

Previous studies have demonstrated that the phyllomedusine hylids possess highly protrusible tongues, a derived characteristic within the family Hylidae. In the present study, the kinematics of the feeding behavior of a phyllomedusine species, *Pachymedusa dacnicolor*, was analyzed using high-speed video (180 frames s^{-1}). Its behavior was compared with that of *Hyla cinerea*, a species with a weakly protrusible tongue. *P. dacnicolor* exhibits a faster rate of tongue protraction, a longer gape cycle and more variable feeding kinematics than *H. cinerea*. In addition, the tongue is used in a unique 'fly-swatter' fashion, to pin the prey to the substratum as the frog completes the lunge. The rapid tongue protraction, extended gape cycle and fly-swatter action may have evolved in response to a diet of large, rapidly moving insects. In addition, several duration variables of the feeding cycle were greater for misses than for captures and drops, which suggests that sensory feedback rather than biomechanics controls gape cycle duration.

Key words: kinematics, feeding behavior, phylomedusine, tongue protraction, treefrog, *Hyla cinerea*, *Pachymedusa dacnicolor*.

Introduction

Recent work on the morphology and kinematics of anuran prey-capture systems has led to the formulation of hypotheses regarding their evolutionary transformations (Emerson, 1985; Nishikawa and Cannatella, 1991; Nishikawa and Roth, 1991; Deban and Nishikawa, 1992; Nishikawa *et al.* 1992; Anderson, 1993; Valdez and Nishikawa, 1993). These studies suggest that several morphological and behavioral traits are plesiomorphic: (1) a tongue of limited protrusibility (less than 60 % of jaw length at maximum extension); (2) a whole-body lunge; (3) head ventroflexion and arching of the body; and (4) jaw prehension. Highly protrusible tongues (greater than 70 % of jaw length at maximum extension) have evolved several times independently among frogs. Behavioral transitions that accompany derived tongue morphology in *Bufo* and *Rana* include the use of the tongue to retrieve the prey and a reduction of the lunge and ventroflexion (Nishikawa *et al.* 1992; Anderson, 1993). Consequently, the head is maintained in a stable position. This stability appears to allow greater coordination of head and tongue movements, which may permit an increase in the precision of prey capture (Nishikawa *et al.* 1992). A similar trend is seen in salamanders, in which primitive species lunge whereas derived species, with highly protrusible tongues, do not (Larsen *et al.* 1989).

Within the treefrog family Hylidae, tongue morphology has been examined in all four subfamilies, including one species of Hemiphractinae, five genera and ten species of Hylinae, two genera and five species of Pelodryadinae, and three genera and three species of Phyllomedusinae (Deban and Nishikawa, 1992; L. A. Gray, K. C. Nishikawa and J. C. O'Reilly, unpublished results). Species within the Hylinae, Hemiphractinae and Pelodryadinae have retained the plesiomorphic tongue morphology and prey-capture behavior patterns (Deban and Nishikawa, 1992). In contrast, phyllomedusines have evolved highly protrusible tongues (Deban and Nishikawa, 1992). However, little is known about the feeding behavior of phyllomedusines.

In addition, there is conflicting evidence in the literature regarding the method of control of the timing of tongue and jaw movements during amphibian feeding. Several kinematic studies (Nishikawa and Cannatella, 1991; Nishikawa and Roth, 1991; Deban and Nishikawa, 1992) and a neurological study (Matsushima *et al.* 1988) support the hypothesis that somatosensory feedback plays a role in controlling the timing of tongue and jaw movements. However, these studies do not rule out the possibility that such events are influenced by biomechanical adjustments in response to the increased mass of the tongue due to adhering prey in capture sequences. Indeed, biomechanical adjustments have been found to cause differences in some kinematic events between successful and unsuccessful prey-capture attempts in the salamander *Bolitoglossa occidentalis* (Larsen *et al.* 1989).

In this study, we investigated feeding kinematics in *Pachymedusa dacnicolor* (a phyllomedusine) and compared it with that of *Hyla cinerea* (a hyline). Our goal was to determine whether the evolution of a highly protrusible tongue within the Hylidae is associated with the acquisition of feeding behavior patterns that are typical of frogs with independently derived, highly protrusible tongues. We also investigated the method of control in the timing of tongue and jaw movements for feeding sequences of *P. dacnicolor*. To achieve this goal, the kinematics of capture sequences was compared with sequences in which the tongue contacts the prey but does not move the prey or capture it (here called drop sequences) and with sequences in which the tongue does not contact the prey (miss sequences). By comparing captures, drops and misses, we determined whether somatosensory input or biomechanics is responsible for the timing of tongue and jaw movement. In drops and misses, there is no increased mass on the tongue. If kinematic differences between drops and misses are found, the likely cause is sensory input that is present only in drops and captures. If there are no differences between drops and misses, but captures are different from both, then biomechanics is more likely to have a role in the timing of these events. Previous studies have not used the distinction between drops and misses to examine this question.

