Kinematics of prey capture in the tailed frog *Ascaphus truei* (Anura: Ascaphidae)

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The kinematics of prey capture by *Ascaphus truei* was investigated. High-speed films (100 fps) of 13 successful and one unsuccessful prey capture sequences from six adult frogs were analysed. *Ascaphus*, the sister group of all living frogs, shares several aspects of feeding kinematics, including rotation of the tongue pad about the mandibular symphysis and mandibular bending during mouth opening and closing, with more derived frogs such as *Bufo marinus*. The times required for tongue retraction, mouth opening and closing are similar in *Ascaphus* and *Bufo*. However, because *Bufo* is much larger and protracts its tongue much farther than *Ascaphus*, the velocities of tongue retraction, mouth opening and mouth closing are relatively lower in *Ascaphus* than in *Bufo*. Differences in prey capture between *Ascaphus* and *Bufo marinus* are (1) the distance of tongue protraction is less in *Ascaphus* (< 0.5 cm) than in *Bufo* (*c.* 2 cm); and (2) lunging of the whole body is more pronounced in *Ascaphus*. Prey capture is highly variable in *Ascaphus*. An intraoral transport sequence is sometimes (7 of 14 observations) inserted into the prey capture cycle before the completion of mouth closing. The gape cycles range from 80–150 ms for sequences with no oral transport and from 130–280 ms for sequences with oral transport. Also, the time required for tongue retraction is significantly longer in the unsuccessful capture attempt. This variability is generally greater than that observed during prey capture in salamanders, and suggests that frogs and salamanders may differ in the importance of sensory feedback in coordinating prey capture.

KEY WORDS:—Anura – *Ascaphus* – kinematics – feeding behaviour.

CONTENTS

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INTRODUCTION

The evolution and kinematics of feeding behaviour in anamniote vertebrates have received much recent attention, especially in salamanders and teleost fishes, for which hypotheses of evolutionary transformation of the feeding system have been developed (Lombard & Wake, 1976, 1977, 1986; Lauder, 1983a,b; Lauder & Shaffer, 1985; Wainwright & Lauder, 1986; Lauder & Reilly, 1988; Larsen, Beneski & Wake, 1989; Reilly & Lauder, 1990). However, much less information on feeding behaviour, especially feeding kinematics, is available for frogs (Emerson, 1976, 1977, 1985; Gans & Gorniak, 1982a,b; Matsushima, Satou & Ueda, 1985). Only the genus *Bufo*, a relatively derived taxon of neobatrachian frogs, has been the subject of detailed kinematic studies (Gans & Gorniak, 1982a,b; Matsushima *et al.*, 1985). Although variation in the morphology of the tongue within anuran taxa has been recognized by systematists for more than half a century (Magimel-Pelonnier, 1924), almost nothing is known about the comparative kinematics of frog feeding behaviour, especially in relatively plesiomorphic taxa.

Since its description, *Ascaphus truei* Stejneger, 1899 has been regarded as a primitive anuran because it has nine presacral vertebrae (rather than eight or fewer as in most other frogs), and a 'tailwagging' muscle which is found in salamanders but which is absent in most other living frogs (Noble, 1922). These primitive features are shared with New Zealand frogs of the genus *Leiopelma*, to which *Ascaphus* was thought to be related. A recent phylogenetic analysis indicates that *Ascaphus truei* is the sister group of all other living frog species, and that although *Ascaphus* and *Leiopelma* share many plesiomorphic features, they are not close relatives (Cannatella, 1985).

Among the primitive characteristics that *Ascaphus* shares with leiopelmatid and other discoglossoid frogs is the presence of a round to oval tongue pad that is closely adherent to the floor of the mouth on all sides (Magimel-Pelonnier, 1924). This tongue morphology, which was employed as the basis for the primitive group Discoglossoidea, is shared by a number of anuran lineages (Cannatella, 1985). Although the characteristic tongue morphology is well known, the detailed kinematics of feeding behaviour have not been studied previously in any species of discoglossoid frog.

Here we describe the kinematics of prey capture in the tailed frog, *Ascaphus truei*. This species is restricted to cold, rocky streams in the humid forests of the Pacific northwest of the United States and Canada (Stebbins, 1985). *Ascaphus truei* lives in cold streams during the day, and emerges to forage in the moist woods whenever the relative humidity is high (i.e., at night or on rainy days). Adult *Ascaphus* feeds on both aquatic and terrestrial prey (Nussbaum, Brodie & Storm, 1983).

Given the current hypothesis of evolutionary relationship of *Ascaphus* to other living anurans, study of its hyolingual morphology and feeding kinematics are of importance to the development of hypotheses of structural and functional transformation of the feeding apparatus during phylogeny. We compare the feeding behaviour of *Ascaphus* with that of the neobatrachian genus *Bufo*, which appears to have a more derived prey capture mechanism (Regal & Gans, 1976; Horton, 1982), and we compare some general features of frog feeding behaviour with those of another lineage of anamniote vertebrates, the salamanders.

MATERIAL AND METHODS

Adult males and females of *Ascaphus truei* were obtained from Tillamook and Lincoln Counties, Oregon between 9 and 10 February, 1987. Feeding sequences were filmed from 19 June to 7 August 1987. We filmed a total of 13 successful and one unsuccessful prey capture sequences using six individual frogs, including one adult female and five adult males (male snout–vent length = 33.5–36.7 mm, $\bar{x}$ = 35.0; female snout-vent length = 41.3 mm). The numbers of feeding sequences per frog were 1, 2, 2, 2, 3 and 4. Only sequences in which the frogs were oriented $90° \pm 10°$ with respect to the camera were included. The frogs were filmed at 100 frames per second using a 16 mm Redlake Locam™ high-speed camera with synchronized strobe illumination, and Kodak™ 4×7277 Reversal Film. Our experience in maintaining *Ascaphus* at room temperature (20–23°C) indicated that the frogs did not feed well and appeared stressed, so they were filmed in a cold temperature room at 15–18°C. At this lower temperature, the frogs feed well and appear to thrive.

Before filming, frogs were placed on a stage with a background of 50 mm grid lines, and on a damp paper towel substrate because they would not sit quietly on a dry substrate. They were allowed to feed unrestrained on the stage after at least 5 min of habituation. Waxworms (*Galleria* sp., *c.* 1.5 cm total length) were placed in front of the frog with forceps.

The films were transferred to VHS format videotape using standard, commercially available techniques which produce 2.5 fields of video data for each 16 mm picture. Thus, the filming rate of 100 pictures per second was maintained. Videotapes were analysed with Peak Performances™ 2d motion analysis software. The resolution of the video image was 39 pixels cm^{-1}. On each frame, the X, Y coordinates of 18 points on the body of the frog (Fig. 1), the prey
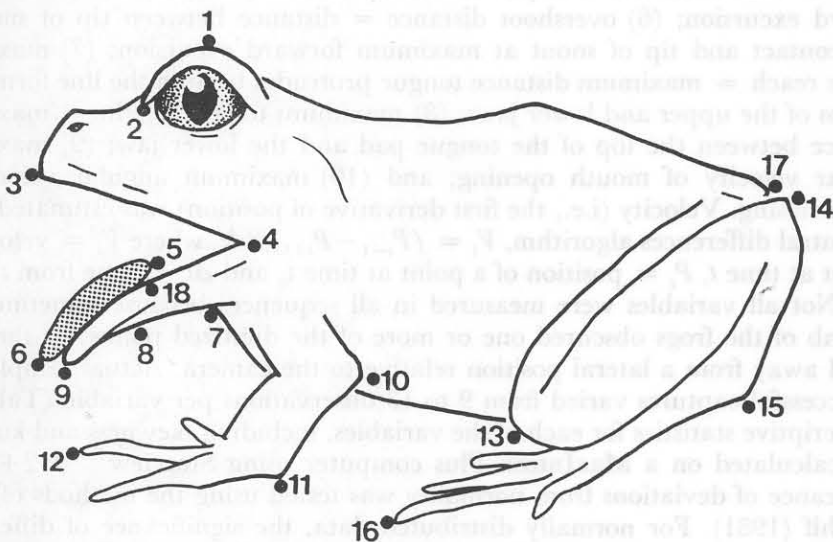

Figure 1. Diagram of the 18 digitized points from which kinematic variables were derived. 1, Top of eye. 2, Anterior corner of eye. 3, Tip of upper jaw. 4, Jaw joint. 5, Posterior tip of tongue. 6, Anterior tip of tongue. 7, Hyoid. 8, Floor of mouth. 9, Tip of lower jaw. 10, Elbow. 11, Wrist. 12, Tip of third finger. 13, Knee. 14, Ankle. 15, Tarsometatarsal joint. 16, Tip of fourth toe. 17, Tip of coccyx. 18, Midlength of lower jaw.

and a non-moving reference point were digitized directly from the video monitor. At least 12 sequential frames were digitized for each sequence.

