

## Terrestrial Prey Capture in *Xenopus laevis*

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*Xenopus laevis* is one of the most intensively studied of laboratory animals, with investigations centered upon developmental, cell and molecular biology (Gurdon, 1996). In contrast, ecological information on the genus *Xenopus* is insubstantial. Fundamental ecological concerns, such as diet, are only sketchily documented from a few studies concerned with gut contents. The distribution of *Xenopus* species in sub-Saharan Africa includes several divergent vegetation types, from savanna to forest, as well as a wide range of altitudes and temperatures (Tinsley et al., 1996). Studies of gut contents include six (of the known 17) species in pools, ponds, and lakes from equatorial forest of West Africa (Noble, 1924; Inger and Marx, 1961; DeBruyn et al., 1996), the Central African highlands (Tinsley, 1973; Tinsley et al., 1979; Kazadi et al., 1986), and temperate savannas of southern Africa (Simmonds, 1985; Schoonbee et al., 1992). In addition to these studies of *Xenopus* in native areas, two further investigations have looked at the diet of feral *X. laevis* in California (McCoid and Fritts, 1980) and South Wales (Measey and Tinsley, 1998). All of these accounts show diets in which aquatic invertebrates predominate. This is not surprising for this genus of aquatic amphibians and reflects a fundamental ecological separation between pipids and most other anurans.

However, although all these studies concur that aquatic organisms dominate the diet of *Xenopus*, all have also found terrestrial invertebrates (and even terrestrial vertebrates, see Inger and Marx, 1961) in stomach contents. Many explanations have been suggested for the presence of terrestrial prey in the stomachs of wild caught *Xenopus*. Tinsley (1975) suggested that some terrestrial arthropods are collected from the surface tension where they become trapped. Inger and Marx (1961) claimed that the large number of terrestrial prey items found in *X. laevis* from Upemba could not be explained solely by these organisms falling into the water. They suggested that, since *X. laevis* is known to wander over land, it may also feed at these times. A similar explanation is given by Kazadi et al. (1986) who considered that *X. laevis* is not restricted to a completely aquatic strategy; terrestrial items may be caught and ingested by animals that wander around on land. Tinsley et al. (1996), in a comprehensive review, suggested

that the terrestrial component of *Xenopus* diets is unlikely to have arisen solely from animals that have fallen or been swept from overhanging vegetation into the water; they concluded that "there is a major need for unambiguous information on this basic point."

The feeding mechanism used by pipids is unique among anurans (Duellman and Trueb, 1986). Pipids lack tongues, and food is transported into the mouth by suction produced by a hyobranchial pump (Sokol, 1969). Water currents, created by intraoral pressure changes, suffice for small prey items, but larger items require mechanical manipulation. Anecdotal descriptions of the mechanisms of *Xenopus* feeding are common (e.g., Rose, 1962; Deucher, 1975) and relate to the forking movements of the forelimbs and the tearing of oversized prey by the claws on the hind feet. Avila and Frye (1977, 1978) and Frye and Avila (1979) provide detailed descriptions of feeding behavior in *X. laevis*, but these studies in common with all other observations do not explain the presence of a terrestrial component in the stomach contents of wild-caught *Xenopus*.

Studies of the feeding mechanisms of amphibians have increased the understanding of the transition from aquatic to terrestrial life by documenting a wide diversity of prey capture methods in both aquatic and terrestrial environments (Lauder and Reilly, 1994). Among anurans, feeding behavior is characterized by three types of tongue projection: mechanical pulling (e.g., *Hyla cinerea*, Deban and Nishikawa, 1992); ballistic (e.g., *Bufo marinus*, Gans and Gorniak, 1982); and hydrostatic (e.g., *Hemisus marmoratum*, Ritter and Nishikawa, 1995). Although accounts include a number of examples of archaebatrachian anurans (see for example Nishikawa and Cannatella, 1991), the feeding mechanisms of pipids, considered to be among the most highly derived and advanced of the archaebatrachians (Cannatella, 1985; Trueb, 1996), have not been investigated comprehensively. Such an investigation would contribute to the understanding of the evolutionary transformation of aquatic feeding systems into terrestrial prey transport designs. This study documents a newly observed capture mechanism by which *X. laevis* can prey on terrestrial invertebrates.

