

Active space of a movement-based signal: response to the Jacky dragon (*Amphibolurus muricatus*) display is sensitive to distance, but independent of orientation

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Accepted 15 November 2006

Summary

The efficacy of any animal signal is constrained by the range over which it remains above the sensory threshold of potential receivers. The spatial area in which reliable detection occurs defines active space; this is influenced by signal structure, the signalling environment and the sensory characteristics of receivers. Identification of the factors influencing active space has provided valuable insights into signal design, particularly in bioacoustics, in which signal distortion and degradation can be easily quantified. In the present study, we consider whether active space can similarly help to explain the design of a movement-based visual signal. The Jacky dragon (*Amphibolurus muricatus*) threat display is composed of five distinct motor patterns delivered in an obligatory sequence: tail-flicks, backward and forward foreleg waves, a push-up and a 'body-rock'. In contrast to other communication systems, the introductory element is characterized by reduced intensity (average speed) but greater duration than subsequent motor patterns. Furthermore, the tail-flick sweeps a three-dimensional (3D) space around the lizard, whereas the motor patterns

that follow are largely restricted to a single plane. Structural properties thus suggest that the active space of the tail-flick might be greater than that of the other motor patterns in the display, which would provide a parsimonious explanation for its use as an alerting component. We tested this prediction in a playback experiment incorporating 3D animations of lizard displays, comparing response probabilities to the factorial combination of three motor patterns, three viewing angles and three distances. Results suggest that the tail-flick does not have a greater active space than other display motor patterns, but that each degrades predictably with distance, thereby providing potential ranging cues. In addition, display components are remarkably robust to variation in receiver orientation, so that efficacy should be maximized in most potential signalling situations. These findings are consistent with the hypothesis that duration is the principal determinant of signal efficacy in this system.

Key words: active space, Jacky dragon, *Amphibolurus muricatus*, signal design, movement-based signal.

Introduction

Animal signals are constrained by both the physical environment (Endler, 1992) and the sensory systems of receivers (Ryan et al., 1990). The environment affects signal transmission by adding noise and altering signal properties (Endler, 1992; Marten and Marler, 1977), whereas receiver characteristics dictate the structural correlates of conspicuousness (e.g. Leal and Fleishman, 2004), audibility (e.g. Klump et al., 1986) and localizability (Wood et al., 2000). These processes have been studied most in bioacoustics; distortion occurs in both the frequency domain (selective attenuation and filtering) and in the time domain (reverberation) (reviewed by Hopp et al., 1998; Bradbury and

Vehrencamp, 1998). Such effects are, in principle, predictable (Morton, 1982), and can provide ranging cues (Whitehead, 1987).

Signals are designed to stimulate the sense organs of intended receivers (Capranica, 1965). In many signalling systems, sensory thresholds define the range-limit for reliable detection. The active space of the signal is defined by the distance at which the probability of detection drops to chance (Brumm et al., 2004; Dupuch et al., 2004; Janik, 2000; Linn and Roelofs, 1989; Lohr et al., 2003). For example, pioneering work by Brenowitz measured the acoustic properties of red-winged blackbird (*Agelaius phoeniceus*) song in the field and determined that the active space of these vocalizations

corresponded with the distance to the edge of the neighbouring territory (Brenowitz, 1982). More recently, studies have demonstrated that signalers can alter the structure of a vocalization to compensate for increased noise, thereby maintaining active space (Brumm et al., 2004; Cynx et al., 1998).

Rather less is known about analogous phenomena in visual signals, although experiments with bees have demonstrated that the probability of detecting colour is influenced by both visual angle (Giurfa et al., 1996) and distance (Hempel de Ibarra et al., 2001). Hempel de Ibarra et al. also identified likely advantages to combining colours with certain spectral properties and in certain spatial arrangements, based on neural mechanisms of colour perception (Hempel de Ibarra et al., 2001). For movement-based visual signals, sensory properties, such as the minimum detectable amplitude of motion (Fleishman, 1992), are similarly likely to determine active space. However, the physical properties of this class of signal have received little systematic study (for reviews, see Fleishman, 1986; Peters and Evans, 2003a; Zeil and Zanker, 1997), and there has been no formal analysis of changes in structure as a function of distance.