For the following events, the time was recorded at which each was first observed, relative to the onset of mouth opening (t = 0): (1) onset of forward head movement; (2) onset of forelimb lifting; (3) onset of tongue protraction; (4) maximum mandibular bending; (5) prey contact; (6) completion of tongue protraction; (7) maximum gape; (8) time of maximum forward excursion; (9) onset of tongue retraction; (10) completion of tongue retraction; (11) onset of mouth closing; and (12) completion of mouth closing.

Variables were calculated as follows: (1) duration of approach = onset of forward head movement to maximum forward excursion; (2) duration of mouth opening = onset of mouth opening to maximum gape; (3) duration of mouth closing = maximum gape to completion of mouth closing; (4) duration of tongue protraction = onset of tongue protraction to maximum tongue protraction; (5) duration that tongue remains at target = prey contact to onset of tongue retraction; (6) duration of tongue retraction = onset of tongue retraction to completion of tongue retraction; (7) duration of feeding sequence = onset of forward head movement to completion of mouth closing; (8) duration of body recovery = maximum forward extension to completion of mouth closing.

The following additional variables were calculated directly from the digitized points: (1) maximum angle of mandibular bending = angle subtended by the jaw joint and the tip of the lower jaw with the midpoint of the lower jaw at the vertex; (2) maximum gape angle = angle subtended by the tips of the upper and lower jaws with the jaw joint at the vertex; (3) maximum absolute gape = distance between tips of upper and lower jaws; (4) distance to prey = distance between tip of snout and prey before onset of forward head movement; (5) lunge distance = distance between position of tip of snout at rest and at maximum forward excursion; (6) overshoot distance = distance between tip of snout at prey contact and tip of snout at maximum forward excursion; (7) maximum tongue reach = maximum distance tongue protrudes beyond the line formed by the tips of the upper and lower jaws; (8) maximum tongue height = maximum distance between the top of the tongue pad and the lower jaw; (9) maximum angular velocity of mouth opening; and (10) maximum angular velocity of mouth closing. Velocity (i.e., the first derivative of position) was estimated using the central differences algorithm, $V_t = (P_{t-1} - P_{t+1})/2\Delta t$, where V_t = velocity of a point at time t, P_t = position of a point at time t, and Δt = time from $t-1$ to $t+1$. Not all variables were measured in all sequences because sometimes the forelimb of the frogs obscured one or more of the digitized points, or the head turned away from a lateral position relative to the camera. Actual sample sizes for successful captures varied from 9 to 13 observations per variable (Table 1).

Descriptive statistics for each of the variables, including skewness and kurtosis, were calculated on a MacIntosh Plus computer using Statview^{TM} 512+. The significance of deviations from normality was tested using the methods of Sokal & Rohlf (1981). For normally distributed data, the significance of differences between one unsuccessful and 13 successful captures, and of correlations between kinematic variables and distance to prey were tested using t-tests and Pearson product-moment correlation coefficients. The onset of tongue protraction ($N = 13$, $G_1 = 1.278$), the time of maximum gape ($N = 12$, $G_1 = 1.56$, $G_2 = 2.56$),

TABLE 1. Sample size (N), range (min value – max value), and mean ± standard error of kinematic variables for feeding sequences with ($N = 6$) and without ($N = 6$) intraoral transport. Observations on the single unsuccessful feeding attempt are presented in the rightmost column, along with the probability that the unsuccessful observation comes from the total population of successful captures (* = $P < 0.05$). All times are relative to the onset of mouth opening ($t = 0$)

Variable	No oral transport			Oral transport			Miss ($N = 1$)
	N	Mean ± SE	Range	N	Mean ± S.E.	Range	
Onset of forward head movement (ms)	6	−23.3 ± 7.1	−50–10	6	−21.7 ± 7.5	−40–0	−60
Onset of forelimb lifting (ms)	6	5.0 ± 6.2	−10–30	6	−1.7 ± 6.0	−20–10	−20
Onset of tongue protraction (ms)	6	1.7 ± 1.7	0–10	6	3.3 ± 2.1	0–10	0
Time of maximum mandibular bending (ms)	6	35.0 ± 4.3	20–50	4	40.0 ± 4.1	30–50	30
Time of prey contact (ms)	6	18.3 ± 4.0	10–30	6	31.7 ± 1.7	30–40	30
Completion of tongue protraction (ms)	6	35.0 ± 5.6	20–50	5	50.0 ± 3.2	40–60	60
Time of maximum gape (ms)	6	36.7 ± 4.9	20–50	5	40.0 ± 5.5	20–50	50
Time of maximum forward excursion (ms)	6	48.3 ± 6.0	30–60	6	61.7 ± 3.1	50–70	80
Onset of tongue retraction(ms)	5	53.3 ± 6.7	30–70	5	72.0 ± 5.8	60–90	70
Completion of tongue retraction (ms)	6	90.0 ± 13.2	40–120	5	118.0 ± 9.2	100–140	170
Onset of mouth closing (ms)	6	46.7 ± 4.9	30–60	5	50.0 ± 5.5	30–60	60
Completion of mouth closing (ms)	6	121.7 ± 13.3	80–150	6	180.0 ± 21.6	130–280	240
Duration of approach (ms)	5	71.7 ± 12.2	40–110	6	83.3 ± 7.6	60–110	140*
Duration of mouth opening (ms)	5	36.7 ± 4.9	20–50	5	40.0 ± 5.5	20–50	50
Duration of tongue protraction (ms)	5	35.0 ± 5.6	20–50	5	46.0 ± 4.0	40–60	60
Duration that tongue remains at target (ms)	6	35.0 ± 5.6	20–60	5	46.0 ± 4.0	30–50	40
Duration of tongue retraction (ms)	6	38.3 ± 7.5	20–60	5	46.0 ± 8.7	20–70	100*
Duration of mouth closing (ms)	6	73.3 ± 11.2	40–100	5	130.0 ± 24.5	80–220	180
Duration of body recovery (ms)	6	71.7 ± 8.7	40–90	6	121.7 ± 23.0	80–230	160
Duration of feeding sequence (ms)	6	143.3 ± 19.6	80–190	6	205.0 ± 25.1	150–310	300
Maximum angle of mandibular bending (°)	3	118.9 ± 4.0	108–129	3	125.0 ± 4.7	116–130	136.0
Maximum gape angle (°)	5	97.2 ± 2.7	90–109	5	93.0 ± 6.6	81–115	99.4
Maximum absolute gape (cm)	5	1.5 ± 0.09	1.2–1.9	5	1.5 ± 0.11	1.1–1.8	1.56
Distance to prey (cm)	6	1.5 ± 0.26	0.92–2.6	6	1.6 ± 0.19	0.94–2.0	3.20*
Lunge distance (cm)	6	2.1 ± 0.34	1.3–3.3	6	2.2 ± 0.29	1.4–3.4	3.72
Overshoot distance (cm)	6	0.79 ± 0.14	0.42–1.4	6	0.60 ± 0.08	0.33–0.81	0.31
Maximum tongue reach (cm)	5	0.23 ± 0.03	0.13–0.36	5	0.34 ± 0.06	0.20–0.55	0.24
Maximum tongue height (cm)	5	0.58 ± 0.08	0.22–0.72	5	0.47 ± 0.04	0.39–0.63	0.27
Maximum velocity of mouth opening (°/ms)	5	2.9 ± 0.24	2.2–3.7	5	2.8 ± 0.23	2.2–3.5	2.0
Maximum velocity of mouth closing (°/ms)	5	1.9 ± 0.25	1.2–2.7	5	1.8 ± 0.14	1.3–2.1	1.7

the onset of mouth closing ($N = 12$, $G_1 = 1.56$, $G_2 = 2.56$), the duration of mouth opening ($N = 12$, $G_1 = 1.56$, $G_2 = 2.56$), the duration of mouth closing ($N = 12$, $G_1 = 1.35$) and tongue reach ($N = 12$, $G_1 = 1.26$) deviated significantly from normality ($P < 0.05$), so these variables were analysed statistically using the Mann-Whitney U-test and Spearman's rank correlation.

