

1 **Receiver psychology and the design of the deceptive caudal luring signal of the death**

2 **adder**

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20

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

39

40 *Keywords:* aggressive mimicry; *Amphibolurus muricatus*; death adder; deceptive signal;
41 Jacky dragon; movement-based signal; receiver psychology; sensory bias; signal design

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

49

50 Other signals are deceptive or 'manipulative' (Dawkins & Krebs 1978), the most
51 studied examples being cases of mimicry. Anglerfish, *Lophius piscatorius*, lure prey to
52 within striking distance by twitching a fleshy prey-like appendage extended in front of the
53 mouth (Wilson 1937). Luring is also a fallback predatory mechanism used by Burton's
54 pygopodid, *Lialis burtonis*. This legless lizard initially strikes prey directly but, if
55 unsuccessful, will wriggle the tip of its tail in an attempt to recapture escaped prey (Murray
56 et al. 1991).

57

58 Caudal luring in snakes is also used to attract prey (Hagman et al. 2008; Reiserer &
59 Schuett 2008). This widespread behaviour, which consists of a distinct wriggling or
60 twitching of the distal portion of the tail, has been reported for species of boid, viperid,
61 elapid and colubrid snakes (Neill 1960; Heatwole & Davison 1976; Sazima & Puerto 1993;
62 Leal & Thomas 1994; Hagman et al. 2008; Reiserer & Schuett 2008). Using lizards as
63 potential prey, we examined the design of caudal luring in death adders, Australian elapid
64 snakes known to lure lizards successfully (Hagman et al. 2008). Unlike its congener
65 *Acanthophis praelongus hawkei* which uses a conspicuously coloured tail as a lure
66 (Hagman et al. 2008), the subspecies *A. antarcticus laevis* used in this study also uses an

67 inconspicuously coloured tail as a lure (Carpenter et al. 1978), suggesting that, in this case,
68 the signal may depend primarily on movement, rather than static conspicuousness.
69 Carpenter et al. (1978) described caudal luring in *A. antarcticus* as slow rippling
70 movements or as rapid thrashing back and forth. *Acanthophis antarcticus* increases its
71 luring behaviour when prey is nearby. Tests with mice, *Mus musculus* and the lizard
72 *Hydrosaurus pustulosus* demonstrate that these movements facilitate attraction and capture
73 (Chiszar et al. 1990; Hagman et al. 2008). Experiments using frogs and lizards as
74 representative prey have shown that caudal luring in other snake species also has a
75 predatory function (Schuett et al. 1984; Sazima 1991; Sazima & Puerto 1993; Reiserer &
76 Schuett 2008).

77

78 While the gross structure of caudal luring in *A. antarcticus* has been reported, the
79 design of this deceptive signal has received little attention in any species (see Reiserer &
80 Schuett 2008). Following observations of the lizard *Anolis carolinensis* ‘grabbing’ the tail
81 of a luring green pit viper, *Bothrops bilineatus*, prior to being attacked and swallowed by
82 the snake, Greene & Campbell (1972) speculated that lizards are attracted to lures because
83 they resemble the lizard’s own prey (aggressive mimicry). Schuett et al. (1984) labelled
84 this phenomenon ‘feeding mimicry’ and found that frogs show similar prey-catching
85 behaviour towards luring rattlesnakes, *Sistrurus catenatus*. Similarly, Reiserer & Schuett
86 (2008) stated that the tail movements ‘resemble an animal’, but the putative models for
87 these functionally effective lures have not been identified.

88

89 Caudal luring is often described as vermiform (worm-like; Green & Campbell
90 1972; Heatwole & Davison 1976; Shine 1980; Chiszar et al. 1990; Sazima 1991; Tiebout
91 1997), yet no work has been done to show whether this movement characteristic is

92 important for lure efficacy. While prey might be attracted to the apparent worm mimicry
93 suggested by the ‘slow undulating movements’ that Carpenter et al. (1978) described, this
94 is clearly not a putative model for the ‘rapid whole-tail thrashes’ also observed in the study.
95