Materials and methods

The feeding behavior of seven *Pachymedusa dacnicolor* Cope was videotaped and analyzed. Capture sequences were compared with published data for a short-tongued hylid *Hyla cinerea* (Schneider) (Deban and Nishikawa, 1992). In addition, capture sequences were compared with drop and miss sequences. Forty-eight feeding sequences were analyzed, comprising 19 captures, 13 drops and 16 misses. The numbers of feeding sequences per individual were 3, 3, 3, 3, 3, 2, 2 for captures, 3, 3, 3, 2, 0, 1, 1 for drops and 3, 3, 3, 1, 2, 2, 2 for misses.

Videotaping and digitizing

Frogs were videotaped between 15 December 1992 and 15 July 1993, using a display Integration Technologies model DIT 660 high-speed, multiframing video camera with synchronized stroboscopic illumination. All sequences were filmed at 180 frames s^{-1} at room temperature (20–24˚C).

Frogs were filmed eating waxworms (*Galleria* sp.) from a lateral position. To videotape a sequence for *P. dacnicolor*, the frog was placed on a stage perpendicular to the camera (90±10 ˚) on a damp paper towel substratum. A background of 1 cm squares was used for scaling and aspect ratio correction. A waxworm was placed facing towards the frog, approximately 5 cm directly in front of it, and was nudged to elicit forward movement to attract the frog's attention. This method has been used successfully in previous studies and has been shown to reduce turning and head tilting (Deban and Nishikawa, 1992).

Video analysis

Video sequences were analyzed with Peak Performance Technologies two-dimensional motion analysis software. Every frame was analyzed for each sequence from the beginning of forward head movement until mouth closure. On each frame, 10 points on the head, two points on the prey item and a non-moving reference point were digitized from the video monitor. Most variables were chosen on the basis of previous studies (Nishikawa and Cannatella, 1991; Deban and Nishikawa, 1992; Nishikawa and Roth, 1991) and were calculated in the same manner. The following kinematic variables were analyzed: (1) duration of approach (time at prey contact minus time of first forward head movement); (2) duration of mouth opening (time at the beginning of the gape plateau minus time of onset of mouth opening); (3) duration of gape plateau (time at onset of mouth closing minus time at onset of gape plateau); (4) duration of tongue protraction (time at maximum tongue reach minus time at onset of tongue retraction); (5) duration of mouth closing (time at completion of mouth closing minus time at onset of mouth closing); and (6) duration of body recovery (time at completion of mouth closing minus time at maximum forward excursion). In addition, the following variables were calculated directly from digitized points: (1) maximum gape angle (the angle formed by the upper and lower jaws); (2) minimum mandible angle (the ventral angle formed by the jaw joint and lower jaw tip, with the mentomeckelian joint at the vertex); (3) distance to prey (the distance from the upper jaw tip to the nearest point on the prey); and (4) maximum tongue reach (the maximum tongue protrusion divided by the jaw length).

The gape plateau is a variable that is not found in previous studies. It is included in the present study because phyllomedusines exhibit an extended plateau in the gape profile. In other anuran species, the onset of mouth closing begins shortly after the mouth is fully opened. Usually, there is only a small plateau, or no plateau, in the gape profiles (Nishikawa and Cannatella, 1991; Nishikawa and Roth, 1991; Deban and Nishikawa, 1992). Tongue retraction variables were not included in the present study because the onset and completion of tongue retraction were difficult to determine for two reasons: (1) the tongue was often forced back into the mouth passively as the frog completed its lunge, and (2) the tongue was often partially obscured by the foreleg during retraction.

Statistical analysis

All comparisons were made with analysis of variance (ANOVA). A two-way ANOVA was used to compare kinematic variables among success categories for *P. dacnicolor*. The factors were individual (random) and success category (fixed). Thus, the individual × success interaction was used as the denominator mean square to test for differences among success categories (Sokal and Rohlf, 1981). To compare *P. dacnicolor* and *H. cinerea*, a one-way ANOVA was used, in which individual was nested within species. In this analysis, however, only eight variables were compared because the two others (duration of gape plateau and duration of recovery) were not available in the literature for *H. cinerea* (Deban and Nishikawa, 1992).