RESULTS

Description of prey capture kinematics in Ascaphus truei

In *Ascaphus truei* prey capture involves movements of the body (approach and body recovery), of the jaws (opening and closing) and of the tongue (protraction and retraction). Photographs from a typical feeding sequence in *Ascaphus truei* are shown in Figure 2. The prey capture sequence is completed in 80–310 ms, depending on the length of the lunge and on whether or not an intraoral transport cycle occurs before mouth closing. Sequences with long lunges and/or with intraoral transport cycles last longer.

Approach. The prey capture sequence begins as the frog moves toward the prey, first rocking forward on its forelimbs. The head is directed slightly downward before a short lunge, and slightly upward before a long lunge. Forward head movement begins 0–50 ms before the onset of mouth opening (Table 1). The frog reaches its maximum forward excursion 30–70 ms after the onset of mouth opening (Table 1), after maximum gape, but before the onset of tongue retraction. The forelimbs always leave the substrate, even in the shortest lunges. The onset of forelimb lifting may occur before or after the mouth opens (Table 1), and the time at which the forelimbs are raised is independent of lunge length ($r = -0.54$, $P > 0.05$). In contrast to the forelimbs, the metatarsals and/or the phalanges of the hind feet remain in contact with the substrate throughout the approach and early body recovery stages. The distance that the hind limbs are extended varies with the distance to the prey. Because the hind feet remain in contact with the substrate, the distance of the lunge appears to be limited to the length of the fully extended frog (i.e. the snout-vent length plus the length of the extended hind limb, excluding the metatarsals and phalanges).

Mouth opening. In every sequence we digitized, the hyoid is always in the retracted position before the mouth begins to open (Fig. 2, 10 ms). The onset of mouth opening occurs after the onset of forward head movement (Table 1). As the mouth opens, the eyes are retracted into the orbits, and the flexible mandible begins to bend downward (Fig. 2, 40–50 ms). In all trials, the mandible is bent to some degree during mouth opening, before the lower jaw has made contact with the substrate. The mandible sometimes reaches its maximum bending before the lower jaw contacts the substrate, and sometimes reaches its maximum bending on impact with the prey or substrate. Maximum mandibular bending (range 108–130°) occurs 20–50 ms after the onset of mouth opening (Table 1). Mouth opening is completed after maximum tongue protraction, but before the onset of tongue retraction (Table 1). In no case was there any indication of a slow opening phase of mouth opening (Fig. 3A–C).

Tongue protraction. Simultaneous with, or shortly after, the onset of mouth opening (range 0–10 ms, Table 1) the tongue appears as a relatively flat, broad pad that is raised slightly above the floor of the mouth (Fig. 2, 50 ms). The onset
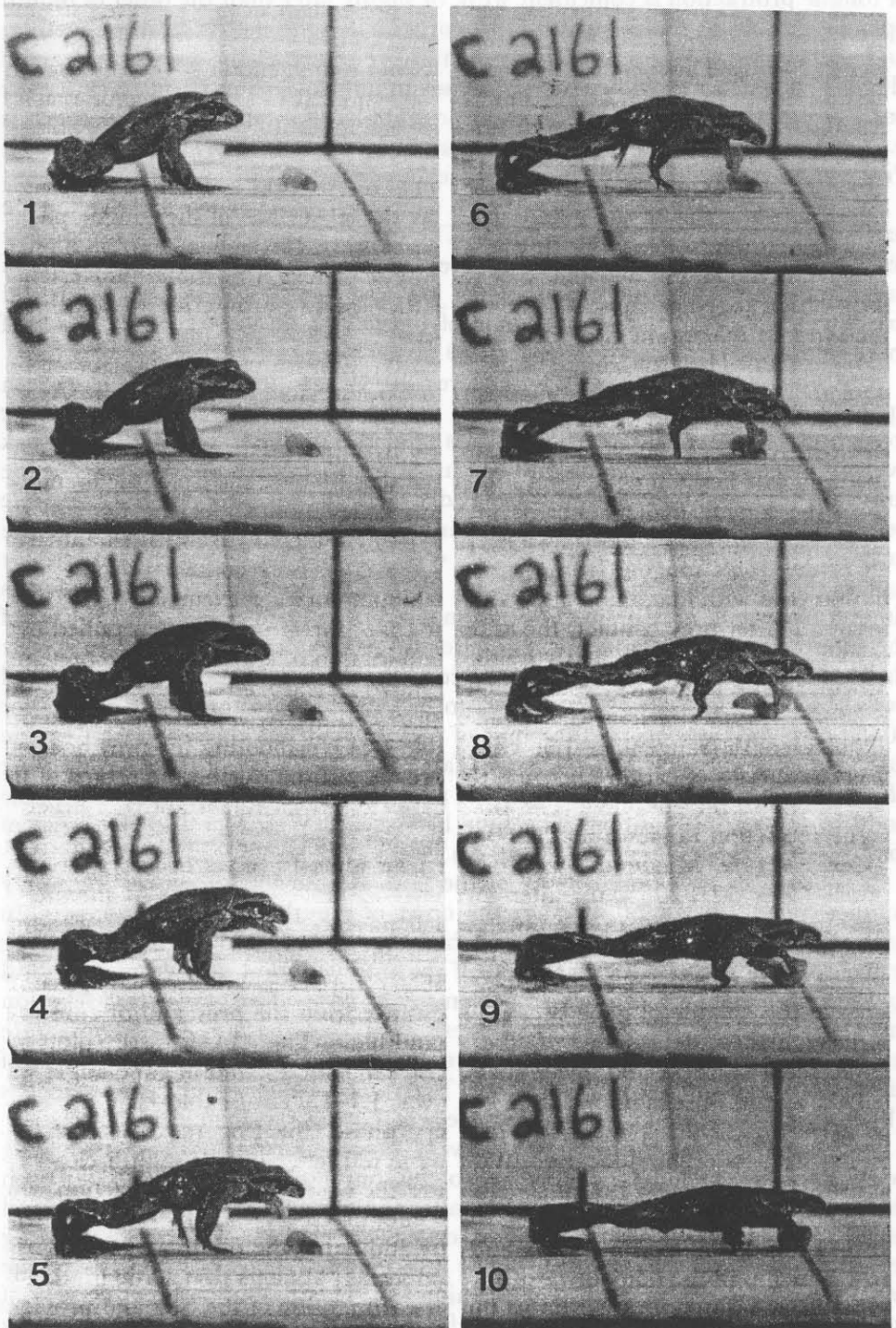
of tongue protraction is coincident with, or slighly later than the onset of mouth opening (Table 1). Subsequently, the posterior tongue pad is elevated further, and the tongue thickens and becomes more compact as the prey is contacted (Fig. 2, 70 ms). The tongue reaches its maximum protraction 20–60 ms after the onset of mouth opening. At maximum protraction, the range of tongue reach is 0.13–0.55 cm and the range of tongue height is 0.22–0.72 cm (Table 1). Protraction is always completed after prey contact.

In *Ascaphus*, tongue protraction is best characterized as rotation of the tongue pad around the tips of the mandibles. The dorsal surface of the tongue pad at rest comes to face ventrally during prey capture through a combination of movements, including depression of the jaw and flexion of the cranioverterbral joint, which together cause the angle of the jaw to lie anterior to the tips of mandibles at maximum gape (Fig. 2, 80 ms).