96 We examined the role of receiver psychology in the design of the caudal luring
97 signal of *A. antarcticus*. In particular, we tested whether motion characteristics of the lure
98 ‘exploit’ biases in the nervous system of the Jacky dragon lizard, *Amphibolurus muricatus*
99 (White 1970). This native Australian agamid lizard, found in coastal heathlands along
100 eastern Australia, is sympatric with *A. antarcticus* and a known prey species of this sit-and-
101 wait predator (Shine 1980; Cogger 2000).
102

103 Visual systems are typically selective in their response to movement. *Amphibolurus*
104 *muricatus* relies heavily on motion cues to detect suitable prey items (Hoese et al. 2008),
105 avoid predators (Carlile et al. 2006) and communicate with conspecifics (Peters & Ord
106 2003). The diet of *A. muricatus* consists mainly of insects and small arthropods (McPhee
107 1963), but it is unknown whether these lizards have evolved a specific preference for
108 certain motion characteristics of these prey (Hoese et al. 2008). Distinctive behavioural
109 responses and normal behaviour in captivity (Ord et al. 2002; Peters & Evans 2003a, b)
110 make *A. muricatus* ideal for exploring this predator - prey system. In particular, the
111 predatory response of *A. muricatus*, which we used as a response assay, consists of
112 orientation towards a target, followed by approach, striking at prey with the mouth open
113 and finally feeding (Hoese et al. 2008).
114

115 A long series of previous studies on *A. muricatus* have successfully used digital
116 video playback and animation techniques to assess the role of visual cues in male - male

117 interactions (Ord et al. 2002; Ord & Evans 2003; Peters & Evans 2003b; Van Dyk & Evans
118 2007, Van Dyk et al. 2007) and prey recognition (Hoese et al. 2008). We began with a
119 ‘calibration’ experiment designed to assess the appropriateness of video playback in this
120 system. In this experiment, we systematically compared the social responses evoked by
121 life-sized simulated video opponents with those evoked by real males confined in a glass
122 tank. Results showed that video stimuli were in every case equivalent to a live conspecific,
123 validating the use of this technique (Ord et al. 2002). We refer readers to Ord et al. (2002)
124 for a critical evaluation of methods for the experimental analysis of the way in which
125 nonhuman animals perceive dynamic visual stimuli, taking into account the remarkable
126 diversity of sensory characteristics. There is broad consensus that, provided the
127 effectiveness of video playback has first been established experimentally, this technique is
128 uniquely well suited to the challenge of reproducing signalling motor patterns (Oliviera et
129 al. 2000) particularly when these are too complex for the alternative approach of robotics
130 (e.g. Göth & Evans 2005; Patricelli et al. 2006). In the present study, we adopted digital
131 video playback to test sensitivity to variation in movement, while controlling for
132 confounding effects such as chemosensory information.

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

141

142 <H1>Experiment 1. Response to Caudal Luring

143

144 <H2>Methods

145

146 <H3>Subjects

147

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

167

168

169 <H3>Video stimuli

170

171 The stimulus was a model death adder created using LightWave 3-D version 8.3
172 animation software (NewTek Inc., San Antonio, TX, U.S.A.). The three-dimensional shape
173 of the model cybersnake was matched precisely to that of a real death adder using
174 techniques developed for studies of opponent recognition (see Van Dyk & Evans 2007;
175 Van Dyk et al. 2007 for details). Texture and colour were imported from a photograph
176 aligned over the model. Bones inserted into the cybersnake allowed it to be positioned over
177 a video exemplar in a loosely coiled ambush posture, such that its head was within striking
178 range of its tail (see Fig. S1 in the Supplementary material). The tapered end of the tail (the
179 lure) was extended in front of the head, henceforth referred to as the ‘neutral’ position.
180 Caudal luring movements were rotoscoped from digital video footage of caudal luring by
181 death adders at 25 frames/s. This method, described in detail elsewhere (Peters & Evans
182 2003b), consists of frame-by-frame synchronization of movement between archival footage
183 and the model, permitting precise reproduction of the motion characteristics of the lure in
184 all three dimensions.

185

186 The Nyquist theorem, which applies to any process in which a continuous function
187 is represented by discrete samples (Hopp et al. 1998), defines the maximum frequency
188 adequately reproduced by the 25 frames/s PAL video standard (12.5 Hz). It is perhaps
189 easier to consider this constraint in terms of the corresponding time interval (80 ms). There
190 is no evidence that complete movements as brief as this occurred in our video footage. In
191 addition, we have previously shown that the PAL frame rate is adequate to capture the

192 velocity characteristics of display motor patterns (Peters et al. 2002; Peters & Evans 2003a)
193 and for playback exploring perceptual processes (Peters & Evans 2003b, 2007).₂ Note that
194 these aggressive signals have both a higher frequency and a larger sweep area than caudal
195 luring movements.

