

Receiver psychology and the design of the deceptive caudal luring signal of the death adder

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Signal design can reflect the sensory properties of receivers. The death adder, *Acanthophis antarcticus*, attracts prey by wriggling the distal portion of its tail (caudal luring). To understand the design of this deceptive signal, we explored perceptual processes in a representative prey species: the Jacky dragon, *Amphibolurus muricatus*. We used 3D animations of fast and slow death adder luring movements against different backgrounds, to test the hypothesis that caudal luring mimics salient aspects of invertebrate prey. Moving stimuli elicited predatory responses, especially against a conspicuous background. To identify putative models for caudal luring, we used an optic flow algorithm to extract velocity values from video sequences of 61 moving invertebrates caught in lizard territories, and compared these to the velocity values of death adder movements. Caudal lures had motion characteristics that matched common invertebrate prey speeds, each corresponding to a peak in a bimodal distribution. Subsequent video playback tests using animations of crickets showed that significantly more attacks were evoked by stimuli moving at common than at rare invertebrate speeds. Overall, these results suggest that biases in the nervous system of the receiver, originally selected for prey recognition, might have been exploited by the design of the caudal luring signal. We suggest that viewing caudal luring from this perspective, rather than thinking of it as aggressive mimicry per se, may help us understand the function and evolutionary origin of this behaviour.

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Signal design is honed by selection to provide maximal efficacy, given the constraints imposed by attributes of the sender, the sensory systems of the receiver and the physical characteristics of the environment (Guilford & Dawkins 1991; Endler 1992). Signals are typically considered to be reliable indicators of the sender's underlying quality, with signal reliability sometimes ensured by cost (Zahavi 1975). Reliable signals can also evolve when there is a conflict between sender and receiver, as in predator–prey interactions (e.g. Hasson 1991).

Other signals are deceptive or 'manipulative' (Dawkins & Krebs 1978), the most studied examples being cases of mimicry. Anglerfish, *Lophius piscatorius*, lure prey to within striking distance by twitching a fleshy prey-like appendage extended in front of the mouth (Wilson 1937). Luring is also a fallback predatory

mechanism used by Burton's pygopodid, *Lialis burtonis*. This legless lizard initially strikes prey directly but, if unsuccessful, will wriggle the tip of its tail in an attempt to recapture escaped prey (Murray et al. 1991).

Caudal luring in snakes is also used to attract prey (Hagman et al. 2008; Reiserer & Schuett 2008). This widespread behaviour, which consists of a distinct wriggling or twitching of the distal portion of the tail, has been reported for species of boid, viperid, elapid and colubrid snakes (Neill 1960; Heatwole & Davison 1976; Sazima & Puerto 1993; Leal & Thomas 1994; Hagman et al. 2008; Reiserer & Schuett 2008). Using lizards as potential prey, we examined the design of caudal luring in death adders, Australian elapid snakes known to lure lizards successfully (Hagman et al. 2008). Unlike its congener *Acanthophis praelongus hawkei* which uses a conspicuously coloured tail as a lure (Hagman et al. 2008), the subspecies *A. antarcticus laevis* used in this study also uses an inconspicuously coloured tail as a lure (Carpenter et al. 1978), suggesting that, in this case, the signal may depend primarily on movement, rather than static conspicuousness. Carpenter et al. (1978) described caudal luring in *A. antarcticus* as slow rippling movements or as rapid thrashing back and forth. *Acanthophis antarcticus* increases its luring behaviour when prey is nearby. Tests

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with mice, *Mus musculus* and the lizard *Hydrosaurus pustolosus* demonstrate that these movements facilitate attraction and capture (Chiszar et al. 1990; Hagman et al. 2008). Experiments using frogs and lizards as representative prey have shown that caudal luring in other snake species also has a predatory function (Schuett et al. 1984; Sazima 1991; Sazima & Puerto 1993; Reiserer & Schuett 2008).

While the gross structure of caudal luring in *A. antarcticus* has been reported, the design of this deceptive signal has received little attention in any species (see Reiserer & Schuett 2008). Following observations of the lizard *Anolis carolinensis* 'grabbing' the tail of a luring green pit viper, *Bothrops bilineatus*, prior to being attacked and swallowed by the snake, Greene & Campbell (1972) speculated that lizards are attracted to lures because they resemble the lizard's own prey (aggressive mimicry). Schuett et al. (1984) labelled this phenomenon 'feeding mimicry' and found that frogs show similar prey-catching behaviour towards luring rattlesnakes, *Sistrurus catenatus*. Similarly, Reiserer & Schuett (2008) stated that the tail movements 'resemble an animal', but the putative models for these functionally effective lures have not been identified.

