Modulation of foraging strategy in response to distinct prey items and their scents in the aquatic frog *Xenopus longipes* (Anura: Pipidae)

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ABSTRACT - Aquatic predators must forage for prey in a complex three-dimensional environment where the availability of different prey types with different spatial niches may vary. Aquatic predators have evolved a number of ways in which they may respond to this variation, including phenotypic adaptation and behavioural modulation. We investigated whether clawed frogs (*Xenopus longipes*) can modulate their foraging behaviour in response to benthic (bloodworms) and pelagic (glassworms) prey species to which they had already been exposed, and whether any response would be elicited by chemosensory prey cues alone. Frogs responded to the presence of prey items by foraging more than in a control treatment (no cues at all) and were able to respond appropriately to prey type, foraging more in the water column for glassworms and on the aquarium floor for bloodworms. This effect was maintained in a second set of trials where frogs were exposed only to the chemosensory cues of the same prey items. These data show that *X. longipes* can modulate its foraging strategy to match the type of prey available and that this behaviour is at least in part informed by chemosensory cues.

INTRODUCTION

It has been established that aquatic predators live in complex environments where the availability of different prey types may vary in both space and time (Ahlgren et al., 1997; Bogan & Lyle, 2007; Downes, et al., 1993; Hart, 1985; Outridge, 1998). Prey abundance in a particular spatial zone may be dependent on season, and the behaviour and ecology of a particular prey species (Beckett et al., 1992). Previous research has shown that, correspondingly, the composition of the diet of such predators can vary seasonally with relative abundance of different species (Fasola & Canova, 1992).

The fitness of a predator may depend partly on the foraging success of individuals in order to invest in reproduction (Blanckenhorn, 1991; Morse & Stephens, 1996), and so predators must be able to cope with spatial heterogeneity of prey types in order to maximise evolutionary success. In some species, morphological phenotypic polymorphisms may allow individuals to specialise more on particular feeding niches and thus improve foraging success (Ehlinger & Wilson, 1998). Alternatively, individual animals may modulate foraging strategies to optimize them for given prey types as and when they are available (Deban, 1997; Ehlinger, 1989; Heiss et al., 2015; Montgomery & Hamilton, 1997; Persson & Greenberg, 1990).

Amphibians have relatively conserved body forms compared with fish and so are more likely to fall into the latter category than the former. They are often an important component of aquatic vertebrate predator assemblages, especially in temporary and fishless waters (Wells, 2007). Amphibians use a variety of sensory organs to detect prey, including eyes and chemosensory organs (e.g. Miles et al., 2004; Placyk & Graves, 2002) and, in aquatic amphibians, mechano- and electro-receptors (e.g. Himstedt et al., 1982; Martin et al., 2013; Reiss & Eisthen, 2008). Species-specific biases exist in their relative importance in prey detection. Some species use multiple senses (e.g. Avila & Frye, 1978; Manenti et al., 2013; Placyk & Graves, 2002; Uiblein et al., 1992), while others may rely almost entirely on single senses (Martin et al., 2013; Miles et al., 2004).

It is well established that once prey has been located, amphibians may modulate their prey seizing (Anderson, 1993; Deban, 1997; Maglia & Pyles, 1995; Monroy & Nishikawa, 2011; Valdez & Nishikawa, 1997) and processing (Avila & Frye, 1978) tactics in response to different prey types, as well as to different feeding environments (Heiss et al., 2013; Manenti et al., 2013). Moreover, search tactics may be modified flexibly to deal with different distributions of the same prey type (Nomura & Rossa-Ferres, 2011). However, little is known about flexibility of the strategies used by amphibians to search their environment for prey prior to encountering prey items. For example, it is not known whether amphibians are capable of exhibiting flexible (i.e. variable according to treatment), if stereotypic (i.e. little variation within treatments), responses (Wainwright et al., 2008) to cues produced by different prey types in order to improve chances of foraging success. In other aquatic predators (mainly fish), such behaviour is well documented (Ehlinger, 1989; Montgomery & Hamilton, 1997; Persson & Greenberg, 1990) and given the similarity of niche, aquatic amphibians are likely to exhibit similar capabilities.

The Lake Oku clawed frog (*Xenopus longipes*) is a

Critically Endangered (IUCN SSC Amphibian Specialist Group, 2017) pipid frog endemic to the highland crater lake of Mount Oku in Cameroon. *Xenopus longipes* is a generalist predator and feeds largely on aquatic invertebrates (Tapley et al., 2016) and will readily feed on prey items at any position in the water column (C. Michaels pers. obs.), although it occupies the benthic zone and mats of submerged vegetation when not foraging. It is equipped with upward-pointing eyes, dermal mechanoreceptors, typical amphibian chemosensory organs and specialised chemosensory subocular tentacles (Loumont & Koebel, 1991), which could all be employed in foraging. We investigated whether these frogs are able to modulate their foraging behaviour in response to cues from different prey type, and whether chemical cues may be important in detecting prey.

