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ORIGINAL ARTICLE

A lure at both ends: aggressive visual mimicry signals and prey-specific luring behaviour in an ambush-foraging snake

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Abstract Aggressive mimic species use signals typically resembling an attractive or harmless model to deceive other organisms in order to increase foraging success. With the exception of a few brood parasitic birds that combine two signals, most known cases of aggressive mimicry involve only a single signal. Here, we used fixed videography, a technique which consisted in setting up continuously recording videocameras focused on ambushing animals, to describe—for the first time—the use of two clearly distinct aggressive visual mimicry signals in the same organism, the puff adder (*Bitis arietans*). Our observational data collected in South Africa revealed that puff adders extended their tongues (lingual luring) and waived their tails (caudal luring), presumably mimicking an invertebrate model, in order to lure prey within striking range. Lingual luring occurred only in the presence of amphibian prey, indicating discrimination between prey types. Our study reveals the diverse predatory strategies and complex decision-making process used by 'sit-and-wait' predators, such as ambush-foraging snakes, to catch prey, and indicates that snakes may have higher cognitive abilities than those usually afforded to them.

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Significance statement Predators exhibit various strategies to increase rates of prey capture. One strategy involves the use of luring behaviours, which are signals designed to attract prey within striking range. Using remote videocameras focused on ambush-hunting puff adders (*Bitis arietans*) in the field, we report—for the first time—the use of two clearly distinct luring behaviours in the same organism: puff adders extended their tongues and waived their tails, which presumably resemble invertebrate prey, to draw prey within striking range. Tongue-luring behaviour was solely used in the presence of amphibian prey, which indicates that puff adders distinguished between prey types. Our research underscores that the predatory decisions made by ambush-foraging snakes are diverse and context-dependent and further demonstrates that these predators possess higher cognitive abilities than first expected.

Keywords Caudal luring · Coevolution · Lingual luring · Predator-prey relationship · Puff adder

Introduction

Predators have evolved a variety of tactics to improve feeding efficiency. One spectacular example is aggressive mimicry in which a predator (the 'mimic') simulates the signal properties of a 'model' to dupe potential prey (the 'receiver'), in order to increase foraging success (Wickler 1968; Pasteur 1982). This deceptive strategy has been reported for a variety of organisms including plants (Schiestl et al. 2003), invertebrate and vertebrate animals (Pough 1988; Sazima 2002; Randall 2005; Christy and Rittschof 2011) and involves various sensory modalities. For example, blue-striped fangblennies (*Plagiotremus rhinorhynchos*) visually mimic juvenile blue-streaked cleaner wrasses (*Labroides dimidiatus*) to approach and feed off the scales of fishes waiting to be cleaned (Wickler 1966; Cheney and Cotê 2005), forked-tailed drongos (*Dicrurus adsimilis*) advertise false alarm calls to pick up the food dropped by other small predators that are deceived into running for their lives (Flower 2011), and web-invading spiders and assassin bugs lure web-building spiders within catching range by producing vibrations that resemble prey entangled in the web (Jackson 1992; Wignall and Taylor 2011).

Mimicry evolves if the receiver is fooled into mistaking the mimic for the model and adjusts its behaviour in a way that benefits the mimic (Dalziell and Welbergen 2016). In almost all known cases, aggressive mimicry involves a single signal or variants of a signal. There are, however, exceptions to this; most notably, some brood parasitic birds combine two signals with different sensory modalities (acoustic and visual) to increase the efficiency of aggressive mimicry. For example, common cuckoos (*Cuculus canorus*) lay eggs that match the colour and pattern of their host's eggs and nestlings mimic the begging of the host brood (Davies et al. 1998; Stoddard and Stevens 2010) and bronze cuckoo (*Chalcites basalis*) nestlings acoustically and visually resemble the host nestlings (Langmore et al. 2008, 2011). Nevertheless, we are not aware of a single previously reported case of aggressive mimicry wherein an organism uses two clearly distinct parts of its body as independent visual luring signals aimed at catching prey.