Caudal luring is often described as vermiform (worm-like; Greene & Campbell 1972; Heatwole & Davison 1976; Shine 1980; Chiszar et al. 1990; Sazima 1991; Tiebout 1997), yet no work has been done to show whether this movement characteristic is important for lure efficacy. While prey might be attracted to the apparent worm mimicry suggested by the 'slow undulating movements' that Carpenter et al. (1978) described, this is clearly not a putative model for the 'rapid whole-tail thrashes' also observed in the study.

We examined the role of receiver psychology in the design of the caudal luring signal of *A. antarcticus*. In particular, we tested whether motion characteristics of the lure 'exploit' biases in the nervous system of the Jacky dragon lizard, *Amphibolurus muricatus*. This native Australian agamid lizard, found in coastal heathlands along eastern Australia, is sympatric with *A. antarcticus* and a known prey species of this sit-and-wait predator (Shine 1980; Cogger 2000).

Visual systems are typically selective in their response to movement. *Amphibolurus muricatus* relies heavily on motion cues to detect suitable prey items (Hoese et al. 2008), avoid predators (Carlile et al. 2006) and communicate with conspecifics (Peters & Ord 2003). The diet of *A. muricatus* consists mainly of insects and small arthropods (McPhee 1963), but it is unknown whether these lizards have evolved a specific preference for certain motion characteristics of these prey (Hoese et al. 2008). Distinctive behavioural responses and normal behaviour in captivity (Ord et al. 2002; Peters & Evans 2003a, b) make *A. muricatus* ideal for exploring this predator-prey system. In particular, the predatory response of *A. muricatus*, which we used as a response assay, consists of orientation towards a target, followed by approach, striking at prey with the mouth open and finally feeding (Hoese et al. 2008).

A long series of previous studies on *A. muricatus* have successfully used digital video playback and animation techniques to assess the role of visual cues in male-male interactions (Ord et al. 2002; Ord & Evans 2003; Peters & Evans 2003b; Van Dyk & Evans 2007; Van Dyk et al. 2007) and prey recognition (Hoese et al. 2008). We began with a 'calibration' experiment designed to assess the appropriateness of video playback in this system. In this experiment, we systematically compared the social responses evoked by life-sized simulated video opponents with those evoked by real males confined in a glass tank. Ord et al. (2002) showed that video stimuli were in every case equivalent to a live conspecific, validating the use of this technique. We refer readers to this paper for a critical evaluation of methods for the experimental analysis of the way in which nonhuman animals perceive dynamic visual stimuli,

taking into account the remarkable diversity of sensory characteristics. There is broad consensus that, provided the effectiveness of video playback has first been established experimentally, this technique is uniquely well suited to the challenge of reproducing signalling motor patterns (Oliveira et al. 2000) particularly when these are too complex for the alternative approach of robotics (e.g. Göth & Evans 2005; Patricelli et al. 2006). In the present study, we adopted digital video playback to test sensitivity to variation in movement, while controlling for confounding effects such as chemosensory information.

We presented *A. muricatus* with a digitized 3D model of *A. antarcticus* performing slow and fast caudal luring displays to measure the efficacy of this signal against three backgrounds of variable environmental 'noise'. To identify potential models for these movement-based signals, we used a motion analysis algorithm to measure the velocity and acceleration characteristics of snake lures and of the lizard's invertebrate prey. Finally, we assessed lizard predatory responses using an animation of a representative prey item moving at a range of prey-derived speeds, both within and outside those found in caudal luring.