Our strategy for analyzing movement-based signals combines quantitative analyses of the structure of signals and noise (Peters and Evans, 2003a) with signal-detection experiments (Peters and Evans, 2003b). We use a native Australian agamid lizard, the Jacky dragon (*Amphibolurus muricatus*), as a model system. Jacky dragon displays are performed in response to conspecific intruders and comprise five distinct motor patterns, delivered in an obligatory sequence (Peters and Ord, 2003). Signals have to be robust to variation in background noise. One strategy to ensure reliable detection is to include particularly conspicuous introductory elements designed to draw the attention of the receiver to the motor patterns that follow. Such alerting components typically have high intensity, delivered over a short duration [auditory: Wiley and Richards (Wiley and Richards, 1982); visual: Fleishman (Fleishman, 1988)]. However, the Jacky dragon employs a different approach (Peters and Evans, 2003a), in which the introductory tail-flick is characterized by longer duration at reduced average speed.

These contrasts in the design of introductory components warranted closer inspection. We began by considering the properties responsible for signal efficacy in the Jacky dragon tail-flick (Peters and Evans, 2003b). We found that duration was more important than speed in evoking an orienting response, with long signals being most successful. Given the efficacy benefit of increased duration, we speculated that the tail-flick might be most suited to this role because it probably has lower energetic costs than other display motor patterns and is less likely to compromise escape. An alternative explanation is suggested by potential differences in active space. The tail-flick sweeps a three-dimensional (3D) region around the animal and is less constrained than the display movements that follow, which are largely restricted to one plane of movement, along the long axis of the body. The active space of the tail-flick may

thus be greater than that of the rest of the display, conferring efficacy that is robust to variation in receiver orientation. This effect could produce a selective advantage independent of duration, or the two parameters could be linked, for example as a consequence of physical or biomechanical constraints.

In the present study, we investigated variation in the probability of response to different signalling motor patterns as a function of distance and angle of view. This is the first experimental analysis of this type for any class of dynamic visual signals. We adapted a strategy analogous to those used in acoustic studies (for a review, see Dooling et al., 2000) and techniques developed in our previous work in the Jacky dragon system (Peters and Evans, 2003b). Signal properties were manipulated using video playback of highly detailed 3D animations. We created an animation of each motor pattern under consideration and then systematically varied the angle of view and apparent distance. We predicted that response to the tail-flick would be less affected by changes in view and increased apparent distance between signaler and receiver than the other motor patterns in the display.

Materials and methods

Subjects

Subjects were 18 adult male Jacky dragons, *Amphibolurus muricatus* (White, ex Shaw 1970), wild-caught from Botany Bay National Park, south of Sydney, Australia. Lizards were treated with an anti-helminthic drug on arrival to reduce endoparasite load and housed indoors in pens (64 cm × 75 cm × 120 cm) with aluminium frames, sides of rigid opaque white plastic sheeting and a clear Perspex® front. Pens contained sand substrates with branches suitable for basking and vegetation for cover, and were arranged so as to maintain visual isolation from other lizards. Room temperature was maintained at approximately 26°C, with ceiling lights on a 14 h:10 h L:D cycle, corresponding to midsummer. Heat lamps (125 W, 240 V Philips Spotone) and UV lamps (300 W Osram Ultra-Vitalux) were suspended above the aquaria. Lizards were fed crickets dusted with vitamin supplements (RepCal, Los Gatos, CA, USA), and mealworms. Water was available in small bowls, and pens were sprayed daily to provide additional moisture. Lizards were subsequently released at the site of capture.

Design

Our goal was to examine the effect of viewing angle and distance on the detection probability of different motor patterns that make up the Jacky dragon push-up display. Digital video playback of 3D animation is the only technique that permits precise definition of both stimulus morphology and movement. Since our stimuli contained no uncontrolled structural variation of the sort that compels sampling when natural recordings are used for playback, we chose to use a single exemplar of each motor pattern. This approach avoided introducing variance that would reduce statistical power and increase the likelihood of Type II error, or require a substantially increased sample size.

We acknowledge that this provides only a direct test of active space variation in the signals produced by a typical lizard. It is conceivable that different response functions might be obtained with individuals substantially smaller or larger than the one chosen; exploration of this sort of morphology–movement interaction is outside the scope of the present study. Our approach is consistent with that adopted in the large corpus of successful playback studies in bioacoustics (reviewed by Gerhardt and Huber, 2002), which underpin current theories of animal communication.