Prey contact. The frog contacts the prey 10–40 ms after the onset of mouth opening (Table 1) and *c.* 15 ms before maximum tongue protraction. As the frog's tongue contacts the prey, the tips of the mandibles are often bent back even farther (Fig. 2, 80–90 ms), apparently by impact with the prey and/or the substrate. The fleshy tongue tip is protruded slightly over the tip of the mandible before the tongue pad reaches its maximum elevation above the floor of the mouth. The worm is almost always ($N = 12$) contacted first with the anterior half of the frog's tongue. In most cases ($N = 12$), prey contact precedes or is simultaneous with maximum gape and maximum forward excursion of the tip of the snout. After prey contact, the anterior tip of the tongue is often pulled over the mandibular tips, apparently by the combination of adhesion to the prey and overshoot. The frog always continues to move forward after prey contact (for 20–50 ms), passing beyond the point of prey contact by about one-half to one full head length (range 0.33–1.35 cm, Table 1). Overshooting the prey does not affect the success of capture because the prey is secured during the return of the body to the resting position. The time between prey contact and the onset of tongue retraction ranges from 20–60 ms.

Maximum gape. Maximum gape of the jaws almost always occurs after prey contact ($N = 12$), 20–50 ms after the onset of mouth opening. At maximum gape, the cranium and upper jaws, which have been following a descending trajectory, are elevated by extension of the intervertebral and craniovertebral joints (Fig. 3A–C; see plots of displacement of upper jaws). Cranial elevation increases the maximum gape because resistance from the prey and/or substrate restricts further depression of the mandibles (Fig. 3A–C; see plots of displacement of upper and lower jaws). The range in maximum gape angle was 81–115° and in maximum absolute gape was 1.1–1.9 cm (Table 1).

Body recovery. During the body recovery phase, the frog returns to resting position near its original location, the tongue retracts, and the mouth closes on the prey. Body recovery begins shortly after the onset of tongue retraction, and usually ceases before the completion of mouth closing (Table 1). The frog returns to its resting position apparently by adducting the thighs and flexing the knees, which pull the body toward the hind feet. It appears that static friction of the hind toes on the substrate limits the forward motion of the frog and provides a fixed point against which muscle contraction can work to return the body to its resting position. As the body nears the resting position, the hind toes are lifted from the substrate. During most of the approach and body recovery, the
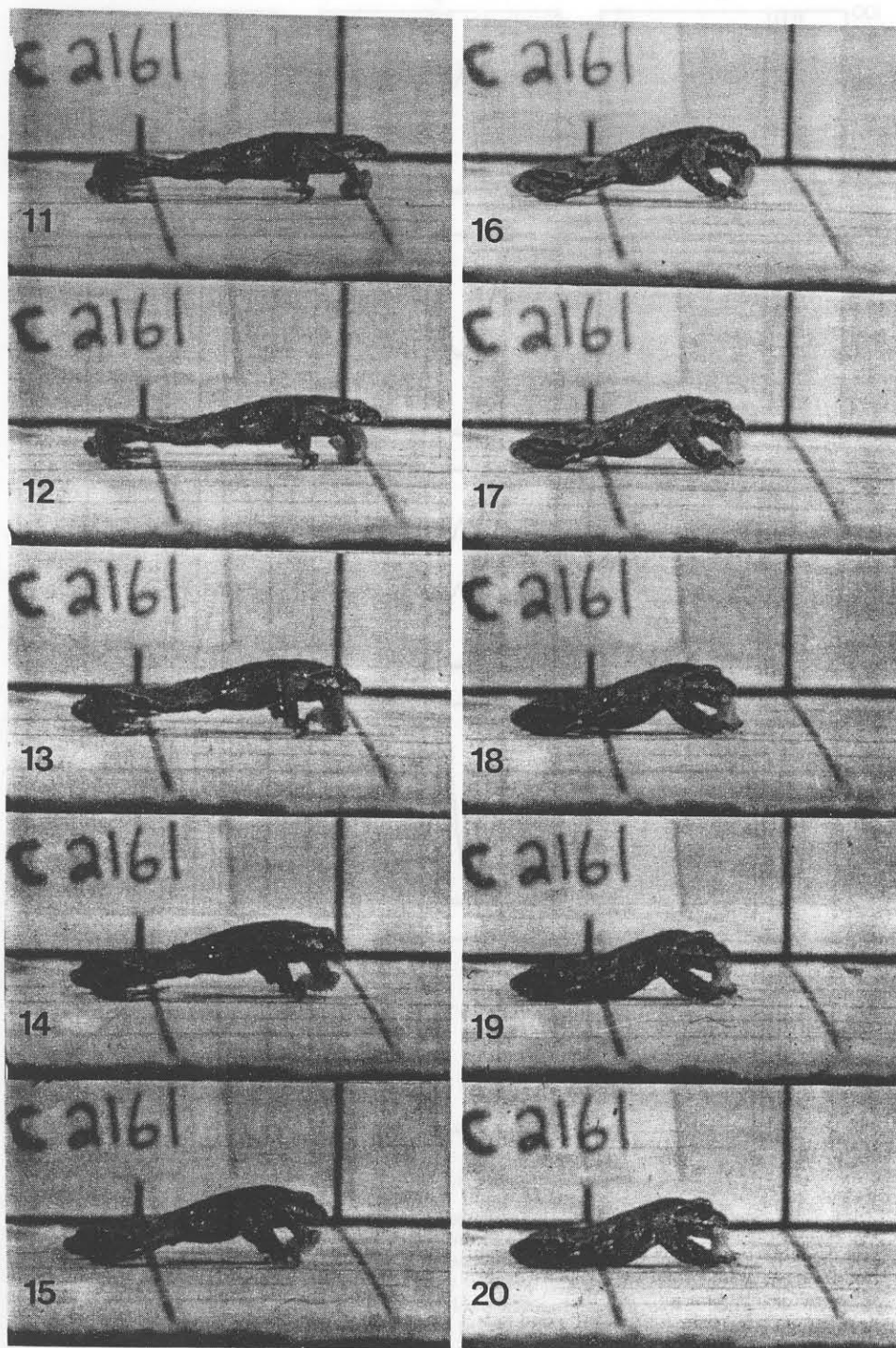
Figure 2. Twenty frames showing the sequence of prey capture. Time (in ms) is indicated by the number on each frame × 10.
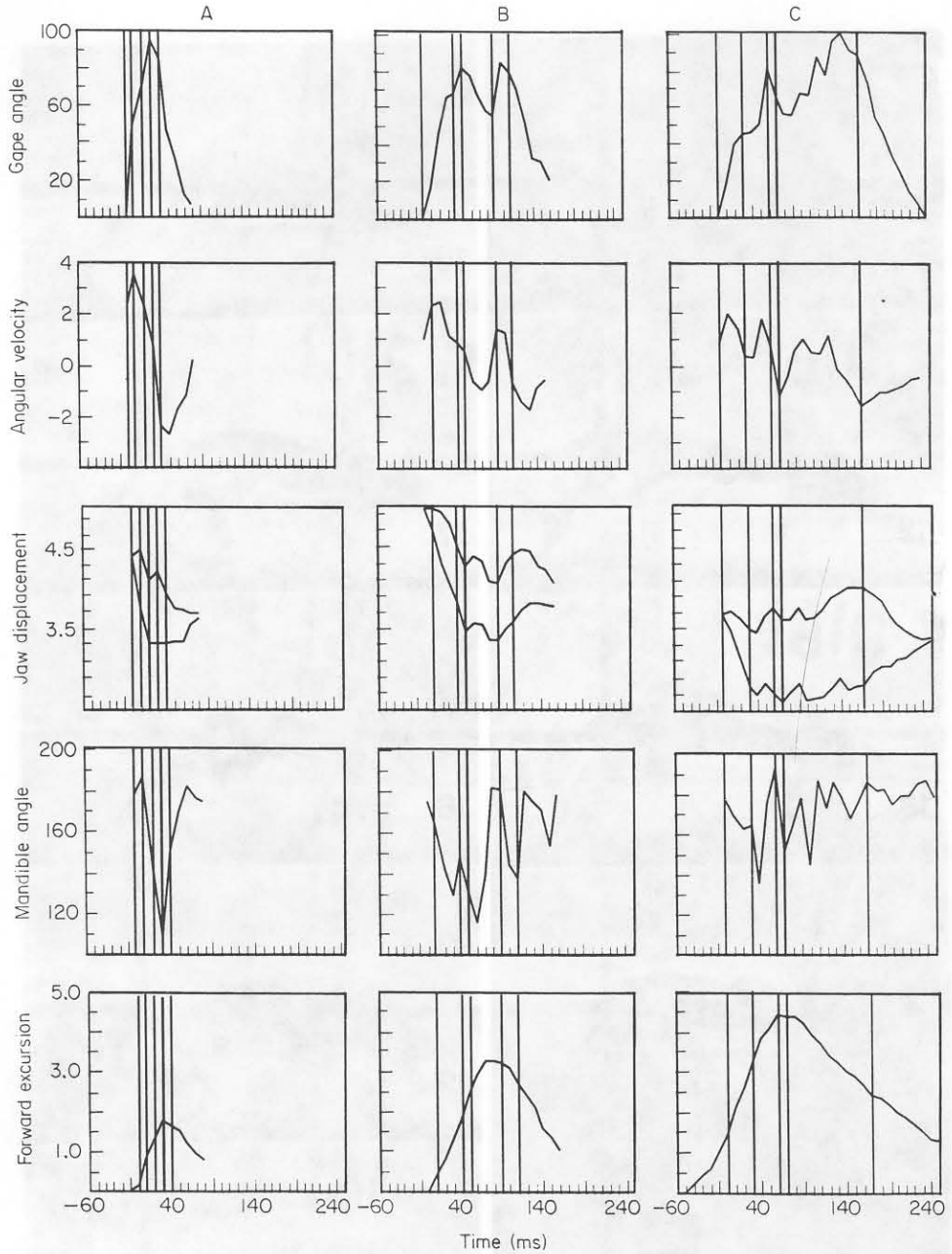
Figure 3. Kinematics of prey capture. A, A prey capture sequence without intraoral transport; B, a prey capture sequence with an intraoral transport sequence inserted before the completion of mouth closing; C, an unsuccessful prey capture sequence. For each sequence, gape angle (°), angular velocity of jaw movements (° ms^{-1}), displacement (cm) of upper jaw tips (top line) and lower jaw tips (bottom line), mandible angle (°) and forward excursion of upper jaw tip (cm) are plotted vs time (ms). Note that cranial elevation is indicated by the change in position of the upper jaw tips while the lower jaw is stabilized at its most ventral position by the substrate or the prey item. Vertical lines indicate onset of tongue protraction, prey contact, maximum tongue protraction, onset of tongue retraction and completion of tongue retraction, from left to right respectively.