Because multiple variables were used in both comparisons, a sequential Bonferroni correction (Rice, 1989) was used to adjust the significance levels to $P=\alpha/(k-i)$ (where k is the number of variables and i is the rank for a given P value). *A posteriori* multiple comparisons were made with Student–Newman–Keuls tests ($P=0.05$; Sokal and Rohlf, 1981). Data were analyzed using Statview II and SuperAnova on a Macintosh computer.

Results

Kinematics of feeding behavior in Pachymedusa dacnicolor

Selected feeding sequences for *P. dacnicolor* are shown in Figs 1 and 2. As found for other frogs (Nishikawa and Cannatella, 1991; Nishikawa and Roth, 1991), the general feeding pattern of *P. dacnicolor* involves movements of the body (lunge and recovery), jaws (opening and closing) and tongue (protraction, prey contact and retraction). The entire capture sequence takes an average of 265±16.0 ms.

The prey-capture sequence begins with a forward lunge. The frog first detaches its hind toes from the substratum and then rotates forward on its forelimbs, initiating the onset of head movement. The time of first forward head movement is somewhat variable, depending on lunge length ($r=0.74$, $P<0.05$), but occurs on average 50±6.3 ms before the onset of mouth opening. The forelimbs leave the substratum as the long hindlimbs extend to propel the frog forward. The average lunge length is 2.2±0.4 cm (Fig. 3A) but varies with prey distance ($r=0.92$, $P<0.0001$). Maximum forward excursion occurs, on average, 139±12.2 ms after prey contact. The hind toes usually remain in contact with the substratum until the feeding sequence is complete, at which time the legs are pulled forward, one at a time, and folded back under the body.

Mouth opening and tongue protraction occur during the lunge. As the mouth opens, the mandible bends downward at the mentomeckelian joint and reaches a minimum angle (maximum bend) of 148±2.7 ° (Table 1) at 64±12.2 ms. The mouth opens in 50±4.4 ms on average, and it remains fully opened for 115±2.5 ms (Table 1; Fig. 3B,C). The tongue begins to protract at 2±0.5 ms (relative to the onset of mouth opening at $t=0$) and reaches an average maximum protraction of 1.2±0.1 cm (Table 1; Fig. 3D) at 9±0.6 ms. The prey is contacted 10±2.0 ms after the onset of mouth opening, as the tongue reaches maximum extension or shortly thereafter. Relative tongue length of *P. dacnicolor* is 1.57 (maximum tongue length 2.0 cm, jaw length 1.04 cm; measured on one