The duration of display motion is likely to be a key parameter mediating probability of detection (Peters and Evans, 2003b); it was therefore necessary to standardize this across stimuli. Four out of the five motor patterns that comprise the Jacky dragon display are both brief (approximately 400 ms) and highly stereotyped. In contrast, the tail-flick is variable and can last as long as 12 s (Peters and Evans, 2003a). We reasoned that presenting each motor pattern in isolation was likely to produce a floor effect in which none of the stimuli evoked a response, or would require repetition of the motor pattern, which would be highly unnatural. We therefore considered logical breaks in the sequence of motor patterns based on Markov analysis (Peters and Ord, 2003), and selected the backward and forward foreleg waves (transition $P=1.0$) as one pair, and the push-up and body-rock components (transition $P=1.0$) as another. The duration of each of these motor pattern pairs was 840 ms (21 PAL video frames). An equal number of frames from a tail-flick sequence, which contained two high-amplitude flicks, was used for comparison.

Next, we considered how to divide the space around the displaying lizard into a manageable number of regions (Fig. 1A). The space to the front of the lizard is most relevant, as Jacky dragons rarely display when they are oriented directly away from the intended receiver. Furthermore, display structure is unlikely to vary much as a consequence of being viewed directly from one side or the other (Fig. 1A; filled and empty circles). An exception to this is the foreleg wave component. As noted elsewhere (Peters and Ord, 2003), the choice of foreleg appears to be arbitrary. It is not restricted to the side nearest the receiver, nor do lizards show an individual left- or right-side bias of the type described in anurans (Vallortigara et al., 1998). To maximize the likelihood of detection in the present experiment, we modeled the foreleg wave using the limb on the receiver's side of the signalling animal's body. We thus restricted our interest to the front side nearest to the receiver, sampling angles orthogonal to the displaying lizard (90°), oblique (45°) and front-on (0°; Fig. 1B). Our manipulation of distance was limited to the range over which we have observed lizards exchanging displays in a large, outdoor enclosure (315 m²; D. Van Dyk, unpublished data). We chose 6 m as the maximum range of a signalling interaction, and added two closer distances of 3 m and 1 m.

The factorial combination of three motor patterns, three viewing angles and three distances resulted in 27 stimulus sequences. To assess the absolute efficacy of display, we also created control sequences of a non-displaying lizard against the