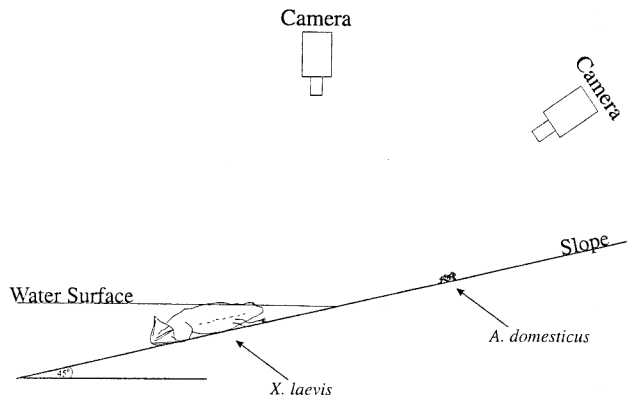


Fig. 1. Experimental apparatus for high-speed video recording of *Xenopus laevis* feeding terrestrially on *Achaeta domestica*.

#### MATERIALS AND METHODS

*Xenopus laevis laevis*, laboratory-reared from stock imported from Cape Province, South Africa (snout-vent lengths 60–65 mm), were maintained in naturalized conditions in a glass aquarium 1.2 m long, 0.35 m wide, and 0.5 m high. The water was maintained at a temperature of  $15 \pm 1$  C and a depth of 0.13 m (55 liters) over a gravel substrate, with spiked water millfoil (*Myriophyllum spicatum*), and large stones that projected from the water surface. Crickets (*Achaeta domestica*), which were placed on top of the stones, supplemented a regular diet of chopped beefsteak.

For filming, the *X. laevis* were placed in a smaller tank ( $320 \times 220 \times 200$  mm) in 3.5 liters of dechlorinated water ( $18 \pm 1$  C) with a ramp projecting beyond the water surface at an angle of  $45^\circ$  (air temperature  $20 \pm 2$  C; Fig. 1). Crickets were allowed to roam on the ramp, and movements of *X. laevis* were recorded from above and from the front with an NAC HSV-400 high-speed video system through a 55 mm Micro Nikkor lens, at 200 frames per second with synchronized stroboscopic illumination. The images were analyzed with Hi-8 tape archived from the camera and using acetates drawn from frozen frames. Measurements of snout-vent length (SVL) were calculated as a percentage of the contracted length, that is the shortest SVL recorded (see Fig. 2H).

#### RESULTS

Observations were made of over 100 terrestrial feeding episodes of *X. laevis* in naturalized conditions. Although not all of these episodes were successful, no quantification of success rate is presented due to the heterogeneity of the naturalized conditions. High-speed video recordings were made of three feeding episodes

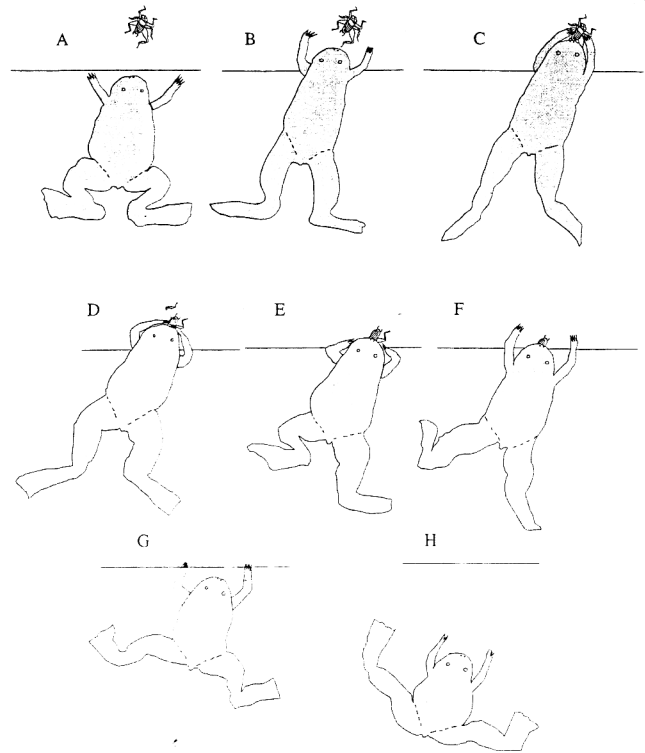


Fig. 2. Terrestrial feeding movements of a female *Xenopus laevis*. In (A), the female is in a preparatory position, and the cricket (*Achaeta domestica*) is walking slowly away. The cricket is siezed in (C) and the frog retreats in (D) to (H). The line represents the edge of the water. Drawn from frozen frames at 0.03-sec intervals of high-speed video recordings.