MATERIALS AND METHODS

Study Animals and Husbandry
In this study, we used adult founder (F0) and captive bred F1 *X. longipes* held as part of the Living Collection at ZSL London Zoo, UK. Details of the source of founder animals and the husbandry of the frogs is reported by Michaels et al. (2015); briefly, frogs were maintained in biologically filtered aquaria containing soft, neutral pH water (Total Dissolved Solids <30mg/L, pH c. 7.2), which were held at 16-20 °C. Before this study, animals were fed on a combination of pelleted food (*Xenopus* Express, USA), live bloodworm (Chironomidae), live glassworm (*Chaoborus*), live earthworm (*Eisenia hortensis*) and water fleas (*Daphnia*), with an equal proportion of blood- and glassworms. Frogs remained part of the Living Collection at ZSL London Zoo after the study was completed. The experimental protocol was reviewed by the Zoological Society of London (Zoological Project Database number: ZDZ58) and was designated as not requiring a Home Office license under the UK Animals (Scientific Procedures) Act 1986, as methods did not diverge significantly from normal husbandry.

Experimental Array
Six groups of six frogs, outside the reproductive period, each group comprising one F1 female, one F1 male, three F0 females and one F0 male, were housed in glass aquaria measuring 45x45x45cm filled with water to a depth of 35cm. This combination of sexes and filial generations was used simply to ensure even distribution of these categories between tanks. Aquaria were part of a filtered system linked to a sump and large external canister filter filled with filter foam and ceramic biological filter media (Eheim, Germany). The return plumbing for each aquarium was equipped with a tap allowing isolation of each enclosure from the system, which prevented the circulation of prey scents between enclosures. Each enclosure was equipped with identical hides (one PVC plastic pipe, one 25x10cm piece of plastic trellis and one granite pebble c. 10cm in diameter). There was no bottom substrate.

Experimental Protocol
Groups of frogs were exposed to two trials between the 13 and 22 April, 2016 (Trial 1 and Trial 2). In Trial 1, each group of frogs was presented with three prey treatments (PreyTypeCue) over three consecutive days, the order of which was systematically varied between tanks so that no group of frogs received the treatments in the same order. The three treatments (PreyTypeCue), presented as 3ml of live prey items, were: *Chaoborus* Glassworms, a pelagic species; Bloodworms (Chironomidae), a benthic species; Control, where tank water was disturbed with a clean, plastic 3ml spoon. Immediately after the stimulus was added to a tank, the animals were scan sampled for 15 minutes with counts made instantaneously every three minutes. This 15 minute period was long enough to capture foraging behaviour. At each three-minute interval, frogs were allocated to combinations of the following two category pairs: 'foraging' (repeated flicking of the front limbs, which aims to push any food items into the mouth and is the primary feeding behaviour in this species) or 'non-foraging' (any other behaviour), and 'on the substrate' (any part of the body in contact with the substrate of the aquarium) or 'off the substrate' (no part of the body in contact with the substrate). These paired categories (e.g. foraging on the substrate) were exhaustive and mutually exclusive such that all frogs were in one of the four paired states. A count of the number of frogs engaged in each category was made using a hard-copy check sheet. All observations were made by a single observer (SD).

In Trial 2, the same experiment was repeated one week later, but rather than presenting prey items, each treatment consisted of the addition of 40ml of Reverse Osmosis (RO) water in which live prey items had been soaked for 24 hours to provide chemosensory cues only; the control treatment consisted of plain 40ml RO water delivered using a clean pipette. Powder-free vinyl gloves were worn for all interactions with the aquaria and these were changed between enclosures to avoid contamination with chemical cues.

Statistical Analyses
For each tank in each treatment, the mean number of frogs foraging in the water column and on the aquarium floor over the six observation intervals was calculated, resulting in a single number for each behaviour-position category per tank per treatment. Given the small sample size (6 tanks) and the repeated measures within the same tank, Friedman's test (Q statistics) and Dunn's post-hoc comparison (Z statistics) were employed to assess the foraging patterns between different prey items or between different chemosensory cues. A Wilcoxon paired signed rank test (W statistics) was used to compare numbers of frogs exhibiting appropriate behavioural responses to Bloodworms and Glassworms between Trials 1 and 2. All analyses were conducted in SPSS 23.0 for Windows.