forelimbs are not in a position to generate forces necessary to return the body to its resting position. The only other structure in contact with the substrate during body recovery is the mandible (Fig. 2, 120–130 ms). Because the mandible is in contact with the substrate after prey contact, one might suppose that the frog could produce a backward recovery force via the mandible. However, in some feeding sequences, the mandible does not touch the substrate after prey contact, and the frog recovers normally.

Tongue retraction. The prey, adhering to the sticky tongue, is transported into the mouth during body recovery from the overshoot. Tongue retraction begins after mouth opening and forward head movement have ceased, 30–90 ms after the onset of mouth opening (Table 1). Retraction is completed 40–140 ms after the onset of mouth opening, but before the mouth is closed (Table 1). The time between prey contact and the onset of tongue retraction varies from 20–60 ms (Table 1). During the initial stages of retraction, the tongue retains its globular appearance (Fig. 2, 110 ms). As retraction proceeds, the tongue pad returns to a more disc-like shape, although it remains elevated. Finally, the tongue returns to its original position in the floor of the mouth.

Mouth closing. Following elevation of the cranium, and during tongue retraction, the head is flexed downward, and the jaws close on the prey. Mouth closing begins 30–60 ms after the onset of mouth opening, coincident with the onset of tongue retraction (Table 1). Mouth closing is completed on average 80–280 ms after the onset of mouth opening (Table 1), and defines the end of the prey capture sequence. The velocity of mouth closing is always less than the velocity of mouth opening (Fig. 3A–C). The longest mouth closing times are associated with sequences in which intraoral transport begins before the final stage of prey capture.

Variation among prey capture sequences

There is a high degree of variation among prey capture cycles in *Ascaphus* (Fig. 4A–D). Four different patterns of sequence duration are found: (1) short sequences with gape cycles less than 100 ms in duration ($N = 2$), in which no intraoral transport cycle occurs after the onset of mouth closing (Figs 3A, 4A); (2) intermediate sequences with gape cycles of 100–200 ms duration ($N = 4$), in which no intraoral transport cycle occurs after the onset of mouth closing (Fig. 4B); (3) intermediate sequences ($N = 5$) with gape cycles of 100–200 ms duration, with an intraoral transport cycle after the onset of mouth closing (Figs 3B, 4C); and (4) long sequences ($N = 2$, including one unsuccessful capture attempt) with gape cycles of more than 200 ms in duration, all of which include an intraoral transport cycle after the onset of mouth closing (Figs 3C, 4D). One of the sequences could not be categorized because the frog turned its head toward the camera shortly after prey contact. These variations were observed among the capture attempts by single individuals, and therefore are not due to individual differences in prey capture strategy.

In seven *Ascaphus* sequences, an intraoral transport cycle was inserted into the capture cycle before the final stages of prey capture. The mouth was re-opened before the tongue had fully retracted and before the jaws closed on the prey. The second mouth opening occurred after the mouth had closed only partially, to
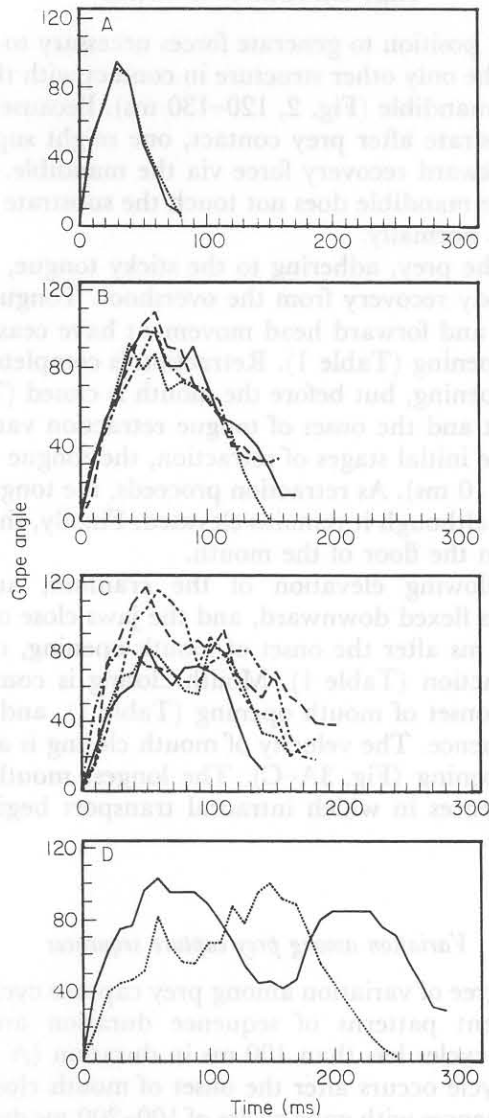
Figure 4. Variability among 12 sequences in gape angle (°). Four different patterns are found. A. Short sequences of less than 100 ms duration ($N = 2$) with no intraoral transport cycle; B, intermediate sequences of 100–200 ms duration ($N = 4$) with no intraoral transport cycle; C, intermediate sequences of 100–200 ms duration ($N = 5$) with an intraoral transport cycle occurring before mouth closing; and D, sequences of more than 200 ms duration ($N = 2$, including an unsuccessful prey capture attempt) both of which include an intraoral transport sequence.

angles of 41°–61.5°. Thus, mouth closing was sometimes but not always interrupted by the onset of the first intraoral transport sequence.

