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SHORT COMMUNICATION

Underwater and Terrestrial Feeding in the Sri Lankan Wart-frog, *Lankanectes corrugatus*

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ABSTRACT

The vast majority of the world's anurans feed terrestrially, with aquatic prey capture having been observed in only a handful of species. We tested the predation behaviour of the strictly aquatic 'fanged' frog *Lankanectes corrugatus* (Nyctibatrachidae) by providing specimens with both aquatic and terrestrial feeding opportunities. The frogs successfully captured prey both underwater and on land adjacent to water. During underwater feeding they located prey purely by tactile stimuli rather than by vision; prey were scooped into the open mouth using both hands. When feeding terrestrially, however, the frogs relied on visual cues alone when attacking prey, capturing prey items by lunging at them, grasping and scooping with the hands. Oral suction and tongue or jaw prehension were not observed in prey capture whether underwater or on land, and the 'fangs' do not appear to play a role in prey capture or ingestion.

Keywords: *Limnonectes*, natural history, Nyctibatrachidae, sub-aquatic feeding, trophic ecology

INTRODUCTION

Lankanectes corrugatus, a nyctibatrachid frog endemic to Sri Lanka, is widely distributed in the island's south-western quarter, from near sea level to elevations of about 1500 m (Manamendra-Arachchi and Pethiyagoda, 2006). Despite being a relatively common species made additionally conspicuous by large size (up to 70 mm snout-vent length) and a loud, distinctive call, very little is known of its natural history, even oviposition being as yet unreported. *Lankanectes* are obligatorily aquatic frogs, usually inhabiting shallow pools in rainforest streams where they rest on the substrate, seated on their haunches, submerged except for their eyes, which protrude above the surface (Fig. 1). Juveniles retain the lateral-line sensory system and exhibit a marked sexual dimorphism: males possess a pair of prominent bony odontoid processes ('fangs') on either side of the mandibular symphysis, the processes being greatly reduced in females (Manamendra-Arachchi and Pethiyagoda, 2006).

Feeding mechanisms of anurans are diverse. Most terrestrial anurans have attached, protrusible tongues and depend heavily on lingual adhesion for capturing prey. A smaller proportion of species uses jaw prehension, while others possess highly specialized jaw-closing mechanisms to capture prey (Nishikawa, 2000). Underwater feeding, however, is rare among anurans and has hitherto not been reported in any Asian species. Feeding in water poses substantially different challenges than capturing prey on land, given the much higher density, viscosity and, in the usual habitats of *L. corrugatus*, also the turbidity of water in comparison to air (Carreno and Nishikawa, 2010).

In 2004, M. M. Bahir (pers. comm.) reported a chance observation of an *L. corrugatus* apparently preying on an aquatic invertebrate underwater at Agrapatana, in the Sri Lankan highlands. Recent field work at the same site provided us with an opportunity to further investigate its feeding behaviour.

MATERIALS AND METHODS

We placed six freshly-collected *L. corrugatus* (38–61 mm SVL) individuals (three of each sex) one at a time in a 30-cm wide glass aquarium with sufficient water for the frogs to rest in their usual posture (Fig. 1). Two earthworms (~5-12 cm) were then dropped into the water and the succeeding sequence was recorded at 300 frames per second (10 × real-time) using a Casio ExilimEX-F1 video camera. Frogs were released to the same stream after between two and four feeding attempts. We also tested terrestrial feeding by building a sand-filled 10-cm wide (*i.e*. greater than the frogs' SVL)

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embankment on one side of the aquarium, on the far side of which a grasshopper was placed.

