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Deceptive digits: the functional significance of toe waving by cannibalistic cane toads, *Chaunus marinus*

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Many ambush foraging predators possess specialized structures and behaviours that plausibly function to attract prey, but this hypothesis has rarely been subject to direct empirical tests. If luring evolved to attract specific prey types then we predict that it will be manifested only if that prey type is present, and only by predators of the size class that feed on that prey type. Also, luring should induce closer approach by prey; and aspects of the behaviour (e.g. frequency of movement of the lure) should have been fine tuned by selection to induce maximal response from prey. We describe a novel luring system: small- and medium-sized (but not metamorph and large) cane toads, *Chaunus marinus*, wave the long middle toe of the hind-foot up and down in an obvious display. In keeping with the functional hypothesis, toe waving is elicited by moving edible-sized objects such as crickets or metamorphic toads. Metamorphic toads are attracted to this stimulus, and trials with a mechanical model show that both the colour and the vibrational frequency of the toe correspond closely with those most effective at attracting smaller conspecifics towards the lure. The independent evolution of visual luring systems in many animal lineages provides a powerful opportunity for robust empirical tests of adaptive hypotheses about signal design.

Keywords: anuran; cane toad; *Chaunus marinus*; luring; mimicry; predator–prey; signal design

Predators use a diverse array of behaviours to locate and capture prey, but a high frequency of parallel and convergent evolution means that broad categories of foraging modes can be defined across a surprisingly wide phylogenetic breadth (Huey & Pianka 1981). One of the most distinctive such modes involve ambush ('sit-and-wait') predation, whereby the predator remains sedentary and relies upon prey movement to create opportunities for capture. Ambush predation has evolved independently in a wide array of invertebrate lineages, as well as in many vertebrate groups (e.g. Perry 1999). Although some predators switch flexibly between active searching and ambush predation (e.g. *Boiga irregularis*: Rodda 1992), or shift ontogenetically in foraging mode (e.g. *Ctenotus taeniolatus*: Taylor 1986), many predator species rely almost entirely upon capturing prey from ambush (e.g. ant-lions: Heinrich & Heinrich 1984).

A broad range of adaptations in morphology, physiology and behaviour have been speculated or reported to enhance success in ambush predation. Most obviously, ambush predators must remain immobile for long periods (e.g. Greene & Santana 1983; Webb & Shine 1997), be highly cryptic so that they are not detected by the approaching prey item (e.g. Shine & Sun 2002; Webb & Manolis 2002) and be able to select ambush sites that provide a high probability of encounter with potential prey items (e.g. lions waiting beside waterholes; pit-vipers waiting beside rodent paths: Schaller 1972; Reinert et al. 1984). Even in such circumstances, however, ambush predators may capture prey less often than do active foragers, because few prey items approach close enough to be captured (Reed & Shine 2002). Presumably in response to this situation, many ambush predators have evolved specialized morphologies and behaviours that are believed to lure prey within striking distance, and hence to increase feeding opportunities for the predator (Gudger 1945; Atz 1950; Pietsch & Grobecker 1978; Drummond & Gordon 1979; Ernst et al. 1994). Different tactics have evolved in different kinds of predators, but broad convergences are common, presumably driven by the limited number of body parts that can be used as lures to mimic the small food items consumed by prey species. For example, the use of tail tips (often distinctively coloured) that are waved in the air to lure prey appears to have evolved

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independently in boid (Radcliffe et al. 1980), colubrid (Sazima & Puorto 1993; Leal & Thomas 1994; Tiebout 1997), elapid (Carpenter 1978; Chiszar et al. 1990), pythonid (Murphy et al. 1978; Simon et al. 1999), and viperid (Allen 1949; Wharton 1960; Henderson 1970; Greene & Campbell 1972; Heatwole & Davison 1976; Jackson & Martin 1980; Sazima 1991; Parellada & Santos 2002; Reiserer 2002; Rabatsky & Waterman 2005) snakes. Similarly, modifications of tongue shape and extrusion rates may function to lure prey in turtles (Ernst et al. 1994) as well as snakes (Goodman & Goodman 1976; Welsh & Lind 2000) and birds (Master 1991).