In tetrapods generally, intraoral transport cycles are similar to prey capture cycles. Both involve movements of the cranium, lower jaw and hyolingual complex (Bramble & Wake, 1985), although the amplitude of cranial, jaw and hyolingual movements may differ between prey capture and intraoral transport cycles. We defined intraoral transport as an increase in gape of at least 10°,

accompanied by rostral movement of the hyolingual apparatus. In *Ascaphus*, the amplitude of tongue protraction is always less during intraoral transport than during prey capture, although the amplitude of mouth opening during intraoral transport may be equal to or greater than during prey capture.

There were also differences between the successful prey captures and the unsuccessful capture attempt. Of all the sequences included in this study, the single unsuccessful capture attempt was the longest lunge at the most distant prey, with the shortest overshoot of the prey item (Table 1). In this attempt, the prey was contacted but was not captured (Fig. 5C, Table 1). The frog spent significantly more time lunging forward in this than in successful sequences, and required significantly more time to retract the tongue than in successful sequences (t – tests, $P < 0.05$, Table 1, Fig. 3C).

The length of the lunge varied nearly three-fold among the 13 successful sequences studied (Table 1). We were interested in whether or not some aspects of prey capture vary with lunge length. Only approach variables, including the distance to prey ($N = 13$, $r = 0.795$), the onset of forward head movement ($N = 13$, $r = -0.579$), the time of maximum forward excursion ($N = 13$, $r = 0.702$) and the duration of approach ($N = 13$, $r = 0.773$) were significantly correlated ($P < 0.05$) with lunge length. Other variables, including mouth opening and closing, tongue protraction and retraction, body recovery and overshoot distance showed no significant correlation with lunge length (all $P > 0.05$).

DISCUSSION

The purpose of this study was to compare the kinematics of feeding in *Ascaphus truei* with that of *Bufo marinus* and other species that possess a more derived feeding apparatus. As with terrestrial salamanders (Larsen *et al.*, 1989), some lizards (Schwenk & Throckmorton, 1989) and *Bufo marinus* (Gans & Gorniak, 1982a,b), *Ascaphus truei* has a lingual prey capture mechanism. A major difference between *Ascaphus* and *Bufo marinus* is that the tongue of *Ascaphus* is much less protrusible because it is more firmly attached to the floor of the mouth and lacks a free flap posteriorly. Other 'discoglossoid' frogs (*Bombina*, *Alytes*, *Discoglossus*, *Barbourula*, *Leiopelma*) also have tongues of very limited protrusibility compared with the neobatrachians *Bufo* and *Rana*. In *Ascaphus*, the anterior tip of the tongue never protrudes more than 5 mm beyond the tip of the mandibles (Table 1), in contrast to *Bufo marinus* and *Rana catesbeiana*, which can protrude the tongue more than 2 cm (Table 2; Gans, 1961, 1962; Gans & Gorniak, 1982b).

In some respects, tongue protraction is very similar in *Ascaphus* and *Bufo*. In both species, tongue movement is most accurately characterized as rotation of the tongue pad about the mandibular symphysis. However, it appears that the conformation of the m. genioglossus and m. hyoglossus (Horton, 1982) are partially responsible for the limited lingual protrusibility in *Ascaphus* (Cannatella & Nishikawa, in preparation).

In both *Ascaphus* and *Bufo*, the mandible is bent downward during mouth opening, presumably by contraction of the m. submentalis acting on the joint between the mentomeckelian bones and the mandibles (Gans & Gorniak, 1982a,b). The m. submentalis is derived from the m. intermandibularis (Gaupp,

TABLE 2. Comparison of feeding kinematics between *Ascaphus* and *Bufo*. *P* = Probability that the mean reported for *Bufo* is taken from the population of successful captures for *Ascaphus truei* (*t*-tests); N.S. = not significant. Data for *Bufo marinus* are taken from Gans & Gorniak (1982b). ~ = Approximate values, exact values not published

Variable	Ascaphus		Bufo		
	Mean	S.E.	Mean	S.E.	P
Duration of approach (ms)	72.9	6.74	180	39	< 0.05
Duration of mouth opening (ms)	43.3	6.07	~ 64	~ 22	N.S.
Duration of tongue protraction (ms)	41.7	3.86	36.8	3.5	N.S.
Duration of tongue retraction (ms)	41.7	5.05	~ 70	—	N.S.
Duration of mouth closing (ms)	96.7	13.84	~ 79.4	21.7	N.S.
Duration of feeding sequence (ms)	177.7	16.76	323	40	< 0.05
Distance of tongue protraction (cm)	0.39	0.05	~ 2	—	< 0.05

1896; Tyler, 1971). It is present in all living frogs, but is reduced and fibrous in *Rhinophrynus dorsalis* (Trueb & Gans, 1983). Pipoid frogs (*Rhinophrynus* and the Pipidae) have secondarily lost the mentomeckelian bones (Cannatella, 1985) and *Rhiniphrynus* has additionally reduced the m. submentalis (Trueb & Gans, 1983). Thus, we predict that mandibular bending during prey capture will be reduced or absent in *Rhinophrynus*. A specialized m. submentalis and discrete mentomeckelian bones are absent in salamanders (Francis, 1934; Duellman & Trueb, 1986), and the mandible does not appear to bend during mouth opening in most salamanders (Larsen *et al.*, 1989; Findeis & Bemis, 1990: fig. 8), although it does bend slightly during mouth opening in *Ambystoma tigrinum* (Reilly & Lauder, 1989a). The presence of a m. submentalis and the presence of mandibular bending can be hypothesized as synapomorphies of Anura (living frogs), assuming that the limited bending in *Ambystoma tigrinum* is independently evolved. If further work verifies our prediction that the mandible of *Rhinophrynus* does not bend during feeding, this would represent a secondary loss.

In terms of overall timing (Table 2), the duration of approach is longer in *Bufo* than in *Ascaphus* (*t*-test, *P* < 0.05), perhaps due to differences in the way prey were presented in the two studies. The duration of the feeding sequence is also longer in *Bufo* than in *Ascaphus* (*t*-test, *P* < 0.05), but this is mostly due to the differences in the duration of approach. The durations of mouth opening and closing and tongue protraction and retraction are similar in the two species (*t*-tests, all *P* > 0.05). A similar pattern of variation, in which overall timing of prey capture is similar although tongue projection distances vary, is observed in plethodontid salamanders (Larsen *et al.*, 1989). The gape cycle is *c*. 100 ms in most salamander species that have been studied, although the different species vary in tongue projection distance from 7 to 44% of snout-vent length.

The similarity in timing between *Bufo* and *Ascaphus* suggests that *Bufo* actually opens and closes the mouth and protracts and retracts the tongue faster than *Ascaphus*, because *Bufo* is larger (*B. marinus*, SVL = 10–15 cm, body mass 264–696 g; *A. truei*, SVL = 33.5–41.3 mm, body mass 4–6 g), and because the tongue of *Bufo* is protruded farther beyond the mandibles in the same time period (Table 2, *t*-test, *P* < 0.05). Physiological times, such as duration of mouth opening or closing, have been observed to vary with body mass$^{-1/4}$ (Lindstedt &

Calder, 1981). Thus, the observed differences between the durations of kinematic events in the two species indicate that the velocities of feeding movements in *Bufo* are much faster than would be predicted if *Bufo* were simply a large ascaphid.

Another difference in feeding between *Ascaphus* and *Bufo* is that, because tongue protraction is limited in *Ascaphus*, whole body lunging plays a much greater role in prey capture. In *Bufo*, all four limbs remain planted on the substrate, even in the longest lunges. The head is moved forward slightly by rotation of the trunk about the forelimbs. In contrast, in *Ascaphus*, the forelimbs leave the substrate even during short lunges of less than one centimetre, and the trunk is propelled forward by extension of the hind limbs. In *Ascaphus*, the forward lunge of the body and head (range 1.33–3.40 cm) contributes much more to prey capture distance than does protraction of the tongue (range 0.16–0.65 cm). Thus, in *Ascaphus*, whole body lunging is the most important mechanism of tongue projection, but lingual projection is necessary for prey capture and transport of the prey into the mouth.