EXPERIMENT 1: RESPONSE TO CAUDAL LURING

Methods

Subjects

Subjects were 31 male Jacky dragons wild caught in La Perouse, Lane Cove and Royal National Parks in Sydney, Australia, between 2004 and 2006. We caught them by noosing and transported them in calico bags to indoor housing facilities at Macquarie University. All lizards were wormed immediately after capture and then moved to individual indoor enclosures (64 × 75 cm and 120 cm high) constructed of rigid, opaque, white plastic sheeting on three sides with a transparent Perspex front for stimulus display and filming. Enclosures were aligned such that lizards were visually isolated from neighbouring males. All pens contained sand substrates, branches suitable for basking and vegetation providing refuge. Water was available in small bowls and enclosures were sprayed daily to maintain humidity levels. Lizards were fed twice weekly with mealworms and crickets (three of each) dusted with multivitamins and calcium supplements (RepCal, RepCal Research Labs, Los Gatos, CA, U.S.A.). Room lights were set at a 14:10 h light:dark cycle during the summer experimental period and heat lamps (120 W, 240 V General Electric Flood) and ultraviolet (UV) lamps (300 W Osram Ultra-Vitalux) provided suitable conditions for thermoregulation and exposure to UV light. Lizards remained healthy throughout the experimental period and were then released at the site of capture. Permission for capture and housing of *A. muricatus* and all related experimental procedures were granted by the New South Wales National Parks and Wildlife Service and the Macquarie University Animal Ethics Committee.

Video stimuli

The stimulus was a model death adder created using LightWave 3-D version 8.3 animation software (NewTek Inc., San Antonio, TX, U.S.A.). The three-dimensional shape of the model cybersnake was matched precisely to that of a real death adder using techniques developed for studies of opponent recognition (see Van Dyk & Evans 2007; Van Dyk et al. 2007 for details). Texture and colour were imported from a photograph aligned over the model. Bones inserted into the cybersnake allowed it to be positioned over a video exemplar in a loosely coiled ambush posture, such that its head was within striking range of its tail (see Fig. S1 in the Supplementary material). The tapered end of the tail (the lure) was extended in front of the head, henceforth referred to as the 'neutral'

position. Caudal luring movements were rotoscoped from digital video footage of caudal luring by death adders at 25 frames/s. This method, described in detail elsewhere (Peters & Evans 2003b), consists of frame-by-frame synchronization of movement between archival footage and the model, permitting precise reproduction of the motion characteristics of the lure in all three dimensions.

The Nyquist theorem, which applies to any process in which a continuous function is represented by discrete samples (Hopp et al. 1998), defines the maximum frequency adequately reproduced by the 25 frames/s PAL video standard (12.5 Hz). It is perhaps easier to consider this constraint in terms of the corresponding time interval (80 ms). There is no evidence that complete movements as brief as this occurred in our video footage. In addition, we have previously shown that the PAL frame rate is adequate to capture the velocity characteristics of display motor patterns (Peters et al. 2002; Peters & Evans 2003a) and for playback exploring perceptual processes (Peters & Evans 2003b, 2007). Note that these aggressive signals have both a higher frequency and a larger sweep area than caudal luring movements.

Playback design

Death adder lures have been described as occurring in two distinct forms: fast and slow (Carpenter et al. 1978). We thus created stimuli representing each of these motor patterns based on video sequences of several bouts of caudal luring in live snakes. The cybersnake began all movements from the neutral position, which was centred in the video frame. Caudal lures were rotoscoped in four distinct 5 s bouts of movement, evenly distributed within a 1 min movement sequence. Although we used a single morph of snake for the animations, the actual 'stimuli' (movement bouts) therefore consisted of four different events for each of the slow and the fast treatments. These bouts were then repeated to create 2 min of stimulus movement for both slow and fast experimental treatments.

Each treatment consisted of 5 min of playback, beginning with 2 min of a motionless cybersnake, so that baseline behaviour could be recorded ('before'). This was followed by a 2 min caudal luring playback ('during'), after which the snake returned to the neutral position and remained still for 1 min ('after'). The control treatment ('still') consisted of 5 min of the cybersnake remaining stationary in the neutral position.

To assess the effects of variation in lure background contrast on the efficacy of luring movements, we animated each stimulus type against three different substrates: white sand (to provide a 'conspicuous' display), leaf litter ('semicamouflaged'), and the same leaf litter background, but with digitally created leaves randomly scattered over the cybersnake ('obscured'). Sequences were then imported into Final Cut Pro 3.0 (Apple Computer), which was used to control stimulus presentation for playback (see movies 1–3 in the [Supplementary material](#)).