RESULTS

Trial 1

There was a significant effect of PreyTypeCue on the number of individuals foraging on the aquarium floor ($Q^2=12$, $P=0.002$). Using Dunn's post-hoc comparisons (see Fig. 1A), Bloodworms significantly increased the number of frogs that were foraging and on the substrate against Control ($Z=-2$, $P=0.001$). The differences in numbers of frogs that were foraging and on the substrate were not significant between Bloodworms and Glassworms ($Z=-1$, $P=0.083$) or between Glassworms and Control ($Z=-1$, $P=0.083$). There was also a difference in the number of frogs that were foraging and off the substrate across treatments ($Q^2=10.182$, $P=0.006$) where Glassworms had a greater number of frogs foraging and off the substrate than Bloodworms ($Z=1.667$; $P=0.004$) and Control ($Z=1.333$, $P=0.021$). No significant difference between Bloodworms and Control ($Z=0.333$, $P=0.564$) was detected.

Trial 2

There was a significant effect of PreyTypeCue on the number of individuals foraging and on the substrate ($Q^2=10.182$, $P=0.006$). Using Dunn's post-hoc comparisons (see Fig. 1B), Bloodworms significantly increased the number of frogs foraging and on the substrate compared to Glassworms ($Z=-1.333$, $P=0.021$) and Control ($Z=-1.667$, $P=0.004$). There was no difference in this respect between Glassworms and Control ($Z=-0.333$, $P=0.564$). There was also a significant effect of PreyTypeCue on the number of frogs that were foraging and in the water column ($Q^2=7.913$, $P=0.019$); Glassworms had a greater number than Control ($Z=1.583$, $P=0.006$) and Bloodworms ($Z=1.592$, $P=0.012$), but there was no significant difference between Bloodworms and Control ($Z=0.667$, $P=0.248$).

Appropriate Response Comparison

The number of frogs foraging and on the substrate did not differ between Trial 1 and two under the Bloodworms treatment ($W=8$, P>0.05). The number of frogs foraging and off the substrate was significantly lower in Trial 2 than in Trial 1 ($W=0$, P<0.05).

DISCUSSION

In Trial 1, the results establish that frogs did indeed respond to the presence of blood- and glass-worms with distinct foraging behaviours. Further, our results show that chemical cues alone (Trial 2) elicit the same prey-specific foraging responses. The small amount of foraging behaviour seen in control frogs was probably a result of a conditioned response to the approach of a human and of a low level of baseline foraging exhibited by the frogs.

Flexible foraging behaviour allows animals to exploit resources efficiently by using prey search behaviour appropriate to the prey detected (Wainwright et al., 2008) and is an alternative to the evolution of prey-specific morphologies (Ehlinger & Wilson, 1998). Such a flexible hunting strategy also suggests that these frogs specifically target prey items in their environment rather than simply
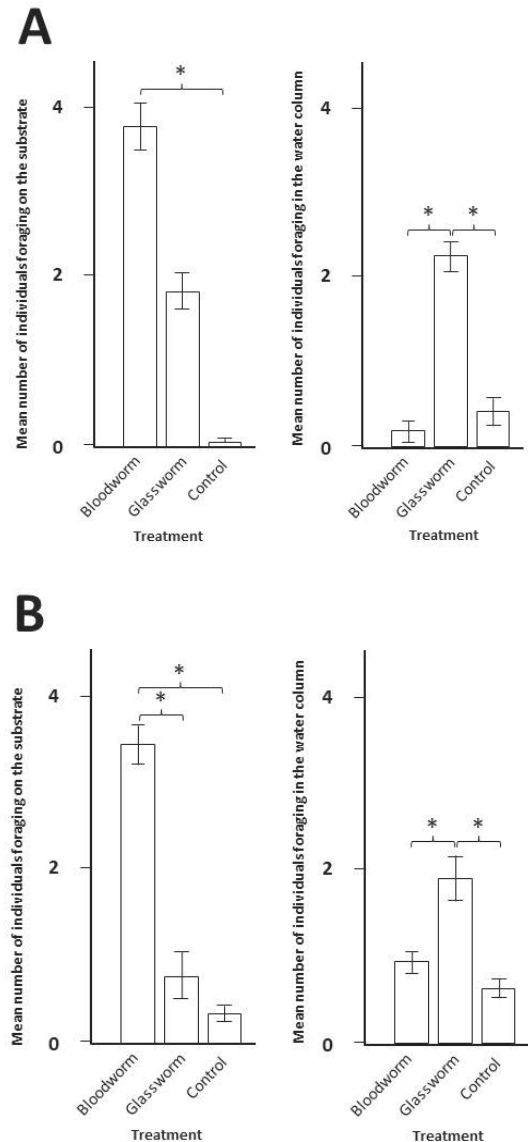