Feeding in *Ascaphus* is perhaps as complex a behaviour pattern as one can observe in a vertebrate, because virtually every striated muscle group in the body plays a role. The axial musculature controls head movements, the appendicular musculature of fore- and hind limbs propels the body forward, the branchiomeric musculature opens and closes the mouth, the hypobranchial musculature stabilizes the hyoid and protracts the tongue, and even the mm. retractor bulbi draw the eyes into the orbits during mouth opening. In the sense that fewer muscle groups are involved in feeding behaviour in *Bufo*, it appears that the complexity of feeding behaviour (i.e. the number of independent muscular contractions which have to be coordinated by the brain) may have decreased during frog phylogeny. A similar trend is found among salamanders, in which relatively primitive species lunge forward to catch prey, whereas more derived species do not (Larsen & Beneski, 1988; Larsen *et al.*, 1989; Miller & Larsen, 1990).

One difference between *Ascaphus* and anamniotes in general (Bramble & Wake, 1985; Larsen *et al.*, 1989; Findeis & Bemis, 1990; Reilly & Lauder, 1990) is that no slow opening phase of mouth opening was observed in *Ascaphus*. Slow opening is also absent in some lizards (Bels & Goosse, 1990).

Ascaphus truei exhibits great individual variability in the timing of events during prey capture. In sequences without intraoral transport cycles, the gape cycle of *Ascaphus* varies from 80–150 ms (Table 1). In sequences with intraoral transport cycles, the gape cycle varies from 130 to 280 ms (Table 1). The low end of the range of gape cycle duration in *Ascaphus* is similar to the fastest gape cycles exhibited by anamniotes (i.e. in aquatic feeding in fishes and salamanders, Wainwright *et al.*, 1989), while the high end is among the slowest reported gape cycles for anamniotes (i.e. that of *Bufo marinus*; Gans & Gorniak, 1982a). Most frogs that have been studied gave gape cycles of between 140 and 280 ms (Emerson, 1985).

The variability in gape cycle duration is much greater in *Ascaphus* than the within- or between-individual variability reported for plethodontid (e.g. Larsen *et al.*, 1989: Fig. 2) or ambystomatid salamanders (e.g. Reilly & Lauder, 1989a: fig. 3), which have gape cycles of *c.* 100 ms duration (Larsen *et al.*, 1989; Reilly & Lauder, 1989a). In salamandrids, gape cycle duration is much longer than in

plethodontid and ambystomatid salamanders (Miller & Larsen, 1990; Findeis & Bemis, 1990), and varies as much as or more than in *Ascaphus* (e.g. *Salamandra terdigitata*, 90–326 ms; Miller & Larsen, 1990). However, Miller & Larsen (1990) report that, although gape cycle duration is highly variable, the shape of the gape profiles was similar both within and between species. In *Ascaphus*, the shapes of gape profiles differ markedly both within and between individual frogs.

There are at least three sources of variability among feeding sequences in *Ascaphus*: (1) variation in distance to prey and lunge length, which appears to affect only approach variables; (2) frequent insertion of an intraoral transport cycle into the prey capture sequence before the end of the first gape cycle; and (3) differences between successful and unsuccessful capture attempts. We know of no previous studies on any frog or salamander species in which insertion of an intraoral transport sequence before completion of jaw closure has been observed. Furthermore, in contrast to *Ascaphus*, several workers have failed to find differences in feeding behaviour between successful and unsuccessful captures in salamanders (Findeis & Bemis, 1990; Miller & Larsen, 1990; Reilly & Lauder, in press). These observations suggest that prey capture is less stereotyped in *Ascaphus* than has been observed in salamanders.

The lack of stereotypy suggests that feeding motor programs are more readily modified by incoming sensory feedback in *Ascaphus* than in salamanders. The interruption of mouth closing by insertion of an intraoral transport cycle (e.g. Fig. 3B, 4C, D) may be due to sensory feedback from the tongue. We propose that the mouth-closing motor program is sometimes overridden by a command to reopen the mouth. Such a command could be triggered, for example, by the position of the prey on the tongue.

The difference between the unsuccessful and successful capture attempts also suggests that sensory feedback may modify events within the prey capture cycle. In the unsuccessful attempt, all kinematic events before prey contact are normal. It is only the completion of tongue retraction that is delayed. A similar pattern of postponement of events that occur after prey contact has been observed in unsuccessful prey captures in the frog *Discoglossus pictus* (Nishikawa & Roth, in press). These observations can be explained by the hypothesis that tongue retraction is postponed by sensory feedback when the prey item is not successfully transported into the mouth.

An alternative explanation is that the unsuccessful attempt was a 'misfire', a pre-programmed motor error (i.e. one which was carried out independent of sensory feedback). However, this explanation would predict that the kinematics of events before as well as after prey contact should be different. Sensory feedback can only affect events that occur after prey contact.

Both insertion of intraoral transport cycles and delayed tongue retraction in unsuccessful prey capture sequences require the existence of a sensory feedback pathway from the tongue surface to the motor neurones controlling tongue and jaw movements. In fact, a sensory projection from the glossopharyngeal nerve (tongue surface sensory fibres) to the motor nuclei controlling tongue and jaw muscles, with a latency of 12–20 ms, has been described in the frog *Bufo japonicus* (Matsushima *et al.*, 1988).

Thexton, Wake & Wake (1977) measured a minimum latency of 12 ms for the tongue-withdrawal reflex in the salamander *Bolitoglossa occidentalis*. They argued that there is not enough time available for sensory feedback modulation of

tongue retraction in *B. occidentalis* because the tongue remains at the target so briefly (9–22 ms). In *Ascaphus*, however, the tongue remains at the target for 20–60 ms. Thus, it would appear that there is enough time for feedback modulation of tongue retraction in *Ascaphus*. While salamandrids have relatively long gape cycles (Miller & Larsen, 1990), the time the tongue remains at the target has not been reported, so it is unknown whether or not they may have enough time for sensory feedback control of tongue withdrawal. However, even if there were enough time for a tongue-withdrawal reflex to occur, there is no evidence of feedback modification of feeding behaviour in any salamandrid species.

In summary, there is no evidence in any salamander that sensory feedback is an important modulator of feeding behaviour. In fact, the stereotypic feeding exhibited by salamanders has been observed in many species (Larsen *et al.*, 1989; Reilly & Lauder, in press; Thexton *et al.*, 1977), as well as in the same species feeding on different prey types (Reilly & Lauder, 1989*b*; Findeis & Bemis, 1990; Miller & Larsen, 1990) or in different media (Lauder & Shaffer, 1988). Sensory feedback may be more important in frogs than in salamanders for the simple reason that the feeding sequence is much longer in frogs, specifically the time the tongue is at the target, so that more time is potentially available for feedback.

CONCLUSIONS

Many aspects of prey capture in *Ascaphus truei* and *Bufo marinus*, including overall timing of events and mandibular bending, are similar. The major differences involve tongue protraction distance, which is shorter in *Ascaphus*, and lunge distance, which is longer in *Ascaphus*. Prey capture is highly variable in *Ascaphus* in ways that suggest a greater role for sensory feedback than appears to characterize the feeding behaviour of salamanders. We suggest that sensory feedback may play a greater role in frogs than in salamanders for the simple reason that more time is available for feedback in frogs.

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REFERENCES

BELS, V. L. & GOOSE, V., 1990. Comparative kinematic analysis of prey capture in *Anolis carolinensis* (Iguania) and *Lacerta viridis* (Scleroglossa). *Journal of Experimental Zoology, 255:* 120–124.

BRAMBLE, D. M. & WAKE, D. B., 1985. Feeding mechanisms of lower tetrapods. In M. Hildebrand, D. M. Bramble, K. F. Liem, & D. B. Wake (Eds), *Functional Vertebrate Morphology:* 230–261. Cambridge: Harvard University Press.

CANNATELLA, D. C., 1985. A phylogeny of primitive frogs (archaeobatrachians). University Microfilms, Ann Arbor, MBA86–08380.