Test procedure

Lizards were randomly assigned a different substrate and luring movement combination treatment on each of 9 test days. The experiment was run in two replicates, in October and December 2006. Stimuli were presented in 3-day blocks with intervening rest days to reduce the likelihood of the lizards becoming habituated to playback. Treatment order was reversed in the second replicate so that stimuli were counterbalanced within subject. We report average responses for these tests. Temperature and humidity were approximately 25 °C and 62%, respectively. Each lizard was tested at the same time each day between 0800 and 1400 hours, when the animals are known to be most active (Ord et al. 2002).

Stimuli were presented using a high-resolution monitor (Sony PVM-1450; resolution 450 lines) mounted on a trolley. Responses

were recorded using a Panasonic WVCP240 CCTV camera with a wide-angle WV-LZ62/2 lens, fitted below the monitor, and a Panasonic AG-MD830 videocassette recorder, located outside the room. Behaviour was monitored from outside the room using a second monitor (Panasonic TC-1470Y), which functioned as a viewfinder for the recording camera. All remaining equipment was operated externally to minimize observer effects. Stimuli were played using an iMac (Apple Computer Inc.) running Final Cut Pro 3.0 and a Canopus ADVC110 for digital to analogue conversion. The large stimulus library required for these tests was stored on an external drive (LaCie d2 250 GB) connected to the iMac via firewire.

Lizards were given time to habituate to the presence of the trolley at the beginning of each trial; recording did not begin until they had oriented away or showed little interest in the display monitor.

Data analysis

Videorecorded behaviour was scored using the 'JWatcher 1.0' event-recorder program (Blumstein et al. 2000). We used four categories: no response, visual response (orienting towards the stimulus), moderate attention (substrate licking, a chemosensory exploratory behaviour, often accompanied by hesitant movement in the direction of the monitor) and predatory response (rapid approach towards the monitor and lunging towards the screen; see movie 4 in the [Supplementary material](#)). Tests were scored for the duration of the test using a 0–3 ordinal scale and then binned in 60 s time bins corresponding to the periods before, during and after luring playback. The data for each lizard were then averaged across time bins for each period and also across the two experimental trials. We used Friedman's analyses of variance (ANOVAs) to compare behaviour between periods to measure the efficacy of luring displays over time, with Dunn's multiple comparisons to compare time periods (SPSS version 16, SPSS Inc., Chicago, IL, U.S.A.).

To test which treatment was most effective at initiating a 'visual grasp' response to caudal luring we measured latency to orient after onset of movement. The nature of this time-to-event (survival) data set required a Cox proportional hazards test for analysis (Cleves et al. 2002). The Cox proportional hazards model is nonparametric, does not assume a particular distribution for the survival times and, having been devised for the analysis of survival times, deals appropriately with right-censored data (for a description of the Cox model see Hosmer et al. 2008). As implemented in Stata version 9 (StataCorp 2005), which was used for these analyses, the Cox model is able to deal appropriately with the correlated observations that arise from repeated-measures analysis, using the method described by Williams (2000) to take account of the clustered data.

In both analyses, we made no more than two comparisons per test, as we were only interested in within-substrate effects and whether slow and fast lures differed from the corresponding control treatment. Significance levels were adjusted using the false discovery rate for multiple comparisons (Benjamini & Hochberg 1995) which provides a good balance between type I and type II error rate. Fisher's exact tests were used to analyse the frequency of predatory responses.

Results

There were significant differences between time periods ($\chi^2_2 = 20.22$, $P < 0.0001$). Caudal luring elicited reliable responses that were significantly greater than those observed during the prestimulus baseline period; an effect that was maintained for 1 min after caudal luring playback had ceased (Fig. 1).

When compared with the still control, latency to orient and maximum response were significantly higher only when the luring

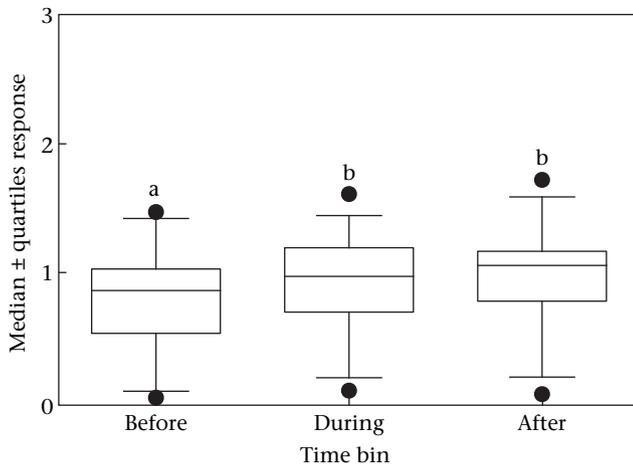


Figure 1. Efficacy of caudal luring. Box plot depicts median response and interquartile range ($N = 31$) for each time bin, whiskers illustrate 5th and 95th percentiles and dots represent outliers. The X axis depicts time relative to the onset of caudal luring. Different letters denote significant differences between comparisons. Response scores: no response = 0; orient = 1; moderate attention = 2; predatory response = 3. See text for details.