196

197 Playback design

198

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

209

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

215

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

223

224 <H3>Test procedure

225

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

235

236 Stimuli were presented using a high-resolution monitor (Sony PVM-1450;
237 resolution 450 lines) mounted on a trolley. Responses were recorded using a Panasonic
238 WVCP240 CCTV camera with a wide-angle WV-LZ62/2 lens, fitted below the monitor,
239 and a Panasonic AG-MD830 videocassette recorder, located outside the room. Behaviour
240 was monitored from outside the room using a second monitor (Panasonic TC-1470Y),

241 which functioned as a viewfinder for the recording camera. All remaining equipment was
242 operated externally to minimize observer effects. Stimuli were played using an iMac
243 (Apple Computer Inc.) running Final Cut Pro 3.0 and a Canopus ADVC110 for digital to
244 analogue conversion. The large stimulus library required for these tests was stored on an
245 external drive (LaCie d2 250 GB) connected to the iMac via firewire.

246

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

250

251 <H3>Data analysis

252

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

265

266 To test which treatment was most effective at initiating a ‘visual grasp’ response to
267 caudal luring we measured latency to orient after onset of movement. The nature of this
268 time-to-event (survival) data set required a Cox proportional hazards test for analysis
269 (Cleves et al. 2002). The Cox proportional hazards model is nonparametric, does not
270 assume a particular distribution for the survival times and, having been devised for the
271 analysis of survival times, deals appropriately with right-censored data (for a description of
272 the Cox model see Hosmer et al. 2008). As implemented in Stata version 9 (StataCorp
273 2005), which was used for these analyses, the Cox model is able to deal appropriately with
274 the correlated observations that arise from repeated measures analysis, using the method
275 described by Williams (2000) to take account of the clustered data.

276

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

283

284 <H2>*Results*

285

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

290

291 When compared with the still control, latency to orient and maximum response
292 were significantly higher only when the luring movement was conspicuous against a sand
293 substrate (Table 1). Lizards were significantly more likely to respond with predatory
294 behaviour (Fig. 2) towards conspicuous slow caudal lures than controls (Fisher's exact test:
295 $P = 0.024$), a trend also apparent with fast lures (Fisher's exact test: $P = 0.052$). However,
296 when caudal luring was semicamouflaged (slow: Fisher's exact test: $P = 0.195$; fast:
297 Fisher's exact test: $P = 0.353$) or obscured (slow: Fisher's exact test: $P = 1.000$; fast:
298 Fisher's exact test: $P = 0.424$), it did not elicit more predatory responses than the control
299 sequence.

300

301 <H1>Experiment 2: Motion Characteristics of Live Prey

302

303 <H2>Methods

304

305 <H3>Field sampling

306

307 We selected 13 Jacky dragon habitats in Lane Cove National Park, Sydney,
308 Australia, and sampled the invertebrate fauna they contained over 7 days in January 2007.
309 Fieldwork was conducted between 0900 and 1300 hours, when lizards are typically active
310 and foraging. The average \pm SEM temperature and humidity during the sampling period
311 were 29 ± 0.36 °C and $57 \pm 4.32\%$, respectively. Individual Jacky dragon territories were
312 located by identifying the animal in its natural surroundings (typically basking on a perch)
313 and then marking a 3 m² quadrat around the lizard.

314

315 Sampling involved sifting soil and leaf litter through a 470 x 300 mm tray with 12 x
316 13 mm grids. The tray sat flush inside a rectangular bin (540 x 350 mm) that caught the
317 sampled material. Unfiltered leaf litter was examined for species too large for the grid.
318 Additionally, all foliage within the quadrat was closely examined for potential prey species.