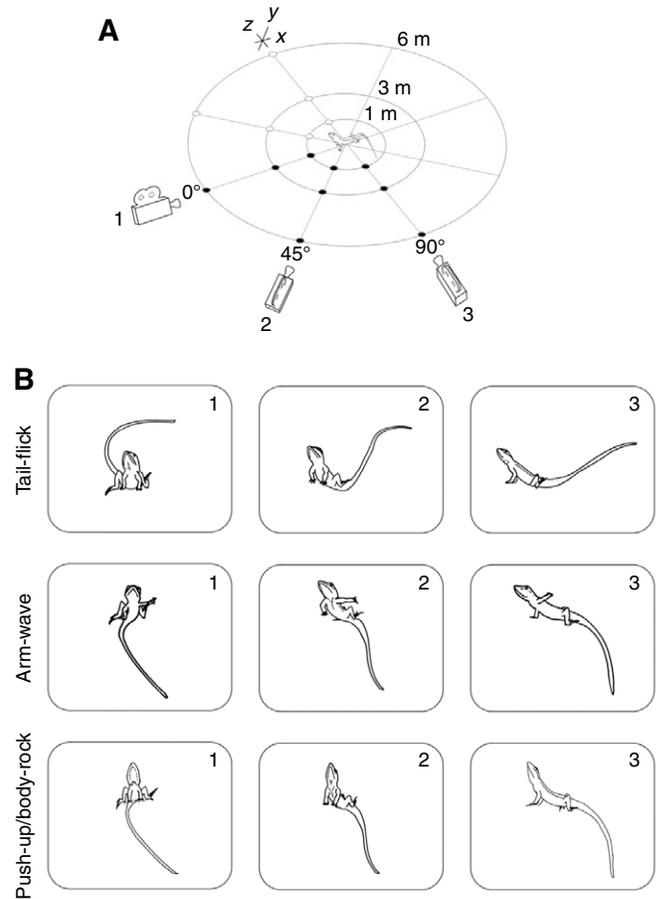


Fig. 1. (A) Illustration of the space around a signalling lizard, divided into 45° sectors and three concentric circles at distances of 1, 3 and 6 m. We created stimulus sequences of each motor pattern by recording at points given by the intersection of the concentric circles and at angles of 0, 45 and 90° (filled circles). The empty circles represent views that were not sampled but which are not likely to be different to the positions chosen. The space behind the lizard was not included, as lizards do not typically display when oriented in a direction away from an intended receiver. (B) A schematic illustration of how the different viewing angles were generated by shifting the location of the camera object in the animation software. The drawings show how changing the location of the camera influenced the view of the tail-flick (top panel), foreleg wave (middle panel) and push-up (bottom panel) for the three camera locations shown in (A).

same background of moving vegetation. Nine such sequences were created, one for each angle of view at each distance. Individual subjects were presented with control sequences from one angle of view only, but at each of the three distances. The total number of sequences for each lizard was thus 30.

Stimulus preparation

Background of windblown plants

Jacky dragon displays are typically seen against windblown plants that generate irrelevant movement in the visual field. The ability of lizard motor patterns to engage visual processing is thus best assessed after the subject has spent a period spent

viewing such background motion. We recorded plant sequences at the field site where these lizards had been caught. A perch site was identified and used as the focal point for video recording, so that we could subsequently embed the computer-generated lizard in the natural scene. Three 10-min sequences were recorded, with a fixed focal length, at distances of 1, 3 and 6 m between the perch and the camera. All sequences were filmed in summer within a one-hour period, on a bright day with no cloud cover. We placed a 300 mm rule in the frame at the beginning of each clip so that we could subsequently scale the animated lizard to be precisely proportional to the background. Plant sequences were edited to 6 min in duration and exported as numbered JPEG sequences.

Lizard animations

Lizard animations were created using LightWave 3D v7 (NewTek Inc., San Antonio, TX, USA). In a previous study, we created a 3D computer-generated Jacky dragon tail using shaping tools within the modeler module of LightWave (Peters and Evans, 2003b). However, ground-up synthesis of a complete Jacky dragon is more challenging. To accurately reproduce morphology, we began with a 3D laser-scan of a taxidermically prepared Jacky dragon. This produced a detailed wire-frame model that represented the shape of the lizard with a mesh of 100 000 polygons. Digital photographs of lizard skin were then used to create a texture map in Adobe Photoshop v6 (Adobe Systems Inc., San Jose, CA, USA); this then overlaid the 3D wire-frame model.

Animation procedures have been described previously (Peters and Evans, 2003b). Briefly, we added a skeleton of artificial 'bones'. These are invisible elements that facilitate adjustment of a model in which there is both global displacement and local movement of some sectors, relative to others. To animate the lizard, we used a 'rotoscoping' technique. This involves superimposing the computer-generated model over sequential digital video frames from an actual lizard display sequence, and then adjusting the limbs and body in all three planes (x , y and z) to match. Weight maps associated with separate regions of the wire-frame model ensured that manipulation of the invisible bones caused deformation of the wire-frame in the appropriate region of the body surface. Although this technique is laborious, it produces a much more faithful reproduction of natural movements than alternative methods that employ 'tweening' algorithms to interpolate between keyframes.

We created separate animations for the tail-flick, foreleg waves and push-up/body-rock. Finished animations had a duration of 6 min. The lizard remained stationary for the first 3 min, then produced one of the three motor patterns, repeating this 60 and 120 s later.

Manipulation of viewing angle and distance was achieved by adjusting the virtual 'camera' in LightWave. Adjusting the location and rotation of the camera in the scene changes the camera's view and the resultant animation, without adjusting the position of the lizard model (Fig. 1A,B). We positioned the camera within the scene using footage of the straight rule in the

Table 1. *The angular size of motor patterns (degree of visual angle) based on a distance of 50 cm between the lizard and the monitor**

Distance	Motor pattern		
	Tail-flick	Foreleg waves	Push-up/body-rock
1 m	18.44	7.50	10.45
3 m	6.65	2.64	3.70
6 m	2.29	0.91	1.27

*Perches were approximately 25 cm from the back wall of the home pens.

unused part of the background sequence (see above) to determine the scale. The relative angular sizes of stimulus motor patterns (Table 1) exceed Fleishman's (Fleishman, 1986) estimate of the minimum required to engage the visual grasp reflex of another lizard species (Genus: *Anolis*; 0.22° of visual angle).