Figure. 1. Mean numbers of frogs foraging on the aquarium floor and foraging in the water column when exposed to glassworms, bloodworms and control treatments in Trial 1 (prey items present; Panel A) and Trial 2 (chemosensory cues only; Panel B). Error bars represent the standard error of the mean. Asterisked brackets reflect significant differences (P<0.05) between the bars at the tips of the brackets identified with Dunn's post-hoc tests; for exact p values, see text. An absence of brackets linking bars implies no significant difference.

ingesting food items when encountered randomly. This specific aspect of plastic foraging behaviour is not well studied in amphibians. Amphibians are known to modulate prey handling behaviour in response to different prey types once encountered (Anderson, 1993; Avila & Frye, 1978; Deban, 1997; Maglia & Pyles, 1995; Monroy & Nishikawa, 2011; Valdez & Nishikawa, 1997), to foraging in different environments (Heiss et al., 2013; Manenti et al., 2013) and to different prey distributions of the same prey type (Nomura & Rossa-Ferres, 2011), but little evidence exists concerning prey searching strategy in this context. It is worth noting that while the frogs in this study displayed

flexible foraging strategies to align their own behaviour with that of the prey item, the method of actually seizing the prey items did not vary noticeably. *Xenopus laevis* is known to use very different means of prey seizure (Avila & Frye, 1978), but this was in response to very different prey forms. In the present study, Bloodworms and Glassworms are probably too similar (both being similarly sized, elongate 'worms') to require different handling behaviours. Chemosensory organs are a dominant sense for prey detection in a number of amphibians (Avila & Frye, 1978; Manenti et al., 2013; Martin et al., 2013; Placykl & Graves, 2002; Telfer & Laberge, 2013). In aquatic species, especially those living in habitats with poor visibility (which does not apply to Lake Oku, which is a relatively low turbidity system – T. Doherty-Bone, pers. Comm.), chemosensory cues may be particularly important (Manenti et al., 2013; Martin et al., 2013; Uiblein et al., 1992). In species where single senses have become highly dominant, other organs are typically reduced (Martin et al., 2013). Although *Xenopus* frogs are able to find prey using olfaction alone (e.g. Avila & Frye, 1978), other sense organs are highly developed including eyes, mechano- and electroreceptors and these are also used to find prey (Elepfandt, 1985; Himstedt et al., 1982). Our data suggest the chemosensory stimuli are an important component of prey detection in *X. longipes*. The number of frogs that were both foraging and in the area in tank occupied by the prey items (or, in Trial 2, where the prey item associated with a chemical would be) did not differ between trials in the Bloodworms treatment. Contrastingly, this was significantly lower in Trial 2, where only olfactory cues were presented, than in Trial 1, where prey items were also present. This suggests that frogs may rely more on chemosensory stimuli to locate Bloodworms than Glassworms, where other senses may be important. *Xenopus longipes* forages for food both during the day and the night in the field (B. Tapley, pers.obs.) and it is also likely that the sensory stimuli used for hunting varies with light levels; in this study, frogs were only fed during hours of light and so any such variation could not be detected. Further work to establish which senses are used for each prey type, any hierarchy in their importance and variation influenced by environmental parameters such as darkness and turbidity, was beyond the scope of this study. The role of learning in the origin of these behavioural strategies is not elucidated by this study, as all frogs had been historically exposed to the prey items used. Given that the prey species used in this study are not sympatric with *X. longipes* in the field, it is unlikely that the prey-specific behavioural response displayed by frogs when presented with both prey and with chemosensory stimuli alone can be explained by innate reflexes. Rather, it is probable that frogs learned to associate particular prey scents with corresponding prey types and locations. *Xenopus laevis* can learn to associate given prey types with particular vibrational signatures (Elepfandt, 1985, 1986; Elepfandt et al., 2000, 2016) and moreover other amphibians show similar associative learning capabilities (Suboski, 1992; Ewert et al., 2001) including using prey chemosensory cues (Dole et al., 1981). The use of naive captive bred frogs may provide insight into the relative importance of innate and learned responses in driving foraging strategy selection. Similarly, as frogs were held in groups for logistical reasons, there may have been a facilitating influence of conspecifics on frog behaviour; however, use of 'tank' as the experimental unit was intended to address this. Further work comparing the behaviour of lone and group-housed frogs in naive and experienced states would allow this to be investigated.

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