DUELLMAN, W. E. & TRUEB, L., 1986. *Biology of Amphibians.* New York: McGraw Hill.

EMERSON, S. B., 1976. A preliminary report on the superficial throat musculature of the Microhylidae and its possible role in tongue action. *Copeia, 1976:* 546–551.

EMERSON, S B., 1977. Movement of the hyoid in frogs during feeding. *American Journal of Anatomy, 149:* 115–120.

EMERSON, S. B., 1985. Skull shape in frogs—correlations with diet. *Herpetologica, 41:* 177–188.

FINDEIS, E. K. & BEMIS, W. E., 1990. Functional morphology of tongue projection in *Taricha torosa* (Urodela: Salamandridae). *Zoological Journal of the Linnean Society, 99:* 129–157.

FRANCIS, E. B. T., 1934. *The Anatomy of the Salamander.* Oxford: Clarendon Press.

GANS, C., 1961. The bullfrog and its prey. *Natural History, 70:* 26–37.

GANS, C., 1962. The tongue protrusion mechanism in *Rana catesbiana. American Zoologist, 2:* 524A (abstract).

GANS, C. & GORNIAK, G. C., 1982a. How does the toad flip its tongue? Test of two hypotheses. *Science, 216:* 1335–1337.

GANS, C. & GORNIAK, G. C., 1982b. Functional morphology of lingual protrusion in marine toads (*Bufo marinus*). *American Journal of Anatomy, 163:* 195–222.

GAUPP, E., 1896. *A. Ecker's und R. Wiedersheim's Anatomie des Frosches.* Braunschweig: Friedrich Vieweg und Sohn.

HORTON, P., 1982. Diversity and systematic significance of anuran tongue musculature. *Copeia, 1982:* 595–602.

LARSEN, J. H. & BENESKI, J. T., 1988. Quantitative analysis of feeding kinematics in dusky salamanders (*Desmognathus*). *Canadian Journal of Zoology, 66:* 1309–1317.

LARSEN, J. H. & GUTHRIE, D. J., 1975. The feeding mechanism of terrestrial tiger salamanders (*Ambystoma tigrinum melanostictum* Baird). *Journal of Morphology, 147:* 137–154.

LARSEN, J. H., BENESKI, J. T. & WAKE, D. B., 1989. Hyolingual feeding systems of the Plethodontidae: comparative kinematics of prey capture by salamanders with free and attached tongues. *Journal of Experimental Zoology, 252:* 25–33.

LAUDER, G. V., 1983a. Neuromuscular patterns and the origin of trophic specialization in fishes. *Science, 219:* 1235–1237.

LAUDER, G. V., 1983b. Functional and morphological bases of trophic specializations in sunfishes (Teleostei, Centrarchidae). *Journal of Morphology, 178:* 1–21.

LAUDER, G. V. & REILLY, S. M., 1988. Functional design of the feeding mechanism in salamanders: causal bases of ontogenetic change in function. *Journal of Experimental Biology, 143:* 219–233.

LAUDER, G. V. & SHAFFER, H. B., 1985. Functional morphology of the feeding mechanism in aquatic ambystomatid salamanders. *Journal of Morphology, 185:* 297–326.

LAUDER, G. V. & SHAFFER, H. B., 1988. Ontogeny of functional design in tiger salamanders (*Ambystoma tigrinum*): are motor patterns conserved during major morphological transformations? *Journal of Morphology, 197:* 249–268.

LINDSTEDT, S. L. & CALDER, W. A., 1981. Body size, physiological time, and longevity of homeothermic mammals. *Quarterly Review of Biology, 56:* 1–16.

LOMBARD, R. E. & WAKE, D. B., 1976. Tongue evolution in lungless salamanders, family Plethodontidae. I. Introduction, theory, and a general model of dynamics. *Journal of Morphology, 148:* 265–286.

LOMBARD, R. E. & WAKE, D. B., 1977. Tongue evolution in the lungless salamanders, family Plethodontidae. II. Function and evolutionary diversity. *Journal of Morphology, 153:* 39–80.

LOMBARD, R. E. & WAKE, D. B., 1986. Tongue evolution in the lungless salamanders, family Plethodontidae. IV. Phylogeny of plethodontid salamanders and the evolution of feeding dynamics. *Systematic Zoology, 35:* 532–551.

MAGIMEL-PELONNIER, O.-L., 1924. La langue des amphibiens. Thèse Facult. Sciences, Paris.

MATSUSHIMA, T., SATOU, M. & UEDA, K., 1985. An electromyographic analysis of electrically-evoked prey-catching behavior by means of stimuli applied to the optic tectum in the Japanese toad. *Neuroscience Research, 3:* 154–161.

MATSUSHIMA, T., SATOU, M. & UEDA, K., 1988. Neuronal pathways for the lingual reflex in the Japanese toad. *Journal of Comparative Physiology A, 164:* 173–193.

MILLER, B. T. & LARSEN, J. H., 1990. Comparative kinematics of terrestrial prey capture in salamanders and newts (Amphibia: Urodela: Salamandridae). *Journal of Experimental Zoology, 256:* 135–153.

NISHIKAWA, K. C. & ROTH, G., 1991. The mechanism of tongue protraction during prey capture in the frog, *Discoglossus pictus. Journal of Experimental Biology;* in press.

NOBLE, G. K., 1922. The phylogeny of the Salientia. I. The osteology and the thigh musculature; their bearing on classification. *Bulletin of the American Museum of Natural History, 46:* 1–87.

NUSSBAUM, R. A., BRODIE, E. D. & STORM, R. M., 1983. *Amphibians and Reptiles of the Pacific Northwest.* Moscow, Idaho: University Press of Idaho.

REGAL, P. J. & GANS, C., 1976. Functional aspects of the evolution of frog tongues. *Evolution, 30:* 718–734.

REILLY, S. M. & LAUDER, G. V., 1989a. Kinetics of tongue projection in *Ambystoma tigrinum:* quantitative kinematics, muscle function, and evolutionary hypotheses. *Journal of Morphology, 199:* 223–243.

REILLY, S. M. & LAUDER, G. V., 1989b. Physiological bases of feeding behavior in salamanders: do motor patterns vary with prey type? *Journal of Experimental Biology, 141:* 343–358.

REILLY, S. M. & LAUDER, G. V., 1990. The evolution of tetrapod feeding behavior: kinematic homologies in prey transport. *Evolution, 44:* 1542–1557.

REILLY, S. M. & LAUDER, G. V., 1990. The strike of the tiger salamander: quantitative electromyography and muscle function during prey capture. *Journal of Comparative Physiology, A, 167:* 827–839.

SCHWENK, K., & THROCKMORTON, G. S., 1989. Functional and evolutionary morphology of lingual feeding in squamate reptiles: phylogenetics and kinematics. *Journal of Zoology, London, 219:* 153–175.

STEBBINS, R. C., 1985. *A Field Guide to Western Reptiles and Amphibians.* Boston: Houghton Mifflin.

SOKAL, R. R. & ROHLF, F. J., 1981. *Biometry,* 2nd edition. San Francisco: W. H. Freeman.

THEXTON, A. J., WAKE, D. B. & WAKE, M. H., 1977. Tongue function in the salamander *Bolitoglossa occidentalis. Archives of Oral Biology, 22:* 361–366.

TYLER, M. J., 1971. The phylogenetic significance of vocal sac structure in hylid frogs. *University of Kansas Publications, Museum of Natural History, 19:* 319–360.

TRUEB, L. & GANS, C., 1983. Feeding specializations of the Mexican burrowing toad, *Rhinophrynus dorsalis* (Anura: Rhinophrynidae). *Journal of Zoology, London, 199:* 189–208.

WAINWRIGHT, P. C. & LAUDER, G. V., 1986. Feeding biology of sunfishes: patterns of variation in the feeding mechanism. *Zoological Journal of the Linnean Society, 88:* 217–228.

WAINWRIGHT, P. C., SANFORD, C. P., REILLY, S. M. & LAUDER, G. V., 1989. Evolution of motor patterns: aquatic feeding in salamanders and ray-finned fishes. *Brain, Behavior and Evolution: 34:* 329–341.