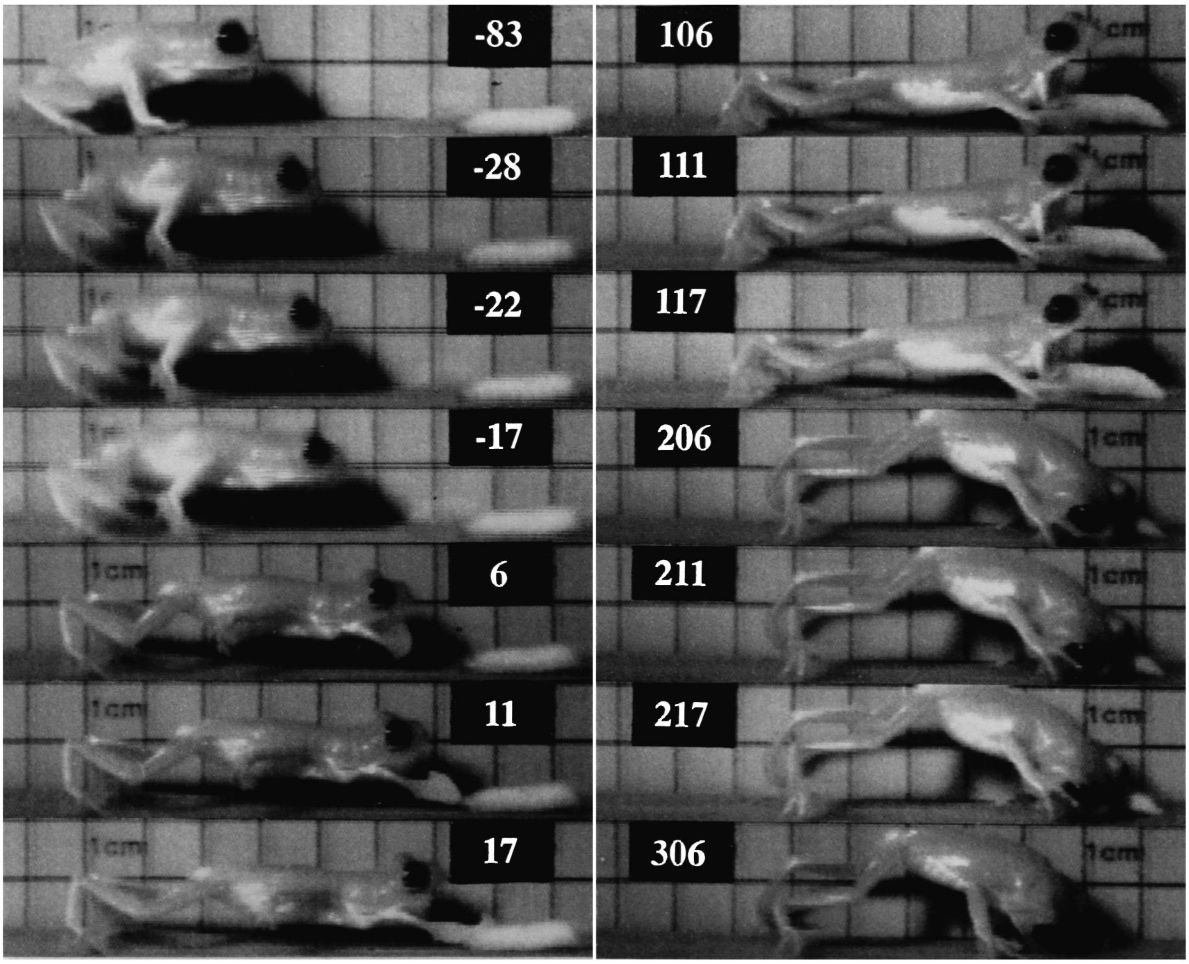

Fig. 1. Selected frames from a typical feeding sequence for *Pachymedusa dacnicolor*. Note the extended lunge, the ‘fly-swatter’ action of the tongue, ventroflexion of the craniovertebral joint and jaw prehension. Time (in ms) is indicated on each frame.