The final stage of the animation process was to add the appropriate background of windblown plants and render each sequence. Digital video footage of vegetation movement was first converted to a series of still frames. These were then loaded sequentially as the background over which the computer-generated lizard was superimposed, creating an uncompressed JPEG image for each of the 9000 frames in each sequence (Fig. 2). We used Final Cut Pro 3 (Apple Computer) to transform these still images into digital video files at full PAL resolution (720×576 pixels). Control sequences were generated in the same way, but with the lizard remaining motionless throughout.

Playback procedure

We used a test set-up similar to that employed in earlier studies (for details, see Peters and Evans, 2003b). All stimuli were presented on a Sony PVM-14M2A colour monitor (resolution >600 lines; screen size 34 cm, measured diagonally). Stimulus sequences were stored on a LaCie d2 external hard drive connected to an Apple G3 iMac running Final Cut Pro 3. Video was streamed as a digital signal to a Sony GV-D300E mini-DV deck, using an IEEE 1394 Firewire interface. The S-video analogue output from the deck was then connected to the Sony monitor.

We used a Panasonic WV-CP240 CCTV camera, with a WV-LZ62/2 lens, and a VHS video deck to record lizard responses. All stimuli were presented with the soundtrack muted, but a marker tone (inaudible to the subject lizard) was dubbed directly to the VHS deck so that responses could later be scored relative to stimulus onset. We performed all playback tests between 08:00 h and 12:00 h, which corresponds with the period of peak activity in our captive population (Ord, 2001).

The study was performed in November and December 2004. We divided testing into six blocks of five days each, with a two-day interval between blocks. Lizards saw one stimulus sequence per day, each in a unique sequence. To control diel variation in behaviour, we standardized presentation time for each subject.

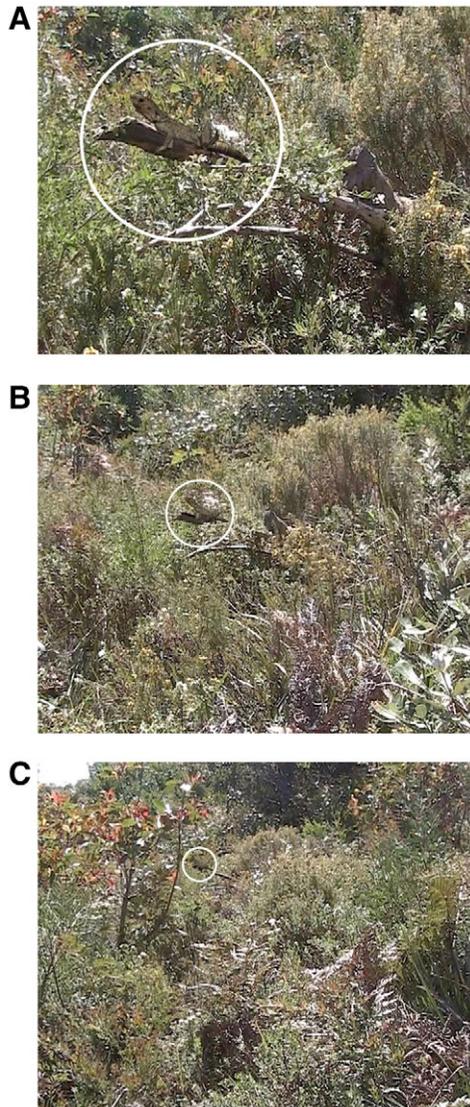


Fig. 2. Representative frames showing the animated lizard (circled) against the background at 1 m (A), 3 m (B) and 6 m (C). Different background plant sequences were used for each relative distance in order to keep the size of the lizard proportional to the background. Although the 3D animated lizard appeared at roughly the same perch site in each of the sequences, the structure of background visual motion varied in an ecologically meaningful way between the sequences.