At first sight, anuran amphibians are poorly suited to luring prey. Many species are ambush foragers, but (at least as adults) they lack elongate body parts, such as tails or slender extrusible tongues. None the less, prey luring occurs in at least two South American frog species, the leptodactylid *Ceratophrys calcarata* (Murphy 1976; Radcliffe et al. 1986) and the phyllomedusid *Phyllomedusa burmeisteri* (Bertoluci 2002). These squat large headed frogs use the toes of their hindfeet as lures, waving the toes when presented with potential prey. *Ceratophrys* eat other anurans (Murphy 1976; Duellman 1978; Radcliffe et al. 1986), and luring responses were elicited more frequently to anuran than to invertebrate prey (Radcliffe et al. 1986). A captive *Phyllomedusa* was reported to wriggle its toes in response to crickets but not cockroaches or mealworms (Bertoluci 2002). In the current paper we report another example of pedal luring in an anuran, but in a species from a different family and showing a different form of the behaviour. Our analysis also is novel in attempting to robustly test specific predictions from the hypothesis that this toe waving behaviour functions to lure prey. Previous work on luring behaviour largely has been descriptive and anecdotal, with little attempt to frame and test specific ideas (e.g. Bertoluci 2002; Parellada & Santos 2002; but see Reiserer 2002).

The scarcity of experimental approaches to this topic is surprising, in that the central hypothesis, that the form and motion of the body part functions to attract prey, is amenable to empirical test rather than relying on subjective evaluation of plausibility. For example, that hypothesis generates the following set of falsifiable predictions:

(1) The putative luring behaviour will be displayed only by predators that eat that prey type (in many species, dietary habits shift with predator body size, thus permitting a direct intraspecific test);

(2) The putative luring behaviour will be elicited only by the presence of specific types of prey;

(3) Potential prey will approach the putative lure, especially when it is being moved about; and

(4) The form and movement of the putative lure are more effective at attracting prey than are most alternative forms and movements.

METHODS

Study Species and Initial Observations

Cane toads *Chaunus marinus* (*Bufo marinus* in earlier literature; see Frost et al. 2006 for generic reallocation) are large (to 240 mm snout-urostyle length, 2800 g) anurans native to South and Central America, but now present in many countries because of deliberate anthropogenic introductions (Lever 2001). These slow moving anurans are classic ambush predators, selecting a suitable foraging site and typically moving only short distances during a foraging bout to take prey items that approach too closely (Zug & Zug 1979; Lever 2001; personal observation). Cane toads feed primarily on terrestrial invertebrates (especially, ants and beetles: Oliver & Shaw 1953; Hinckley 1962; Krakauer 1968; Zug & Zug 1979; Evans & Lampo 1996; Grant 1996) but occasionally take vertebrates, including smaller conspecifics (Lever 2001). Most previous analyses of toad diets appear to have been based on large toads (where size of sampled animals is given: Hinckley 1962; Krakauer 1968; Grant 1996) and our own data suggest that cannibalism may be common in smaller toads. For example, we dissected 28 juvenile cane toads (snout-urostyle lengths 21–55 mm) collected beside a water body in northern NSW on 21 December 2005, and found that other cane toads made up 64% of the total of 149 prey items (M. Hagman & R. Shine, unpublished data). These data suggest that cannibalism may be more common than previously reported, especially in small- and medium-sized toads.

Our study animals were collected by hand from a population near the toad invasion front in tropical Australia during March 2005 (Adelaide River floodplain, Northern Territory, 12°45′11.33′S, 131°29′13.82′E), and housed at the University of Sydney. During the 5-h transport from the capture site to Sydney, the toads were placed individually in moist cloth bags inside ventilated plastic containers. We could not detect any negative effects of transport on their health (i.e. no mortality or signs of stress and illness). We collected (and held) the toads under a licence from the New South Wales Department of Primary Industries (number NIA-0205) and The University of Sydney Animal Ethics Committee (number L04/5-2004/3/3908). The toads were originally collected to form a breeding colony for a long-term project at The University of Sydney; they were not captured specifically for the purpose of this study. Thus they are still held in captivity under the conditions described below. In addition to the permits mentioned above we also have University of Sydney Animal Ethics approval for the study presented here (approval number L04/1-2007/1/4516). The cane toad is nonindigenous to Australia and highly invasive. As a condition of the permits mentioned herein, we are not allowed to release our study animals.

The toads were housed in glass aquaria (120 × 60 cm floor area). Each cage housed five medium- or large-sized toads or 20 small (metamorph) toads. We kept large- and medium-sized toads on a substrate of green synthetic turf and provided them with two containers of water (30 × 30 cm and 6 cm). Small toads were kept on a substrate of moist sand that covered two-thirds of the floor area. The remaining third of the enclosure was filled with water to a depth of 4 cm. All toads were provided with hiding shelters, rocks and plastic plants. The enclosures were illuminated by means of two fluorescent tubes that we placed above each tank (photoperiod light:dark