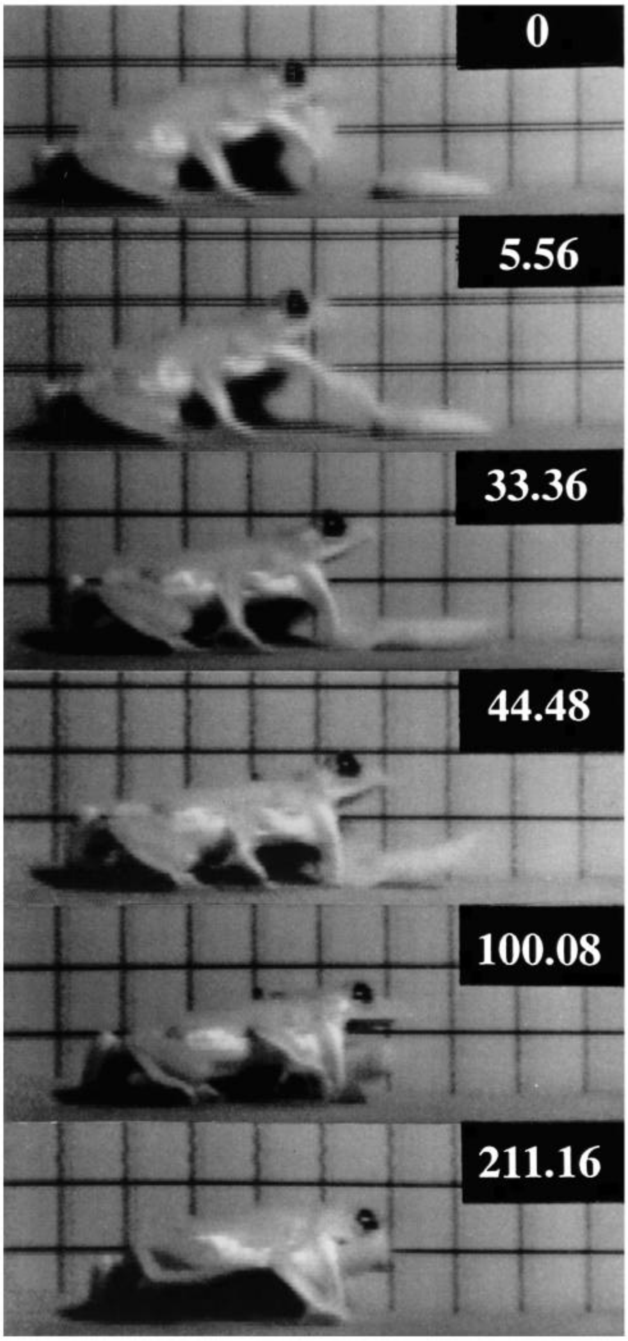

Fig. 2. Selected frames from a feeding sequence for *Pachymedusa dacnicolor* in which the tongue retrieves the prey and ventroflexion and jaw prehension are absent. Time (in ms) is indicated on each frame. Background grid is 1 cm squares.

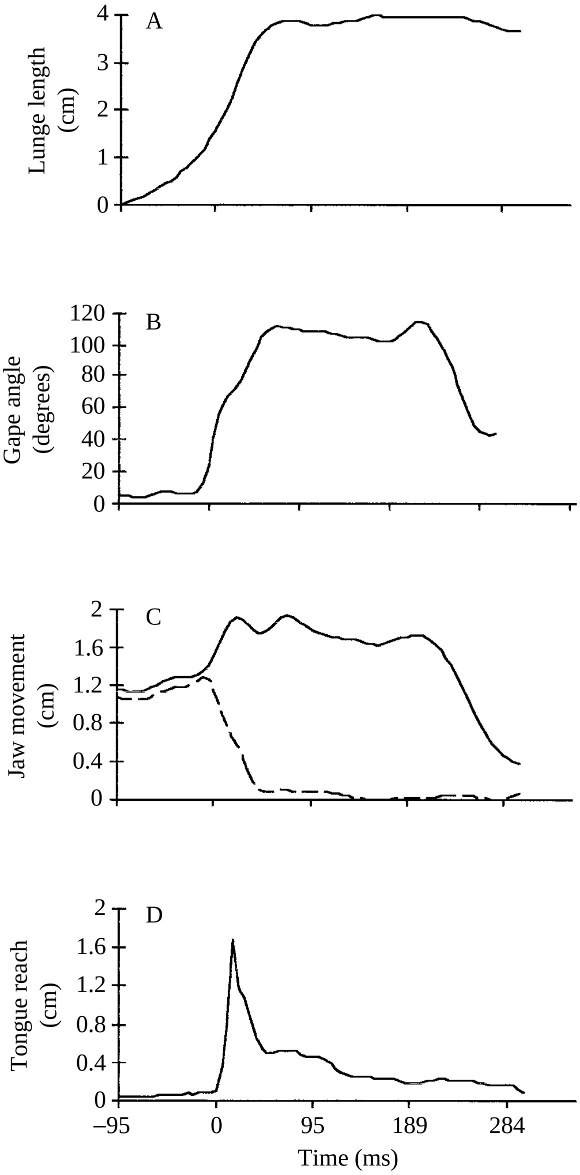

Fig. 3. Four kinematic profiles for a ‘typical’ feeding sequence for *Pachymedusa dacnicolor*. (A) Forward movement of the body. (B) The gape profile (note the rapid mouth opening and closing, and the extended plateau). (C) Movements of the upper (solid line) and lower (dashed line) jaws. (D) Tongue movements. The average duration of capture feeding sequences is 265 ms (range 139–400 ms). Because profiles vary in shape, an ‘average’ sequence with error bars is not illustrated.

specimen). The average maximum gape distance is 1.7±0.1 cm, and the average maximum gape angle is 116±2.9 °. The duration of mouth closure (56±4.5 ms) is about the same as the duration of mouth opening (50±4.4 ms).

P. dacnicolor exhibits variable feeding kinematics. Generally the craniovertebral joint is ventroflexed and the back is arched as the mouth closes over the prey (Fig. 1), but ventroflexion and arching may be reduced or absent (Fig. 2). The duration of the gape cycle may also be reduced, and the lunge is of variable length. In addition, in 45 out of 48 sequences, the tongue acts as a ‘fly-swatter’, reaching the prey ahead of the mouth and pinning it to the substratum as the frog completes the lunge (Fig. 1). However, in three sequences the fly-swatter action of the tongue is absent. In these sequences, the tongue adheres to the prey and then flips it up into the mouth (Fig. 2).