Statistical analyses

Our dependent measure was the orienting response, which we operationally defined as an observable movement of the head toward the monitor. As we were primarily interested in the propensity of each signal to attract attention, we considered only response probabilities to the initial display at the third minute. The data were analysed with non-parametric tests of significance for repeated measures. Friedman's analyses of variance (ANOVAs) were used when comparing more than two conditions, whereas Wilcoxon signed-ranks tests were used for pair-wise comparisons (Siegel and Castellan, 1988). For

ANOVAs, we calculated partial η^2 from the parametric ANOVA model as an estimate of effect size. Partial η^2 can be interpreted as the amount of variation explained by a parameter after controlling for that explained by the other parameters (Cohen, 1988). The effect size for pair-wise comparisons, h , was calculated as the absolute difference between probability values following arcsine transformation (Cohen, 1988):

$$h = |2\arcsine \sqrt{P_1} - 2\arcsine \sqrt{P_2}|,$$

where P_1 and P_2 are the probability values to be compared.

First, a Friedman's ANOVA was performed to assess variation in the probability of response over all stimuli. Second, we grouped responses to stimuli by each of the three structural parameters (motor pattern, angle of view and distance) and tested for main effects using Friedman's ANOVAs. These were followed by Wilcoxon signed-ranks tests for pair-wise comparisons between conditions. Our third series of analyses again used Friedman's ANOVAs and Wilcoxon signed-ranks tests, but considered interactions between two variables collapsed across the third variable; for example, we examined the effect of distance within angle of view, pooling data across motor patterns.

Results

Of the 54 presentations of a control sequence (three to each lizard), only two spontaneous orienting responses were observed. We therefore restricted statistical comparisons to stimulus sequences of display movement. Response probabilities across the stimulus set are presented separately for each motor pattern in Fig. 3. A Friedman's ANOVA revealed significant variation in orienting probability as a function of movement characteristics ($\chi^2=51.004$, d.f.=17, $P=0.002$).

We next considered the main effects for motor pattern, angle of view and distance. Friedman's ANOVAs indicated no overall effect of motor pattern ($\chi^2=0.102$, d.f.=2, $P=0.950$) or angle of view ($\chi^2=1.910$, d.f.=2, $P=0.385$). However, there was a strong effect of distance ($\chi^2=15.574$, d.f.=2, $P=0.0001$). Wilcoxon signed-ranks tests revealed significantly higher response probability to 1 m than both 3 m ($z=2.898$, $P=0.004$, $h=0.17$) and 6 m ($z=3.198$, $P=0.001$, $h=0.22$), whereas the probability of responses did not differ between displays at 3 and 6 m ($z=0.574$, $P=0.566$, $h=0.05$).

Our final set of analyses considered interactions between two variables, while pooling data across the third variable. Results from Friedman's ANOVAs are summarized in Table 2. We found no significant variation in response probability to different motor patterns when considered within angle of view or viewing distance. Similarly, angle of view did not affect response probability when considered within motor pattern or the distance category. However, the effect of distance was robust. This was clearly significant at each angle of view. When we considered the effect of distance and motor pattern, we found a pronounced effect for tail-flicks and push-up/body-rocks, but only a non-significant trend for foreleg waves.