RESULTS

All six frogs attempted to capture earthworms under water. During these predation events the frogs did not respond to the worms until one of the prey made contact. They then either dived (Fig. 2A) or sank (Fig. 2B,C) to the prey, mouth agape, using both hands (manus) to capture the prey and shove it into the mouth (Movement 1, sensu Gray *et al*., 1997), the hands being inserted into the oral cavity in their entirety. The mouth was agape well before scooping commenced, which suggests that oral suction plays no role in the capture of the prey used here. The frogs evidently did not use visual cues to locate prey, never attacking a worm unless a tactile stimulus was received. Of the 35 attempted underwater feeding events observed, 14 were unsuccessful, the frog initiating a dive but being unable to locate the prey despite it being within a head-length of its eyes, which suggests that visual cues are not used to locate prey underwater. As is evident from Fig. 2, when feeding on earthworms underwater, *L. corrugatus* does not employ oral suction or tongue or jaw prehension: it appears to rely wholly on scooping to force prey into the mouth.

During terrestrial feeding, using visual cues alone the frogs attacked the prey by lunging, squashing them against the substrate using their hands, and then grasping and pushing the prey into the mouth using both hands. Tongue or jaw prehension was not observed during this action. The frogs then retreated to the water by scrambling backwards immediately once the prey was secured, and resumed their resting posture. All four terrestrial feeding attempts observed were successful.

DISCUSSION

We report these observations because underwater feeding and/or the use of hands in feeding have been recorded in very few species of anurans. The vast majority of frogs and toads possess protrusible tongues and employ lingual adhesion as the primary means of prey capture (Nishikawa and Schwenk, 2002).

The majority of aquatic-feeding anurans use "terrestrial" methods such as jaw, tongue or forelimb prehension for aquatic prey capture (Dean, 2003). The other method of underwater prey capture by anurans is inertial suction feeding, which occurs only in the tongue-less frogs of the family Pipidae (Carreno and Nishikawa, 2010). For frogs feeding on large prey, however, the forelimbs play a significant role in prey manipulation. Here, the jaws are used to capture prey and the forelimbs used to transport prey into the oral cavity (Gray *et al*., 1997).

Figure 1. The usual resting posture of *Lankanectes corrugatus*

Figure 2. The underwater prey-capture sequences of *Lankanectes corrugatus*. A, an unsuccessful attempt, diving; B, a successful attempt, sinking; C, a successful attempt, sinking (in frontal view). Elapsed time is shown in milliseconds from the commencement of each strike.

In contrast, when feeding on smaller prey, these frogs transfer the prey into the oesophagus without the involvement of the forelimbs. Gray *et al*. (1997), who identified five distinct forelimb-movement patterns used for prey manipulation in frogs, suggested that the 'scooping' movement is primitive, widespread and well developed among aquatic anuran taxa. This method of feeding, however, may depend on the size and type of prey.

Although anurans are able to locate prey on the basis of tactile, olfactory or even auditory cues alone, vision appears to be the dominant sensory modality that most frogs use to detect prey (Monroy and Nishikawa, 2011). Frogs frequently use alternative kinematic strategies to deal with variation in particular attributes of their prey, such as size, shape, velocity or location, as is evident also in our observations. *Lankanectes corrugatus* usually inhabit shallow regions of seasonally turbid streams in which vision would likely be of limited use in locating prey underwater, whereas in terrestrial feeding visual cues alone were clearly sufficient for locating prey.

The diet of *L. corrugatus* is poorly known, as is much of its natural history. The gut contents of a few specimens have revealed aquatic beetles, cockroaches, millipedes, centipedes and dragonflies (M. Meegaskumbura, pers. comm.) suggestive of a broad, primarily terrestrial diet. In the aquarium, *Lankanectes* feed readily on earthworms, grasshoppers and other arthropods that match its size (H.S., pers. obs.).

It is also noteworthy that the 'fangs' of *Lankanectes* (analogous structures occur also in other anuran lineages, *e.g.* the dicroglossid genus *Limnonectes*) do not appear to play a role in prey ingestion or defence: the frogs did not attempt to bite when handled. As their sexual dimorphism suggests, their function is likely to be associated with combat or threat behaviour between males, as in *Limnonectes* (Tsuji and Matsui, 2002).

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