movement was conspicuous against a sand substrate (Table 1). Lizards were significantly more likely to respond with predatory behaviour (Fig. 2) towards conspicuous slow caudal lures than controls (Fisher's exact test: $P = 0.024$), a trend also apparent with fast lures (Fisher's exact test: $P = 0.052$). However, when caudal luring was semicamouflaged (slow: Fisher's exact test: $P = 0.195$; fast: Fisher's exact test: $P = 0.353$) or obscured (slow: Fisher's exact test: $P = 1.000$; fast: Fisher's exact test: $P = 0.424$), it did not elicit more predatory responses than the control sequence.

EXPERIMENT 2: MOTION CHARACTERISTICS OF LIVE PREY

Methods

Field sampling

We selected 13 Jacky dragon habitats in Lane Cove National Park, Sydney, Australia, and sampled the invertebrate fauna they contained over 7 days in January 2007. Fieldwork was conducted between 0900 and 1300 hours, when lizards are typically active and foraging. The average \pm SEM temperature and humidity during the sampling period were 29 ± 0.36 °C and $57 \pm 4.32\%$, respectively. Individual Jacky dragon territories were located by

Table 1
Responses to slow and fast caudal lures compared to the still control

Versus still control		Maximum response		Latency to orient					
		t_{30}	P	HR	Z	P	95% CI		
							Low	High	
Conspicuous	Slow	-2.872	0.007	1.48	3.05	0.002	1.15	1.90	
	Fast	-2.352	0.025	1.54	2.75	0.006	1.13	2.10	
Semicamouflaged	Slow	-0.194	0.847	1.03	0.16	0.874	0.74	1.43	
	Fast	-0.334	0.740	1.08	0.49	0.626	0.79	1.48	
Obscured	Slow	0.561	0.579	1.07	0.45	0.651	0.79	1.46	
	Fast	-1.085	0.287	1.21	1.26	0.209	0.90	1.62	

HR: hazard ratio. Two different analyses are presented. $N = 31$ for both. Significance is adjusted according to the false discovery rate (Benjamini & Hochberg 1995), where alpha (α) = 0.025 for the smaller P value of the two comparisons within each substrate treatment, and (α) = 0.05 for the larger P value.

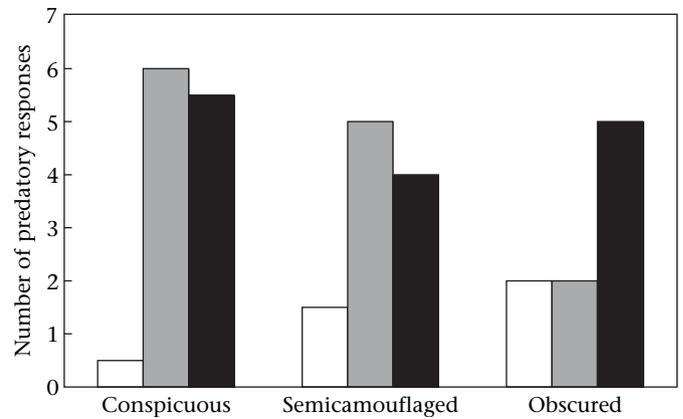


Figure 2. Predatory responses (approach, lunge) to caudal luring playbacks ($N = 31$). Data are averages from a repeated-measures design. Bars represent still control (white bars), slow (grey bars) and fast (black bars) caudal lures shown against each of the substrate types.

identifying the animal in its natural surroundings (typically basking on a perch) and then marking a 3 m² quadrat around the lizard.

Sampling involved sifting soil and leaf litter through a 470 × 300 mm tray with 12 × 13 mm grids. The tray sat flush inside a rectangular bin (540 × 350 mm) that caught the sampled material. Unfiltered leaf litter was examined for species too large for the grid. Additionally, all foliage within the quadrat was closely examined for potential prey species.