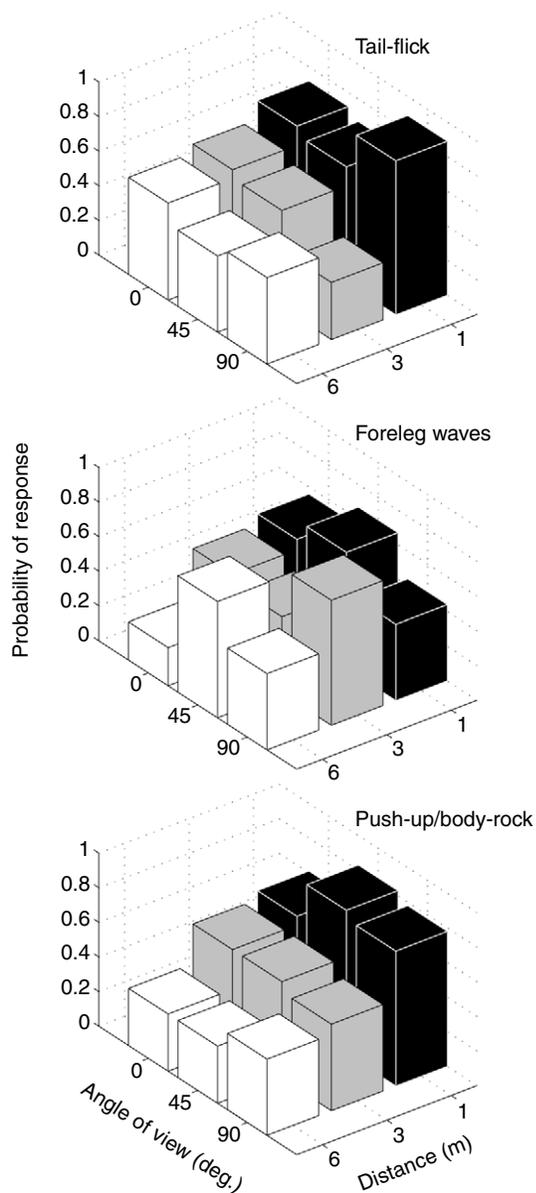


Fig. 3. Column graphs depicting response probabilities to the 27 sequences featuring lizard displays as a function of angle of view (0, 45 and 90°) and the distance between signaler and receiver. Separate plots are presented for the tail-flick (top), backward and forward foreleg waves (middle) and push-up/body-rock (bottom), with shading representing the distance in each plot: 1 m (black), 3 m (grey) and 6 m (white).

Discussion

Our results suggest that detection of each motor pattern is sensitive to distance, but independent of orientation. This is the first such demonstration for a movement-based signal, although the general phenomenon of decreased efficacy with increased signaler–receiver distance has been documented in other sensory modalities (Brenowitz, 1982; Linn and Roelofs, 1989). We attribute this effect to the reduction in visual angle

Table 2. Results of Friedman's ANOVAs comparing response probabilities

	χ^2 ^a	<i>P</i> -value	Partial η^2
Motor pattern			
Main effect	0.102	0.950	0.029
Within angle of view			
0°	3.261	0.196	0.096
45°	0.593	0.744	0.009
90°	0.286	0.867	0.005
Within distance			
1 m	3.098	0.212	0.062
3 m	0.269	0.874	0.010
6 m	2.821	0.244	0.074
Angle of view			
Main effect	1.910	0.385	0.020
Within motor pattern			
Tail-flick	0.140	0.932	0.017
Foreleg waves	1.920	0.383	0.049
Push-up/body-rock	2.000	0.368	0.025
Within distance			
1 m	0.237	0.888	0.010
3 m	0.367	0.832	0.007
6 m	1.959	0.375	0.056
Distance			
Main effect	15.574	0.0001	0.390
Within motor pattern			
Tail-flick	9.320	0.009	0.212
Foreleg waves	5.930	0.052	0.120
Push-up/body-rock	11.210	0.004	0.348
Within angle of view			
0°	7.815	0.020	0.213
45°	10.034	0.007	0.212
90°	9.102	0.011	0.240

^aAll tests performed have two degrees of freedom.

subtended by display movements at 3 m and 6 m (Fleishman, 1992) (Table 1).

Perhaps surprisingly, we were unable to detect any variation in responsiveness due to angle of view. It is possible that those structural properties of display motor patterns that influence detection do not vary appreciably with orientation, which might reflect selection for efficacy under the possible viewing conditions. Alternatively, this finding could be a Type II error, attributable to assay insensitivity. Although we cannot rule out such an interpretation, it is important to note that our response measure and sample size were sufficient to detect a robust effect of distance. We conclude that any putative effect of receiver viewing angle must be small, relative to that of signaler range.

Our results reveal that the active spaces of the movements that make up Jacky dragon displays are statistically

indistinguishable. We had predicted an interaction between motor pattern, angle of view and distance, because the 3D sweep of the tail-flick contrasts with the essentially single-plane movement of the push-up/body-rock and foreleg waves. There was a slight hint of an interaction between motor pattern and distance in the failure to detect a range effect with foreleg waves (Table 2). However, these data are highly variable, in contrast to the orderly changes in efficacy found with the other two motor patterns (Fig. 3), and we are reluctant to interpret them further.

Our design systematically sampled a portion of the space around a signalling lizard (Fig. 1, filled circles). It is logical to expect stimuli defined by these points in the horizontal plane to have effects comparable with those that would be evoked by corresponding stimuli on the other side of the signaler (Fig. 1, empty circles). To keep the total size of the stimulus set manageable with the limited number of subjects available, we also restricted manipulation of camera position to a single plane. As Jacky dragons are semi-arboreal and typically display from raised perches, it will be important to consider variation in display height in future experiments. It is conceivable that responses to the motor pattern examined in this study might be differentially affected by the vertical position of receivers, relative to signalers.