In this study, we report two forms of aggressive visual mimicry, namely lingual and caudal luring, in an ambush-foraging snake, the African puff adder (*Bitis arietans*). These techniques consist of displaying the tongue and waiving the tail, respectively, in a way that presumably mimics a generalised invertebrate larva to lure prey within striking range. These behaviours have previously been reported but never concomitantly in a single species. We used a videographic dataset of puff adders foraging in the field to describe these two luring behaviours and examine the prey specificity of lingual luring. To our knowledge, this is the first evidence for two independent forms of aggressive visual mimicry in the same organism, and our study emphasises the diverse predatory strategies and complex decision-making process used by 'sit-and-wait' predators, such as ambush-foraging snakes, to catch prey.

Methods

Study site and species

The study took place in the Dinokeng Game Reserve, a ca. 18,500-ha area in the Gauteng Province of South Africa (−25.38 S, 28.31 E; ca. 1100 m. a.s.l.). The site, which is composed of a mosaic of savannas and open woodlands, falls within the Savanna Biome (Driver et al. 2005) and is seasonal with hot, wet summers and mild, dry winters (Shulze 1997).

The puff adder is a heavy-bodied medium-sized viperid snake (ca. 700–900 mm snout-to-vent length [SVL]), which occurs in savannas and open woodlands throughout most of sub-Saharan Africa and parts of the Arabian Peninsula. It is a primarily nocturnal, ambush-foraging snake that—in our population—feeds largely on small mammals and amphibians and occasionally on birds and lizards (XG and GJA unpublished data; this study). In the area of study, puff adders are most active from the onset of the rain season, typically in late October–November, to the beginning of the dry season in June–July. During the coldest months of the austral winter (July–August), puff adders do not hibernate but generally remain inactive on the surface, in burrows, under rocks or in termitaria.

Radiotelemetry and fixed videography

As part of a large radiotelemetric study on puff adders, we implanted radiotransmitters (model SI-2, 13 g; Holohil Ltd., Ontario, Canada) into the body cavity of 86 puff adders (42 males, 44 females) in accordance with established procedures (Reinert and Cundall 1982; Reinert 1992; Alexander 2007). Transmitter mass never exceeded 5% of the snake body mass. We released snakes at their capture locations typically 3–4 days following surgery and located snakes every 2–3 days using a R1000 radio receiver (Communications Specialists, Inc., CA, USA) with a two- or three-element Yagi antenna (Africa Wildlife Tracking, Gauteng, South Africa).

From 23 Sep 2013 to 23 Dec 2015, we used fixed videography to monitor the feeding behaviour of radio-tagged puff adders in the field. This method consisted in setting up continuously recording videocameras focussed on ambushing animals and is a powerful technique for recording precise feeding data on ambush-foraging snakes (Clark 2006). Each videocamera unit was made of a closed-circuit television surveillance camera (model PC177IRHR-8, Supercircuit Inc., TX, USA) connected to a recording mini digital video recorder (model MDVR 14-4, Supercircuit Inc., TX, USA; 30 frames per s) and powered by a 12-V sealed lead-acid battery. The videocameras recorded in colour during the day and automatically switched to night-time vision using built-in infrared LEDs at low light levels. We located radio-tagged snakes using radiotelemetry and set up the videocamera units ca. 70 cm in front of ambushing snakes. The following day, we collected the memory cards and reviewed recordings to quantify prey encounter (prey that came within 50 cm of a snake) and capture (successful strikes at prey) rates, prey type and luring behaviour of snakes (lingual or caudal luring). It was not possible to record data blind because our study involved focal animals in the field. We considered an animal as prey based on a sample of 116 puff adder prey items recorded from dissecting museum specimens or observations of free-ranging radio-tagged snakes feeding (XG and GJA unpublished data). Finally, we quantified the number and duration of luring bouts to the closest second using the time stamped on the videos and characterised the duration of chemosensory tongue flicks (i.e. the alternative tongue function) by recording the number of frames when snake tongues were visible (one frame equalled ca. 0.03 s).

Statistical analysis

We conducted all statistical analyses using STATISTICA, version 12.5 (StatSoft Inc. 2014), and SPSS, version 23.0 (IBM Corp. 2015). Values given are means ± SD, and all reported P values are two-tailed. Significance level for all tests was $\alpha = 0.05$.