Invertebrates were collected in jars and transferred to the laboratory where they were filmed less than 2 h after capture. In total, we collected 61 potential prey items from eight different orders (Araneae, Blattodea, Coleoptera, Diplopoda, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera), as well as unidentified caterpillars. Although no studies have investigated the diet of *A. muricatus* in detail, McPhee (1963) stated that they eat moths, caterpillars, grasshoppers and beetles. We have observed them consuming many of these items in addition to a variety of spiders. We therefore consider it likely that at least some of the invertebrates that were found in *A. muricatus* habitat must constitute potential prey. This diversity of potential prey created a wide range of motion characteristics for analysis.

Filming

Filming was conducted in a laboratory, with temperature and humidity controlled at approximately 28 °C and 67%, respectively. Prey items were videorecorded (PAL standard: 25 frames/50 fields per s) in an open-fronted glass terrarium (920 × 380 mm and 360 mm high) with a sand substrate to facilitate natural movement. Three broad-spectrum Dedolight DLH4 Aspherics2 lights (24 V, 150 W), positioned approximately 240 mm from the terrarium, provided lighting. Prey items were recorded on DV tape using a Canon XL1 digital video camcorder mounted on a tripod. Focal length was constant throughout.

Analysis of image motion

We used an optic flow algorithm to quantify motion characteristics from digital video sequences. This technique uses local changes in image intensity to characterize velocity; it has been used in recent analyses of visual signal design in both lizards (Peters & Evans 2003b) and spiders (Elias et al. 2006; see Peters et al. 2002 for full details).

Up to 5 s of side-to-side movement were selected for each prey item ($N = 61$) and exported as AVI files for subsequent analysis. The selection criterion for each video sequence was that it contained

lateral movement that kept the invertebrate within the field of view for 1–5 s. For comparison, we also converted footage of the cyber-snake from each of the eight rotoscoped bouts of movement into AVI format. All sequences were exported as a stream of uncompressed images at 25 frames/s.

Results

Invertebrate prey found in habitats of *A. muricatus* moved at a wide range of average speeds, which produced a complex bimodal distribution. The average speeds of slow and fast caudal lures matched the typical speed ranges of invertebrates (Fig. 3).

Invertebrate speed, initially visualized as a histogram with the percentage of invertebrate individuals expressed along the ordinate and mean speed of locomotion along the abscissa (Fig. 3), was used to derive which speeds were commonly found among the range of invertebrates sampled. This was done by sorting the percentage of invertebrates found by the number of speed bins in which that percentage was represented, such that, for example, four speed bins represented invertebrates in the 1–2 percentile range and three speed bins represented invertebrates in the 9–10 percentile range (see Fig. 3). Two discontinuous groups were found. Invertebrates that moved at ‘common’ speeds (i.e. the speeds of the majority of potentially encountered prey) accounted for 74% of the sample population. The ‘rare’ category made up the remaining 26% of the invertebrate sample. Subsequent analyses used this split to perform

a posteriori tests. These species generated two conspicuous peaks in the speed distribution (0.1–0.6 and 0.9–1.1 pixels/frame; Fig. 3).

EXPERIMENT 3: RESPONSE TO PREY MOTION

Methods

Subjects and materials were the same as for experiment 1.

Video stimuli

We wished to test lizard sensitivity to variation in prey motion. Rather than use original digital video recordings, containing a range of sizes, shapes and colours, we standardized morphological characteristics by using a cricket modelled in LightWave as a representative prey item. This design afforded control over all factors except speed.

Playback design

Regions of interest were chosen from the distribution of invertebrate prey velocity data (Fig. 3) so that suitable speeds could be assigned to the ‘cybercricket’ for playback experiments. Three regions were chosen within the caudal luring range: a slow peak (0.5–0.6 pixels/frame), a fast peak (0.9–1.0 pixels/frame) and a trough that spanned the intermediate range (0.6–0.9 pixels/frame). Two extreme regions, very slow (0.1–0.2 pixels/frame) and very fast (1.1–1.5 pixels/frame), together with a control (no movement) were selected for comparison. Each region (excluding the control) corresponded to velocity estimates for five to eight invertebrates; values that were then averaged to determine a representative speed for each group. The six treatments had motion velocities of 0, 3.35, 12.26, 16.83, 20.77 and 28.32 mm/s, or 0, 0.48, 1.76, 2.41, 2.97 and 4.06 °/s (based on the assumption that the lizard was in the middle of its pen).