Table 1. *Kinematic variables for 'capture' (*N*=19), 'drop' (*N*=13) and 'miss' (*N*=16) feeding sequences of* Pachymedusa dacnicolor

Variable	Capture	Drop	Miss	*F*	*Post hoc* comparison
Duration of approach (ms)	183±12.5	194±18.4	213±21.7	0.441	
Duration of mouth opening (ms)	50±4.4	46±5.5	51±3.8	4.763	
Duration of gape plateau (ms)	115±12.5	154±15.3	339±55.5	9.144*	C=D<M
Duration of tongue protraction (ms)	7±0.6	8±0.8	7±0.7	0.04	
Duration of mouth closing (ms)	56±4.5	70±7.1	88±12.8	3.517	
Duration of body recovery (ms)	88±13.7	136±24.3	334±62.1	10.851*	C=D<M
Maximum gape angle (degrees)	116±2.9	117±2.3	123±3.0	0.945	
Minimum mandible angle (degrees)	148±2.7	159±3.8	156±2.1	6.386	
Distance to prey (cm)	1.9±0.3	2.8±0.5	4.2±0.3	6.019	
Maximum tongue reach (cm)	1.2±0.1	1.2±0.1	1.4±0.1	2.92	

*Significant difference at $P\leqslant 0.05$ (Bonferoni-corrected).

Values are means ± s.e.m. for each variable.

Also shown are *F* values from ANOVA comparing success categories.

C, capture; D, drop; M, miss.

Table 2. *Kinematic variables taken from Deban and Nishikawa (1992) for capture sequences of* Hyla cinerea *(*N*=12)*

Variable	Mean	*F*
Duration of mouth opening (ms)	57±4.1	1.15
Duration of feeding sequence (ms)	152±8.1	93.01*
Duration of tongue protraction (ms)	37±3.3	36.5*
Duration of mouth closing (ms)	68±4.3	2.33
Maximum gape angle (degrees)	79±2.2	135.9*
Minimum mandible angle (degrees)	155±1.0	6.79
Distance to prey (cm)	2.5±0.2	4.3
Maximum tongue reach (cm)	0.3±0.02	577.6*

*Significant difference at $P\leqslant 0.05$ (Bonferroni-corrected).

Mean values ± s.e.m. are given for each variable.

Also shown are *F* values from ANOVA comparing *Hyla cinerea* with *Pachymedusa dacnicolor*.

All times are relative to the onset of mouth opening (t=0).

Comparisons between P. dacnicolor *and* H. cinerea

There appear to be fundamental differences in feeding kinematics between the long-tongued *P. dacnicolor* and the short-tongued *H. cinerea* (Table 2). Both species launch the entire body at the prey, but only *P. dacnicolor* uses the tongue as a fly-swatter. In *H. cinerea*, the tongue is protruded only a short distance beyond the tip of the jaw, it remains in contact with the prey for only 32 ms (Deban and Nishikawa, 1992) and jaw prehension is used to bring the prey into the mouth. In addition, *H. cinerea* exhibits a gape profile which is similar to that of *Bufo* and archeobatrachian species (Deban and Nishikawa, 1992; Nishikawa *et al.* 1992), but very different from that of *P. dacnicolor*. *H. cinerea* opens and closes its mouth at a similar rate to *P. dacnicolor*, but it does not maintain its mouth fully opened. As a result, the gape profile lacks a plateau and the duration of the feeding sequence is reduced by more than 100 ms. Also noteworthy are the differences in the duration of tongue protraction. Tongue protraction in *H. cinerea* takes 4–5 times longer than in *P. dacnicolor*, even though *H. cinerea* has a tongue only one-quarter as long (Deban and Nishikawa, 1992). In addition, *H. cinerea* captures prey at a greater distance (2.5 cm) than *P. dacnicolor* (1.9 cm) and has a smaller maximum gape angle (79°) and larger minimum mandible angle (155°) than *P. dacnicolor* (116° and 148° respectively).

Comparisons between successful and unsuccessful capture attempts

The duration of the gape plateau is significantly longer in miss sequences (339±55.5 ms) than in drops (154±15.3 ms) or captures (115±12.5 ms; Table 1; Fig. 4). As a result of this difference, miss sequences also have a significantly longer mean duration of body recovery (334±62.1 ms) than drops (136±24.3 ms) and captures (88±13.7 ms, Table 1). Because the kinematics of drops are more similar to those of captures than to those of misses, the hypothesis that sensory feedback controls the timing of mouth closing is supported.