319

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

330

331 Filming

332

333 Filming was conducted in a laboratory, with temperature and humidity controlled at
334 approximately 28 °C and 67%, respectively. Prey items were videorecorded (PAL
335 standard: 25 frames/50 fields per s) in an open-fronted glass terrarium (920 x 380 mm and
336 360 mm high) with a sand substrate to facilitate natural movement. Three broad-spectrum
337 Dedolight DLH4 Aspherics2 lights (24 V, 150 W), positioned approximately 240 mm from
338 the terrarium, provided lighting. Prey items were recorded on DV tape using a Canon XL1
339 digital video camcorder mounted on a tripod. Focal length was constant throughout.

340

341 <H3>Analysis of image motion

342

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

347

348 Up to 5 s of side-to-side movement were selected for each prey item ($N = 61$) and
349 exported as AVI files for subsequent analysis. The selection criterion for each video
350 sequence was that it contained lateral movement that kept the invertebrate within the field
351 of view for 1 - 5 s. For comparison, we also converted footage of the cybersnake from each
352 of the eight rotoscoped bouts of movement into AVI format. All sequences were exported
353 as a stream of uncompressed images at 25 frames/s.

354

355 *<H2>Results*

356

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

360

361 Invertebrate speed, initially visualized as a histogram with the percentage of
362 invertebrate individuals expressed along the ordinate and mean speed of locomotion along
363 the abscissa (Fig. 3), was used to derive which speeds were commonly found among the
364 range of invertebrates sampled. This was done by sorting the percentage of invertebrates

365 found by the number of speed bins in which that percentage was represented, such that, for
366 example, four speed bins represented invertebrates in the 1 - 2 percentile range and three
367 speed bins represented invertebrates in the 9 - 10 percentile range (see Fig. 3). Two
368 discontinuous groups were found. Invertebrates that moved at 'common' speeds (i.e. the
369 speeds of the majority of potentially encountered prey) accounted for 74% of the sample
370 population. The 'rare' category made up the remaining 26% of the invertebrate sample.
371 Subsequent analyses used this split to perform a posteriori tests. These species generated
372 two conspicuous peaks in the speed distribution (0.1 – 0.6 and 0.9 – 1.1 pixels/frame; Fig.
373 3).

374

375 <H1>Experiment 3: Response to Prey Motion

376

377 <H2>Methods

378

379 Subjects and materials were the same as for experiment 1.

380

381 <H3>Video stimuli

382

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

387

388 <H3>Playback design

389

390 Regions of interest were chosen from the distribution of invertebrate prey velocity
391 data (Fig. 3) so that suitable speeds could be assigned to the ‘cybercricket’ for playback
392 experiments. Three regions were chosen within the caudal luring range: a slow peak (0.5 -
393 0.6 pixels/frame), a fast peak (0.9 - 1.0 pixels/frame) and a trough that spanned the
394 intermediate range (0.6 - 0.9 pixels/frame). Two extreme regions, very slow (0.1 - 0.2
395 pixels/frame) and very fast (1.1 - 1.5 pixels/frame), together with a control (no movement)
396 were selected for comparison. Each region (excluding the control) corresponded to velocity
397 estimates for five to eight invertebrates; values that were then averaged to determine a
398 representative speed for each group. The six treatments had motion velocities of 0, 3.35,
399 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
400 assumption that the lizard was in the middle of its pen).

401

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

409

410 The cybercricket began centred in the field of view for all treatments. The position
411 of the leaves in the horizontal plane varied, since each treatment required different
412 trajectory lengths. The cybercricket was fully exposed for 5 s while moving in either
413 direction in all treatments. However, owing to the differing speeds, the number of
414 transitions (two to four) had to be varied. Total movement time hence varied from 80 to 92

415 s. This also affected latency to emerge from the leaves (3 - 7 s). Each stimulus treatment
416 consisted of 5 min of playback with the same temporal structure (i.e. before, during and
417 after periods) used in experiment 1.

418

419 <H3>Test procedure

420

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

425

426 <H3>Data analysis

427

428 Data were scored as for experiment 1. Baseline behavioural scores were subtracted
429 from those that occurred during stimulus movement to isolate responses evoked by the
430 simulated prey item. We divided six treatments according to their relation to the prey
431 motion distribution into three 'common' and three 'rare' speeds. The behavioural responses
432 of these groups were then averaged to give each lizard a single estimate of response to
433 common and to rare prey motion, which were compared using paired-sample *t* tests.