Results

We reviewed 4634 h (193 continuous days!) of video recordings of snakes foraging (18 females and 18 males). Average time recorded in ambush per snake was 129 ± 119 h (range 1.6–496), and the number of foraging sites used per snake was 6 ± 7 (1–35). Overall, 12 females and 10 males encountered 132 potential prey (43 amphibians, 24 birds, 39 mammals and 26 reptiles) during recordings. Of these 132 prey, one amphibian species, the bubbling kassina (*Kassina senegalensis*), was seemingly not eaten by puff adders: although snakes often struck at other amphibian prey (48%, 11/23), they never did at *K. senegalensis* despite many close encounters (0/20; Fisher's exact test, $P = 0.0002$). We removed this species from our prey encounter dataset, except in one instance when a snake lingual-lured one (see below). Therefore, in total, snakes encountered 112 prey (plus one *K. senegalensis*) and successfully caught 24 of them, a 21.4% capture success.

We observed lingual luring in nine adult individuals (6 males and 3 females; SVL 767 ± 94 mm; mass 663.4 ± 234 g; see Fig. 1 below for an example and online supplementary materials A, B, C, D, E, F, G, H, I, J, K) on 11 occasions and could determine prey identity for nine of these. Lingual luring only occurred in the presence of amphibians (Fisher's exact test; $P < 0.0001$): snakes lingual-lured amphibians on 37.5% (9/24) of encounters but never did in the presence of non-amphibian prey (0/89). Lingual luring largely occurred with bufonid toads ($N = 8$; 6 *Schismaderma carens*, 1 *Amietophrynus* sp., 1 unknown bufonid) and once with *K. senegalensis*. We examined if lingual luring increased amphibian capture success by snakes using a binomial repeated measure logistic regression to account for multiple observations on the same snakes. We removed three cases of lingual luring when prey likely did not see the lure ($N = 2$; prey had their back turned on the snakes) or when the species was seemingly not a prey item ($N = 1$; *K. senegalensis*). Strike success was 66.6% (4/6) for luring snakes and 35.3% (6/17) for non-luring snakes, but this difference was not statistically significant ($P = 0.36$).

We were able to accurately quantify the number and duration of luring bouts for eight observations. Snakes lingual-lured 4.1 ± 7.6 times (range 1–22) for 7.9 ± 4.9 s (3–30) per bout. On five occasions, snakes first lured 20.6 ± 38.9 s (1–90) after the appearance of amphibian prey in the camera's field of view, and on three occasions, amphibian prey entered the field of view 95 ± 83 s (46–191) after the snakes initiated luring. Whenever possible, we quantified the characteristics of chemosensory tongue flicks in a 5-min period either prior the appearance of prey or after the disappearance of prey from the camera's field of view or in cases where snakes successfully caught prey after puff adders resumed their ambush position. We used a general linear model with ln-transformed tongue flick duration as the dependent variable and accounted for multiple observations on the same individuals by averaging the values in the model to avoid pseudoreplication. Lingual luring bouts ($N = 36$) lasted significantly longer compared to chemosensory tongue flicks ($N = 145$; $F_{1,7} = 112.9$, $P < 0.0001$), which averaged 0.5 ± 0.26 s (0.1–1.5 s).

Because of the relatively low resolution of our field video recordings, we were unable to accurately quantify other metrics, but lingual lures varied qualitatively within and between individuals (online supplementary materials A, B, C, D, E, F, G, H, I, J, K). In some cases, the tongue clearly pointed toward the prey, but in others, it was seemingly extended straight relative to the orientation of the head. While extended, the tongue either moved up and down or from side to side. The tips of the tongue were typically stretched out and pointed in opposite directions, but in two cases, they were held close together with the tongue curling downward seemingly making contact with the ground.