We manipulated apparent distance by moving the camera component of the 3D layout, thus varying the angular size of the animated lizard. Such variation is potentially ambiguous; it might be perceived as change in absolute size, rather than in range (Zeil, 2000). Potential depth cues include motion parallax, binocular stereopsis and accommodation. It is important to note that the background sequences we used scaled appropriately with simulated distance (Fig. 2), thus ensuring that the visual angle subtended by the lizard animation was proportional to the visual motion of the surrounding plants. This relative scaling was designed to introduce additional depth cues.

Notwithstanding such considerations, the findings of this study do not support our initial prediction that the structural properties of the introductory tail-flick would confer efficacy superior to those of the motor patterns that follow it, at least in terms of active space. It thus seems unlikely that active space alone is sufficient to explain the almost invariant sequence of motor patterns found in natural Jacky dragon displays (Peters and Ord, 2003). Results are instead consistent with previous experimental findings suggesting that duration is the principal determinant of signal efficacy (Peters and Evans, 2003b). We have also shown that signalling movements contrast reliably with those of wind-blown vegetation, when viewed at the same viewing distance (Peters and Evans, 2003a).

Alternative explanations for why the tail-flick serves an introductory role include reduced conspicuousness to predators and lower energetic costs. Increased display activity has been shown to reduce survivorship in another lizard, *Sceloporus jarrovi* (Marler and Moore, 1988; Moore and Marler, 1987), although it is difficult to know whether predators are selectively attentive to visual displays or if increased activity

levels in general render the lizard more vulnerable to attack. Experimental investigations of the relative conspicuousness to predators of different motor patterns will be required to resolve this question. A useful approach is suggested by recent field studies investigating the 'survival' of artificial moths varying in levels of camouflage (Schaefer and Stobbe, 2006; Stevens and Cuthill, 2006). Analogous tests of movement-based signals could be performed using programmable robots (Martins et al., 2005; Patricelli et al., 2002). In addition to reduced conspicuousness to predators, it is likely that the tail-flick motor pattern requires less energy. The energetic cost of display behaviour has been investigated in several systems [e.g. fiddler crabs, genus *Uca*, Matsumasa and Murai (Matsumasa and Murai, 2005); lizards, *Cnemidophorus exsanguis*, *C. sonorensis*, *Sceloporus virgatus* and *S. jarrovi*, Pough and Andrews (Pough and Andrews, 1985)]. These studies consistently demonstrate a cost to the signaler. However, common techniques such as measuring oxygen consumption in a respirometer, or determining lactate levels, do not allow for comparisons between multiple components produced in a rapid sequence within a single display as in the Jacky dragon; infrared cameras that permit measurement of heat levels in real-time may provide a useful proxy for energy expenditure.

The diversity of animal signals we see today reflects a history of selective forces and a variety of constraints (Endler and Basolo, 1998; Ord et al., 2001; Ord et al., 2002). Constraints can be inherent to the signaler, as in the case of physical or morphological limitations (Podos, 2001), as well as those imposed by the sensory system of receivers (Aho et al., 1988; Fleishman, 1992), which must perceive and process the signal. External factors such as the transmission environment contribute by defining the optimal structure for minimizing masking by background noise (Brumm et al., 2004). Similarly, the need to avoid detection by predators influences both signal design (Marler, 1955; Stoddard, 1999; Wood et al., 2000) and the timing of signalling (Endler, 1987). A greater understanding of any communication system can be achieved through careful consideration of these factors; meta-analyses across communication systems and sensory modalities allow for the refinement of prevailing models of signal evolution.

We thank Libby Eyre from the Biological Sciences Museum at Macquarie University for the loan of the taxidermic lizard, Karen Bell for assistance during the experiment and Terry Ord and Jochen Zeil for comments on earlier drafts. C.S.E. was supported by grants from the Australian Research Council and Macquarie University. Housing and experimental procedures were approved by the Macquarie University Animal Care and Ethics Committee (Protocol No. 2001/014) and the NSW National Parks and Wildlife Service (License No. S10397).

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