Other variables were not significantly different among captures, drops and misses. However, *post hoc* comparisons were also performed on the non-significant variables in order to rule out the possibility that variables for drops and captures were artificially grouped as a result of the low statistical power associated with the Bonferroni correction. The *post hoc* tests indicated differences in three of the variables that were not significant based on the overall ANOVA: (1) distance to prey; (2) minimum mandible angle; and (3) duration of mouth closing. These differences suggest that the ANOVA for these variables might have been significant if the sample sizes used had been larger. The difference among success categories for prey distance suggests that there may be an optimum prey distance at which *P. dacnicolor* is most successful. Prey distance was greater for misses than for captures and was

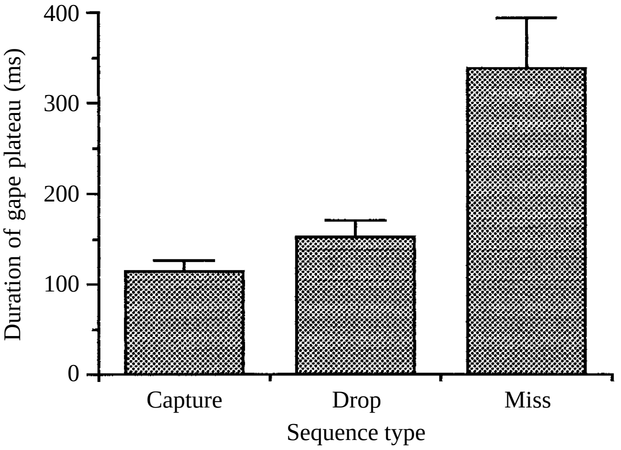

Fig. 4. Mean duration of gape plateau (time that mouth is fully opened) in capture (N=19), drop (N=13) and miss (N=16) sequences for *Pachymedusa dacnicolor*. The average duration in miss sequences is significantly longer than in drops and captures. Standard errors are indicated.

intermediate for drops. The minimum mandible angle was the only variable for which drops grouped with misses. The *post hoc* test indicated that the mandible angle was smaller in captures than in drops and misses. Because this is not a duration variable, this result does not refute the hypothesis that sensory feedback controls the timing of mouth closing.

Discussion

Feeding behavior of phyllomedusines and basal hylids

The highly protrusible tongue of phyllomedusines may have evolved under different selection pressures from lineages with independently derived long tongues. In frogs such as *Bufo marinus*, long tongues have apparently evolved as a mechanism to increase the precision of prey capture (Nishikawa *et al.* 1992). These frogs exhibit a relatively stereotypic prey-capture behavior pattern. The body is not launched forward during the feeding sequence, so a stable head position is maintained, and head and body movements are accurately coordinated (Nishikawa *et al.* 1992). Because phyllomedusines usually exhibit a full body lunge during prey capture, a different explanation is required for the evolution of a highly protrusible tongue within this lineage.

It is likely that long tongues evolved in the phyllomedusines as an adaptation for feeding on large, rapidly moving insect prey. Large orthopterans appear to be the primary natural prey item of *Phyllomedusa tarsius* (Duellman, 1978). Although we are not aware of any other field studies on diets of phyllomedusines, *P. dacnicolor* and *Agalychnis callidryas* (also a phyllomedusine) prefer crickets and moths in the laboratory. In contrast, the most common prey items consumed in the field by the short-tongued *H. cinerea* are slow-moving insect larvae (lepidopteran and coleopteran species; Freed, 1982). More field studies are needed to determine whether other *Hyla* species also eat slow-moving prey. In phyllomedusines, the extremely rapid rate of tongue protraction in combination with a whole-body lunge allow the frog to pin the prey quickly to the substratum before it completes the lunge and engulfs the prey. This behavior pattern is likely to reduce the chances of prey escape. A study comparing the capture efficiencies of hylines and phyllomedusines on different types of prey is currently in progress.

Another unusual aspect of the feeding behavior exhibited by phyllomedusines is the extended plateau phase in the gape profile. A plateau phase is a common feature of terrestrially feeding salamanders (Lauder and Reilly, 1994) and is found in some frogs (Emerson, 1985; Nishikawa *et al.* 1992). However, the plateau is considerably longer in *P. dacnicolor* than in any other caudatan or anuran species investigated to date and results in an extremely long gape cycle. *P. dacnicolor* has a gape cycle ranging from 56 to 411 ms for captures and from 166 to 1107 ms for misses. In contrast, most other species have a gape cycle of between 140 and 280 ms (Emerson, 1985).