We observed caudal luring behaviour in four individuals (two males and two females; SVL 688 ± 73 mm; mass 456 ± 68.6 g; see online supplementary materials L, M, N, O, P) for a total of five observations, but never saw a prey entering the field of view. Luring bouts lasted 655 ± 888 s ($N = 3$). In two cases, the tail was held almost vertical and undulated from side to side, and in one case, the tail was held nearly horizontal and waived up and down. The two remaining snakes used a combination of both. The waiving tail was typically positioned toward the rear of the body ($N = 3$), and in one case to the side of the snake, but never held right above the snake's head. It is worth mentioning that caudal luring displays were dramatically more obvious for males, which have longer tails in our population (ANCOVA; ln-transformed tail length with SVL as covariate; $F_{1,73} = 1254$, $P < 0.0001$), compared to females. Interestingly, two of the snakes that caudal-lured also used lingual luring, either just prior or during caudal luring.

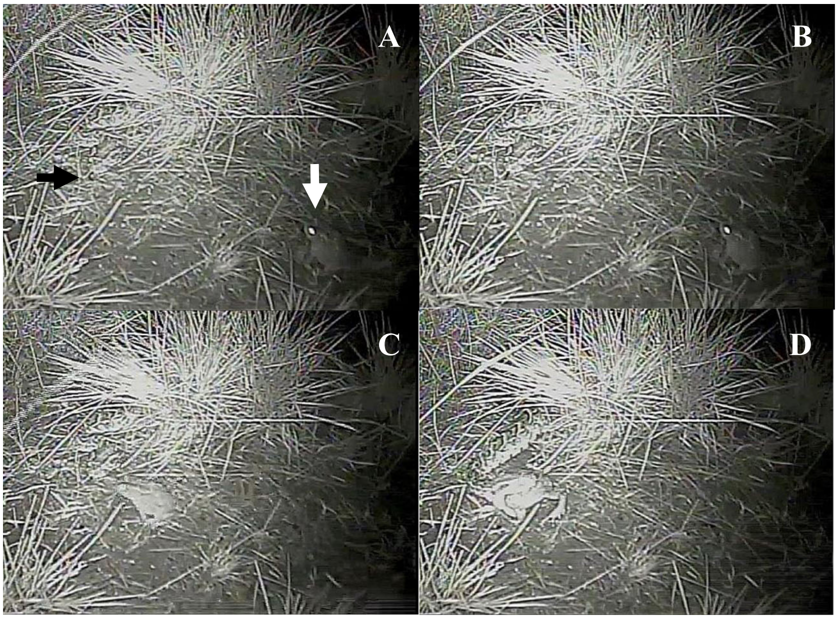

Fig. 1 Lingual luring of a toad by a puff adder. **a**, **b** The snake tongue flicks to lure the toad. **c** The toad approaches the snake to investigate. **d** The snake captures the toad. The *black* and *white arrows* in **a** show the snake and toad's locations, respectively. The tongue of the snake, which resembles a small black worm, is clearly visible on **a**, **b**

Finally, we tested whether the luring behaviours differently affected detection of prey in our video recordings (we removed the two snakes that both caudal- and lingual-lured): despite our small sample size, lingual luring was strongly and positively associated with prey presence in the camera's field of view compared to caudal luring (Fisher's exact test; $P = 0.005$). However, the luring behaviours did not differently affect prey capture (Fisher's exact test; $P = 0.49$).

Discussion

Our study reports two previously undescribed behaviours, lingual and caudal luring, in the ambush-foraging puff adder, which provides the first case of two independent forms of aggressive visual mimicry in the same organism. Further, although our data are observational, we were able to demonstrate the prey specificity of lingual luring. Thus, our study emphasises the diversity of predatory strategies used by ambush-foraging predators to capture prey and contributes to the growing body of evidence which demonstrates that snakes have higher cognitive abilities than first recognised (Reiserer 2002; Glaudas 2004; Putman and Clark 2015a).

Lingual luring has previously been recorded only in a few predators foraging on aquatic prey, namely four species of natricine snakes (Czaplicki and Porter 1974; Welsh and Lind 2000; Hansknecht 2008), a turtle (Drummond and Gordon 1979) and a bird (Master 1991). Therefore, our description of this behaviour is new for predators foraging on terrestrial prey (but see Goodman and Goodman 1976; Lillywhite and Henderson 1993 for other possible snake cases). In our study, we recorded lingual luring only with amphibian prey, and 82% (9/11) of our observations were made with amphibians in the camera's field of view. These observations strongly suggest that this signal is typically used in a predatory context, specifically target amphibian prey as receivers, and that the presence of amphibians is the stimulus that elicits lingual luring.