We used the high-contrast white sand image that elicited the highest responses towards caudal luring in experiment 1 as a background. Owing to the speed of the fast treatments it was necessary for the cricket to turn around several times to complete a 2 min block of movement. This led to the inclusion of two 3D modelled leaves, which were placed at each end of the cybercricket’s movement trajectory, such that reversal of direction occurred behind the leaf. This eliminated the possibility of lizards reacting to the conspicuous acceleration associated with a sudden 180° turn.

The cybercricket began centred in the field of view for all treatments. The position of the leaves in the horizontal plane varied, since each treatment required different trajectory lengths. The cybercricket was fully exposed for 5 s while moving in either direction in all treatments. However, owing to the differing speeds, the number of transitions (two to four) had to be varied. Total movement time hence varied from 80 to 92 s. This also affected latency to emerge from the leaves (3–7 s). Each stimulus treatment consisted of 5 min of playback with the same temporal structure (i.e. before, during and after periods) used in experiment 1.

Test procedure

The experiment was run over 6 days in March–April 2007. Lizards were randomly assigned a different treatment on each day. All other aspects of experimental procedure were identical to experiment 1. Each lizard was tested twice in a repeated-measures design, with the second series in reverse order to counterbalance habituation effects.

Data analysis

Data were scored as for experiment 1. Baseline behavioural scores were subtracted from those that occurred during stimulus movement to isolate responses evoked by the simulated prey item.

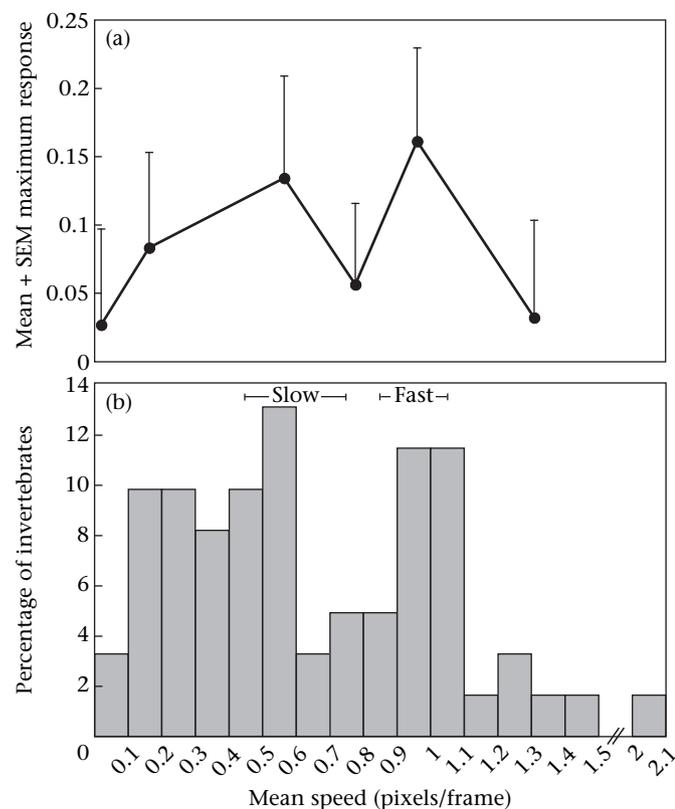


Figure 3. Prey speeds and lizard predatory responses. All stimuli used for characterization of motion were filmed such that they were life sized on the playback screen, allowing us to compare the motion characteristics of invertebrates and snakes directly. (a) Maximum predatory response, after subtracting baseline behaviour, of *A. muricatus* ($N = 31$) towards the cybercricket moving at speeds within the range found in invertebrates. The six treatments had motion velocities of 0, 3.35, 12.26, 16.83, 20.77 and 28.32 mm/s. (b) Distribution of speeds for 61 invertebrate prey items found in *A. muricatus* territories. Speed bins are 0.10 pixels/frame (25 frames/s). Lines above histogram depict speed ranges for the two types of caudal lure presented in experiment 1.

We divided six treatments according to their relation to the prey motion distribution into three ‘common’ and three ‘rare’ speeds. The behavioural responses of these groups were then averaged to give each lizard a single estimate of response to common and to rare prey motion, which were compared using paired-sample *t* tests.