434

435 *<H2>Results*

436

437 The predatory responses of Jacky dragons towards the cybercricket moving at
438 different speeds were clearly bimodal (Fig. 3). Speeds that fell within the range of those
439 commonly found among invertebrates in nature elicited higher overall predatory responses

440 than those that were rarely experienced (Fig. 3). The mean \pm SEM behavioural responses to
441 the three common prey speed stimuli (0.14 ± 0.04) was significantly greater than that
442 towards the three rare prey speed stimuli (0.03 ± 0.04 ; $t_{30} = 2.376$, $P = 0.024$).

443

444 <H1>DISCUSSION

445

446 We carried out a detailed experimental analysis of the design of a snake caudal

447 luring signal. Our results suggest it is possible that death adders mimic the motion

448 characteristics of invertebrates using a deceptive signal to attract agamid lizards.

449 *Amphibolurus muricatus* responded most strongly towards two ranges of movement speeds

450 common in invertebrates found in their habitat, and likely to be prey. These ranges each

451 overlap with the motion of one of the two luring movements seen in death adders. We

452 conclude that the caudal luring signal may have been shaped by aspects of receiver

453 psychology (Guilford & Dawkins 1991).

454

455 Recent experiments have measured peripheral motion sensitivity in the Jacky

456 dragon (Woo & Burke 2008; Woo et al. 2009b) using random dot kinematograms. These

457 simple stimuli are highly effective at evoking visual responses, but they are explicitly

458 nonbiological and do not engage higher-order cognitive processes, such as recognition or

459 categorization. Woo & Burke's (2008) and Woo et al.'s (2009b) results show that the Jacky

460 dragon visual system is broadly tuned and is particularly sensitive to high-speed motion.

461 Responses increase monotonically with speed over the range 10 - 160 °/s, although all these

462 speeds are faster than those experienced by the lizards in our tests.

463

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

472

473 As a heuristic, it is worth considering the most likely a priori scenarios for a process
474 of perceptual exploitation. We might have expected: (1) a flat response function with no
475 sensory or perceptual tuning; (2) unimodal tuning (either a bell curve or a curve skewed
476 towards fast speeds, as in basic movement sensitivity); or (3) a probability-based tuning
477 response that tracked the properties of target movement. The first situation predicts an
478 equal response to all speeds, posing the fewest constraints on caudal luring signal design.
479 The second scenario allows for two hypotheses, depending on the position of the response
480 curve. *Amphibolurus muricatus* might be tuned to a central mean of prey speeds.
481 Alternatively, lizards might be more sensitive towards fast speeds, such as those
482 characteristic of intraspecific displays (Peters & Evans 2003a, b), rendering the slow lure
483 ineffective. In the probability-based scenario, responses should be higher towards common
484 prey speeds, regardless of velocity, than towards those that are rarely seen in nature. Our
485 results are consistent with this last hypothesis: *A. muricatus* responded more strongly
486 towards common prey speeds (both 'fast' and 'slow') than rare ones (Fig. 3). While it is
487 possible that prey movement was different in our sand substrates than in leaf litter, there
488 appears to be an extraordinary correspondence between prey characteristics, lure design

489 and lizard response intensity, suggesting that the snake's deceptive signal may be modelled
490 from common invertebrate movements and that it achieves efficacy by engaging
491 recognition processes. If this hypothesis is correct, we would predict that future studies
492 using these methods and changing the speed of the caudal lure to speeds outside the range
493 of common prey will elicit fewer predatory responses from the lizards. We believe that this
494 is the first experimental evidence that receiver psychology may have shaped the design of
495 caudal luring.

496

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

505

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507

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511

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695

696 **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

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

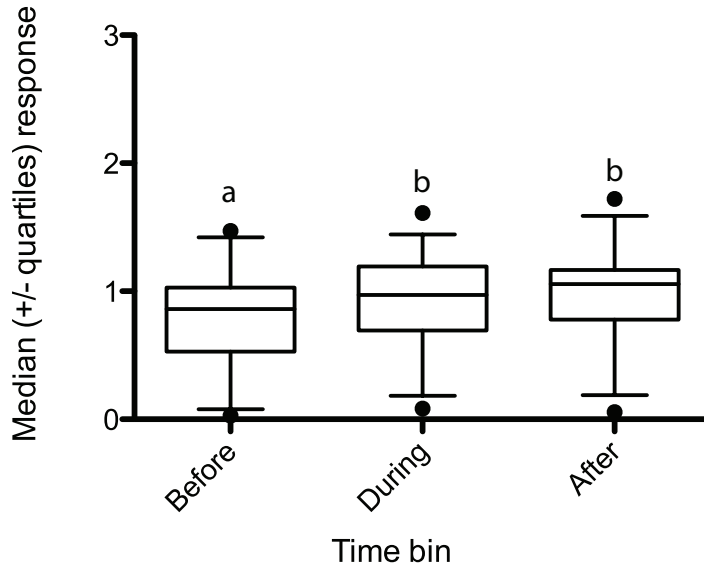
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705 **Figure legends**