We also quantitatively demonstrated that luring tongue flicks differed greatly from chemosensory tongue flicks: the range of duration between luring and chemosensory tongue flicks did not overlap, and average length of time for luring tongue flicks was more than an order of magnitude longer. This finding is similar to that reported for two aquatically foraging natricine snakes (Welsh and Lind 2000; Hansknecht 2008) and therefore provides further indirect evidence that the tongue flicks were used as an aggressive mimic signal. Prior to our study, reports of lingual luring in snakes were limited to four closely related natricine snake species, and hence, the occurrence of this behaviour in a distantly related snake suggests an independent evolutionary origin.

Caudal luring is more taxonomically widespread than lingual luring in the animal kingdom. It has been recorded in several species of snakes—particularly juveniles of ambush-foraging snakes (Rabatsky 2008)—as well as in lizards (Murray et al. 1991; Pernetta et al. 2005) and odonate insects (Edgehouse and Brown 2014). For snakes, the receivers of caudal luring signals are typically frogs and lizards (Schuett et al. 1984; Reiserer 2002) and occasionally birds (Andrade et al. 2010; Fathinia et al. 2015). For example, the Iranian spider-tailed viper (*Pseudocerastes urarachnoides*) has evolved a stunningly elaborate tail tip, presumably mimicking an arachnid model, which is seemingly used to attract birds on which it feeds (Fathinia et al. 2015).

Although we never saw prey entering the camera's field of view in response to puff adder caudal luring, it is highly likely that it functions as an aggressive mimic signal (but see Putman and Clark 2015b; Clark et al. 2016 for an unknown tail display function in rattlesnakes). First, this behaviour is relatively common in vipers (Rabatsky 2008), including congeners (FitzSimons 1962; Reiserer 2002). Second, we never observed tail displays by puff adders in a defensive context (e.g. an alternative function; Greene 1973, 1988), despite our extensive experience with this species in the field and laboratory. Finally, all snakes were in ambush when they caudal-lured.

It could be argued that puff adders waived their tail to divert prey's attention from the snake's head, a behaviour called caudal distraction (Mullin 1999). However, this is extremely rare in squamate reptiles (Foster and Martin 2008), has only been described in a distantly related snake species, the grey rat snake (*Pantherophis spiloides*), and typically involves the predator slowly creeping toward prey while the attention of the latter is focussed on the tail (Mullin 1999), which we never observed in puff adders. Thus, despite our lack of conclusive data, the most parsimonious explanation is that puff adders used their tail to lure prey within striking range. Because our videocameras were generally focussed on the snake's head, in many instances, we could not see the snake's tail and this behaviour may be more commonly used by puff adders than reported here.

We examined whether the luring behaviours differently attracted prey into the camera's field of view: lingual luring was comparatively more efficient in doing so than caudal luring. We interpret this as evidence that lingual luring is a more effective aggressive mimicry signal for puff adders. This may partly explain why we observed lingual luring more often than caudal luring if the foraging benefits acquired through the use of the former are higher than the latter, although prey capture success did not differ between luring behaviours. However, this lack of statistical difference is not surprising given our small sample size, and the figures suggest that lingual and caudal luring may not be equally efficient: snakes that caudal-lured never successfully caught a prey (0%, 0/3), whereas snakes that lingual-lured experienced a 44% capture success (4/9). We speculate that this difference in attracting prey may be linked to the difference in size between the tongue and the tail. That is, puff adders, and specifically males, have quite thick tails that may dissuade amphibian prey to attack it, in contrast to the snake's tongue, which clearly resembles a small harmless worm. Another possible—and not necessarily mutually exclusive—explanation may involve the disruptive coloration between the tongue and the head, which may increase the camouflage of puff adders by breaking their outline, whereas the comparatively more uniform colour between the tail and the rest of the body may not.