(of three different animals) from overhead and one from an anterior position. The movement has been subdivided into four phases: preparatory, fast, opening; closing; and recovery (Lauder and Reilly, 1994).

Preparatory behavior was characterized by the following criteria. The rear limbs were not outstretched but flexed so that the splayed feet were held symmetrically and slightly posterior to the vent (Fig. 2A). Measurements of SVL in this position (from stilled video frames) averaged 107% of the contracted length. A part of the animal touched the substrate under the water, often the outside toes of the hind feet or the ventral surface of the frog. The eyes and nares protruded from the water surface, with the surface tension held around the orbital and parietal lateral-line organs. Depending on the slope on which the animal rested, this meant that other parts of the frog, such as the fingers, may also emerge above the water surface. In this position, animals were able to wait without moving for long periods of time.

Fast opening of the mouth was combined with a lunge, triggered by the movement of a cricket on the slope within 50% of the contracted body length of the waiting frog. Crickets re-

maining still within this area were ignored, as were crickets moving outside this area. During this movement, the frog launched itself out of the water toward the prey item. The power of the movement was provided by the hind feet pushing backward in the water. The position of the pelvis extended to the maximum length, with respect to the vertebral column, making the SVL its greatest (119% of contracted body length). Forelimbs were held stretched forward, and hind limbs were at maximum stretch, the toes together (see Fig. 2C). The mouth of the frog was held wide open and ventroflexed toward the target prey. The movement from waiting to full stretch was timed from video frames as  $60 \pm 5$  msec ( $n = 3$ ). The prey was seized at the end of the fast opening phase.

Closing of the mouth followed the intake of the prey in a successful capture event. The forelimbs closed together behind the prey item, the fingers interlocking and pulling the item toward the open mouth.

Recovery followed the closing phase whether or not the cricket was successfully grasped. This phase involved the rapid movement of the frog backward into the water. The hind feet were brought directly back toward the vent, with toes splayed and webbing taut, SVL simultaneously shortening. The feet then moved quickly out to the sides until level with the head, pushing water forward. At this point, SVL was at its shortest. If the cricket was held in the mouth, the forelimbs moved outward away from the mouth and were held parallel in front of the frog (Fig. 2F).

During some of the observed events, crickets, which were not immediately taken into the mouth during the closing phase, were pulled back by the forelimbs during recovery and subsequently brought into the mouth. In other instances, the mouth closing on a leg of a cricket was enough to retrieve it into the water where it was manipulated by the forelimbs for full ingestion, which always occurred underwater. Any distraction made by the investigators during filming (including movements over and around the tank) led to withdrawal of the *X. laevis* away from the water surface under any furnishings present. The speed at which this occurred depended upon the suddenness of the movement.

#### DISCUSSION

The feeding mechanisms of aquatic and terrestrial Salamandridae have been compared by Özeti and Wake (1969) who found that terrestrial species have large mouth openings and aquatic species smaller mouths, increasing the

efficiency of their hyobranchial pump method of feeding. In semiaquatic salamandrids returning to water, labial lobes, which increase the velocity of inflowing water by reducing aperture, redevelop and are most important to efficient aquatic feeding. Like aquatic salamandrids, *Xenopus* lack a protrusible tongue but do not have these other adaptations to aquatic feeding. The morphological characteristics seen in *Xenopus* suggest a versatility of function, of which the terrestrial component probably plays an important part.