Results

The predatory responses of Jacky dragons towards the cyber-cricket moving at different speeds were clearly bimodal (Fig. 3). Speeds that fell within the range of those commonly found among invertebrates in nature elicited higher overall predatory responses than those that were rarely experienced (Fig. 3). The mean \pm SEM behavioural responses to the three common prey speed stimuli (0.14 ± 0.04) was significantly greater than that towards the three rare prey speed stimuli (0.03 ± 0.04 ; $t_{30} = 2.376$, $P = 0.024$).

DISCUSSION

We carried out a detailed experimental analysis of the design of a snake caudal luring signal. Our results suggest it is possible that death adders mimic the motion characteristics of invertebrates using a deceptive signal to attract agamid lizards. *Amphibolurus muricatus* responded most strongly towards two ranges of movement speeds common in invertebrates found in their habitat, and likely to be prey. These ranges each overlap with the motion of one of the two luring movements seen in death adders. We conclude that the caudal luring signal may have been shaped by aspects of receiver psychology (Guilford & Dawkins 1991).

Recent experiments have measured peripheral motion sensitivity in the Jacky dragon (Woo & Burke 2008; Woo et al. 2009) using random dot kinematograms. These simple stimuli are highly effective at evoking visual responses, but they are explicitly nonbiological and do not engage higher-order cognitive processes, such as recognition or categorization. Woo & Burke's (2008) and Woo et al.'s (2009) results show that the Jacky dragon visual system is broadly tuned and is particularly sensitive to high-speed motion. Responses increase monotonically with speed over the range 10–160 °/s, although all these speeds are faster than those experienced by the lizards in our tests.

Even under weak signal conditions in which signal to noise ratios are low, performance with high-speed motion in the range of conspecific displays remains almost perfect, but there is a marked deterioration in performance at the slower speeds of cricket prey or the serpentine locomotion of a death adder (Woo & Burke 2008). This pattern of movement sensitivity clearly predicts a greater response to the fast lure, but slow and fast lures were equally effective at eliciting responses in lizards. Together, these findings suggest that our results are best explained not by the detection processes of the sensory periphery, but by higher-order prey recognition.

As a heuristic, it is worth considering the most likely a priori scenarios for a process of perceptual exploitation. We might have expected: (1) a flat response function with no sensory or perceptual tuning; (2) unimodal tuning (either a bell curve or a curve skewed towards fast speeds, as in basic movement sensitivity); or (3) a probability-based tuning response that tracked the properties of target movement. The first situation predicts an equal response to all speeds, posing the fewest constraints on caudal luring signal design. The second scenario allows for two hypotheses, depending on the position of the response curve. *Amphibolurus muricatus* might be tuned to a central mean of prey speeds. Alternatively, lizards might be more sensitive towards fast speeds, such as those characteristic of intraspecific displays (Peters & Evans 2003a, b), rendering the slow lure ineffective. In the probability-based

scenario, responses should be higher towards common prey speeds, regardless of velocity, than towards those that are rarely seen in nature. Our results are consistent with this last hypothesis: *A. muricatus* responded more strongly towards common prey speeds (both ‘fast’ and ‘slow’) than rare ones (Fig. 3). While it is possible that prey movement was different in our sand substrates than in leaf litter, there appears to be an extraordinary correspondence between prey characteristics, lure design and lizard response intensity, suggesting that the snake's deceptive signal may be modelled from common invertebrate movements and that it achieves efficacy by engaging recognition processes. If this hypothesis is correct, we would predict that future studies using these methods and changing the speed of the caudal lure to speeds outside the range of common prey will elicit fewer predatory responses from the lizards. We believe that this is the first experimental evidence that receiver psychology may have shaped the design of caudal luring.

Tantalizingly, a recent finding regarding the caudal luring of sidewinder rattlesnakes, *Crotalus cerastes*, showed that lizards were highly attracted to the lure, but only if they were sympatric with the snake species (Reiserer & Schuett 2008). The authors noted this result by stating ‘Despite the fact that nonsympatric lizards are not natural prey for *C. cerastes*, it has been assumed that [caudal luring] involves mimicry of a general category of potential prey’ and they suggested that there is more to caudal luring than morphological mimicry of vermiform prey. Our results may provide a potential explanation for their results.

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Supplementary Material

Supplementary material associated with this paper is available, in the online version, at doi:10.1016/j.anbehav.2009.12.011.

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