706

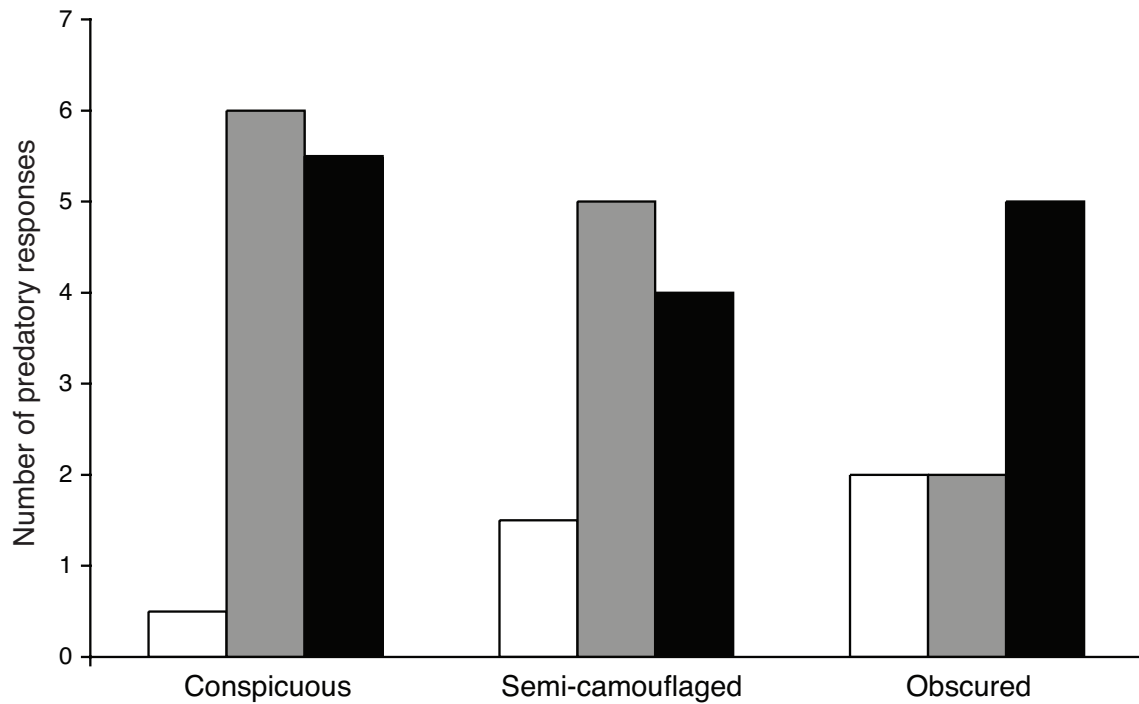
707 **Figure 1.** Efficacy of caudal luring. Box plot depicts median response, Q1 and Q3 ($N = 31$)

708 for each time bin, whiskers illustrate 5th and 95th percentiles and dots represent outliers.