Lauder and Reilly (1994) recommended a standard terminology for phases in amphibian feeding behavior, emphasizing the importance of the fast opening phase in prey capture. In this study, it was not possible to carry out the precise measurements needed to further analyze gape and hyoid features due to the low number of successful film recordings of terrestrial prey capture. However, it seems clear that, of the mechanisms by which this aglossal aquatic anuran feeds terrestrially, the fast body lunge is more important than the fast opening of the mouth. This is in keeping with studies of terrestrial anurans that have also highlighted the importance of lunging (e.g., Nishikawa and Roth, 1991; Deban and Nishikawa, 1992; Gray and Nishikawa, 1995).

In the preparatory phase, the floor of the buccal cavity can be seen to move as the hyoid apparatus is raised and lowered to assist ventilation (Brett and Shelton, 1979). This action may also allow air to be analyzed for olfactory cues, since *X. laevis* possesses two classes of olfactory receptors, one aquatic and one terrestrial (Freitag et al., 1995). Refraction of the eyes in *X. laevis* is for vision in air, which suggests that a major function for vision is analysis of the environment out of the water (Elepfandt, 1996). When the dorsally positioned eyes protrude from the surface (see Fig. 1), the visual field extends over the total emergent area enabling the location of potential predators and prey items (Graydon and Giorgi, 1984). Graydon and Giorgi (1984) also found a faint visual streak corresponding to minimal improvement for horizontal directions. The lateral-line organs can give information about possible predators or prey in the water behind and below the animal (Elepfandt, 1984; Elepfandt and Weidemer, 1987).

During the lunge, the iliosacral joint between the sacrum and ilium of the pelvic girdle is at full stretch. The sliding of the ilia and sacral diapophyses is very important in accelerating the lunge and recovery in this feeding mechanism. The joint has been previously studied,

and pipids are one of the few anuran families known to be uniformly characterized by a Type-I iliosacral articulation (Emerson, 1979; Trueb, 1996). Very fast striking movements (around 10 msec<sup>-1</sup>) minimize the risk of attack by predators and maximize the chances of capturing prey with rapid escape reflexes. This movement is faster than any other previously recorded for *Xenopus*. The very great acceleration produced by the coccygeo-iliac muscles during swimming have been previously demonstrated. Videler and Jorna (1985) recorded a maximum speed of 1 msec<sup>-1</sup> during swimming, and Miller and Camilliere (1981) recorded swimming speeds of 1.5 msec<sup>-1</sup> after physically training *X. laevis*.

The lunge seemed to be triggered by movement of the prey item. Therefore, it is presumed that only vision was used, in contrast to aquatic prey detection. The eyes were not used during the strike because the prey falls below the frog (see above). No observations were made of *Xenopus* catching terrestrial prey more than one body length from the water's edge. However, during the whole of this study, the frogs were well fed, and the possibility exists that they would have ventured further had they been more hungry.

Recovery involved a similar movement to the fast dive from the water surface described by Videler and Jorna (1985), principally using the ilio-lumbar muscles. Following the recovery (Fig. 2F), one of the rear feet would be moved out, whereas the other held close to the head producing a wheeling motion, turning the frog through 180° and enabling it to swim immediately forward into deeper water. This wheeling movement is also seen following the compression after a fast dive (pers. obs.). In their natural habitat, *Xenopus* often live in turbid conditions; thus, as soon as they are below the surface, effective escape is made from terrestrial predators (see Tinsley and Kobel, 1996, and references therein).

The mechanism described in this study explains the presence of some of the terrestrial components in the diet of *Xenopus*, although it seems likely that there are other mechanisms through which terrestrial prey may be acquired. These mechanisms include leaping out of the water to catch volant prey items (Simmonds, 1985). The responses of *X. laevis* to wave stimuli are well documented (Elepfandt, 1992) and are thought to relate to the ability of *Xenopus* to catch invertebrates trapped in the surface tension. *Xenopus wittei* has been observed to catch crickets walking on *Lemna minor* thalli (Measey and Tinsley, 1997); the mechanism for this is

essentially the same as that of *Xenopus* responding to wave stimuli.

The proportion of the terrestrial component of gut contents may be exaggerated in some studies, in which a *Xenopus* population has eaten all aquatic prey in a water body, and is likely to be seasonal in many natural habitats. However, this study redefines the ecological niche of *X. laevis* and prompts reconsideration of assumptions made about competition with other amphibians (Tinsley et al., 1996).

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