Aggressive mimics must often make context-dependent predatory decisions, which may drive the evolution of higher cognitive functions (Jackson and Cross 2013). A prime example is that of web-invading spiders, which lure web-building spiders on which they feed, by generating vibrations mimicking an insect caught in the web (Jackson 1992). These spiders learn to fine-tune the appropriate signal to attract and capture a particular prey species by trial and error (Jackson and Wilcox 1993). Although not as sophisticated, snakes similarly make context-dependent predatory decisions, because luring behaviour is prey specific. For example, northern death adders (*Acanthophis praelongus*) caudal-lured more often in the presence of lizards and introduced cane toads compared to native frogs (Hagman et al. 2008, 2009), and syntopic lizard prey was more effective at eliciting caudal luring by sidewinder rattlesnakes (*Crotalus cerastes*) than allopatric lizards (Reiserer and Schuett 2008).

We observed puff adders lingual luring only in the presence of amphibians, indicating that they have the ability to discriminate between prey types. Further, our observations also suggest that they may be able to differentiate among amphibian species. In our population, puff adders feed on several amphibian species but never fed on *K. senegalensis* despite many close encounters (note than one snake lingual-lured one once). This frog has a highly distinctive banded pattern and walks instead of hoping/jumping, two characteristics shared by the sympatric and toxic, but distantly related species, banded rubber frog (*Phrynomantis bifasciatus*; du Preez and Carruthers 2009). We speculate that *K. senegalensis* is a Batesian mimic of *P. bifasciatus*, or alternatively, these two species could be each other's Mullerian mimics. In any case, lingual luring was largely associated with bufonid toads, whose predatory behaviour is released by small moving objects (Ingle 1968; Ewert 1970). Hence, puff adders possibly evolved lingual luring by exploiting the sensory biases of hunting toads.

Tests of the adaptive significance of facultatively used luring behaviours are surprisingly rare. Although a few studies have shown that luring can be effective in attracting prey toward the predator, no studies that we are aware of statistically demonstrated that luring increases prey capture rate. For example, cane toads (*Rhinella marina*) that waived their toes attracted more prey than those that did not (Hagman and Shine 2008), and the caudal luring of pigmy rattlesnakes (*Sistrurus miliarius*) and death adders attracted frogs and lizards, respectively (Jackson and Martin 1980; Chiszar et al. 1990; Hagman et al. 2008; Nelson et al. 2010), but there was no report of prey capture success in these studies. Furthermore, snowy egrets (*Egretta thula*) that lingual-lured in the field did not experience increased foraging success compared to those that did not (Master 1991). In our study, prey capture success was approximately twice as high for snakes that lingual-lured compared to those that did not. However, this difference was not statistically significant, possibly because of our low sample size and/or our inability to control for many variables due to the field nature of our study.

Given that the puff adder is one of Africa's most widespread, iconic, common and medically important snakes

(Barlow et al. 2013) and is routinely kept in captivity for the production of antivenin and for public display, we are surprised that neither lingual nor caudal luring has previously been reported for the species. This demonstrates that even common, widespread species of snakes are not as well known as is often assumed and that their behavioural repertoires may demand higher cognitive abilities than those usually afforded to snakes. Additionally, our observations demonstrate the power of telemetry-videography combination as a tool for the study of snake behaviour in a natural setting. Clearly, observations made in captivity do not comprehensively capture the breadth, diversity and complexity of snake biology.

The predator-prey system that we describe here provides a unique opportunity to test many of the proximate and ultimate factors that are implicated in luring behaviours. Are both of these behaviours triggered by and used to catch amphibian prey, and do they increase prey capture rate? What factors affect the decision made by an individual to select one or the other strategy or to use them simultaneously? Is their effectiveness affected by frequency use in the population, or is their use related to prey density? Further studies are required to answer these questions that could ultimately improve our understanding of the ecology and evolution of facultatively used luring signals.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted (University of the Witwatersrand, animal protocol no. 2012-42-04). Specimens were collected under scientific research permits CPF6-0167 and CPF6-0024, issued by the Gauteng Department of Agriculture and Rural Development.

Informed consent Informed consent was obtained from all individual participants included in the study.

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