Emerson's (1985) model predicts that frogs eating fast-moving prey will have a faster rate of tongue protraction than those eating slow-moving prey and that frogs eating small prey will have a shorter overall gape cycle than those eating large prey. The rationale is that a short gape cycle will result in a rapid recovery, so that the frog will quickly be ready to eat again. This model predicts that, for frogs eating large prey, the length of the gape cycle is not critical and so selection pressures for short gape cycles are relaxed. Because *P. dacnicolor* probably preys on large, rapidly moving insects, rapid tongue protraction and a long gape cycle fit the predicted patterns.

H. cinerea has a slower rate of tongue protraction and a shorter average gape cycle than phyllomedusine species. The slower rate of tongue protraction in *H. cinerea* can be predicted from the Emerson (1985) model. However, according to this model, the gape cycle should be equally long in both groups because both eat relatively large prey. Perhaps the difference in gape cycle length between these two species is related to differences in the method of prey capture. *H. cinerea* retrieves prey with its tongue and may need to close its mouth rapidly to prevent prey escape. In contrast, *P. dacnicolor* pins the prey to the substratum and, therefore, may have no need for rapid mouth closure.

P. dacnicolor also exhibits more variability than *H. cinerea* in prey-capture behavior patterns. Three major components of prey-capture behavior which may vary are: (1) lunge length; (2) ventroflexion of the craniovertebral joint and arching of the body; and (3) use of the tongue to pin the prey to the substratum or to transport it to the mouth. Lunge length is adjusted according to prey distance (r=0.92), but it is unclear what factors influence the degree of ventroflexion and arching, or the use of the tongue to retrieve or immobilize the prey. These components are not correlated with lunge length (r<0.37; P>0.05 for both variables) and do not appear to result from prey characteristics (size, shape and movement) because the same prey type elicited the entire range of behavior patterns. Perhaps motivational factors (for example, satiation or fear) interacting with prey distance result in specific combinations of behavior patterns. In other species for which more than one behavior pattern has been observed (*Cyclorana novaehollandiae* and *Rana pipiens*), prey-capture behavior is modified in response to prey type (Anderson, 1993; Valdez and Nishikawa, 1993).

Neural control of timing of kinematic events

For several species of frogs, some kinematic duration variables are longer in unsuccessful prey-capture attempts than in successful attempts (Nishikawa and Cannatella, 1991; Nishikawa and Roth, 1991; Deban and Nishikawa, 1992). The variables typically related to prey-capture success are the duration variables that occur after prey contact, such as the durations of tongue retraction, mouth closing and recovery. These results suggest that somatosensory stimuli associated with prey contact result in tongue retraction and mouth closing. A neurological study on the Japanese toad *Bufo japonicus* (Matsushima *et al.* 1988) found a sensory feedback pathway from sensory receptors on the tongue surface to the tongue retractor motor neurons, with a latency of 12–20 ms. It has not yet been determined whether this pathway is widespread among frogs.

An alternative explanation for the differences between successful and unsuccessful capture attempts is that they are a result of a purely biomechanical phenomenon. In successful prey-capture attempts, the timing of tongue retraction and mouth closing may be altered as a result of the increased mass of the tongue due to the prey. A waxworm has about the same mass as the tongue of a 250 g *Bufo marinus* (K. C. Nishikawa, unpublished observations) and thus may exert a considerable load. Larsen *et al.* (1989) concluded that biomechanical adjustments were the cause of differences in jaw rotation between successful and unsuccessful prey-capture attempts in the salamander *Bolitoglossa occidentalis*.

For *P. dacnicolor*, differences between successful and unsuccessful prey-capture attempts are best explained by a sensory feedback control mechanism. In captures and drops (but not in misses), the tongue touches the prey. In drop sequences, the tongue does not pick up or move the prey, so there is no increase in mass. Because drops resemble captures more than they resemble misses, simple biomechanical adjustments in response to the mass of the prey on the tongue do not appear to play a role in controlling the timing of kinematic events.

In conclusion, *P. dacnicolor* has a faster rate of tongue protraction, a longer gape cycle and more variable feeding kinematics than *H. cinerea*. In addition, the tongue is used as a fly-swatter to pin the prey to the substratum. The fast tongue protraction, extended gape cycle and fly-swatter action may have evolved in response to a diet of large, rapidly moving insects. Kinematic similarities in capture and drop sequences, and differences between captures and misses, suggest that sensory input is important in controlling the timing of jaw and tongue movements.

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