709 The X axis depicts time relative to the onset of caudal luring. Different letters denote

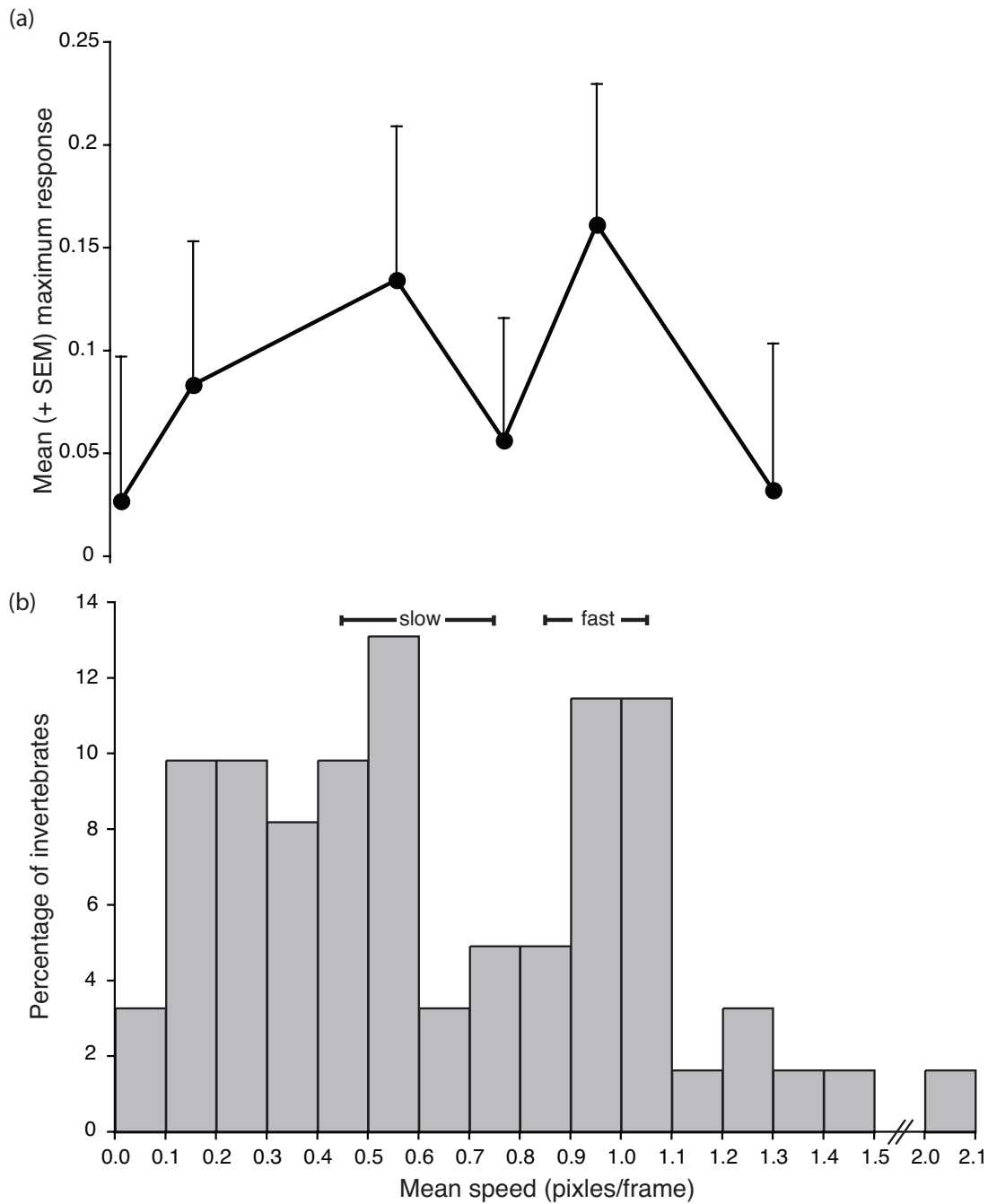
710 significant differences between comparisons. Response scores: no response = 0; orient = 1;

711 moderate attention = 2; predatory response = 3. See text for details.



712

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



717

718 **Figure 3.** Prey speeds and lizard predatory responses. All stimuli used for characterization
 719 of motion were filmed such that they were life sized on the playback screen, allowing us to
 720 compare the motion characteristics of invertebrates and snakes directly. (a) Maximum
 721 predatory response, after subtracting baseline behaviour, of *A. muricatus* ($N = 31$) towards

722 the cybercricket moving at speeds within the range found in invertebrates. The six
723 treatments had motion velocities of 0, 3.35, 12.26, 16.83, 20.77 and 28.32 mm/s. (b)
724 Distribution of speeds for 61 invertebrate prey items found in *A. muricatus* territories.
725 Speed bins are 0.10 pixels/frame (25 frames/s). Lines above histogram depict speed ranges
726 for the two types of caudal lure presented in experiment 1.
727