



Digital video playback and visual communication in lizards

TERRY J. ORD*†, RICHARD A. PETERS*‡, CHRISTOPHER S. EVANS*‡ & ALAN J. TAYLOR‡

*Animal Behaviour Laboratory, †Department of Biological Sciences and ‡Department of Psychology,
Macquarie University

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Experimental analyses of dynamic visual signals have to overcome the technical obstacle of reproducing complex motor patterns such as those found in courtship and threat displays. Video playback offers a potential solution to this problem, but it has recently been criticized because of sensory differences between humans and nonhuman animals, which suggest that video stimuli might be perceived as deficient relative to live conspecifics. Quantitative comparisons are therefore necessary to determine whether video sequences reliably evoke natural responses. Male Jacky dragons, *Amphibolurus muricatus*, compete for territories using complex displays delivered in a rapid stereotyped sequence. We evaluated video playback as a technique for studying this visual signal. Digital video sequences depicting a life-sized displaying male were indistinguishable from live male conspecifics in the rate and structure of aggressive displays evoked. Other measures of social behaviour suggested that video stimuli were more effective in this context. Lizards produced significantly more appeasement displays and had higher rates of substrate licking and locomotor activity in response to video playback than to confined male opponents, which failed to produce aggressive displays. Lizards tracked temporal changes in the display rate of video stimuli and were also sensitive to individual differences in morphology and behaviour between video exemplars. These results show that video stimuli are appropriate for the experimental analysis of Jacky dragon aggressive displays. We compare the potential shortcomings of video playback with those of other techniques and conclude that no approach offers a panacea, but that several have complementary characteristics.

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The design of animal signals reflects selection from both environmental factors (e.g. Wiley & Richards 1982; Endler 1992) and properties of the receiver (reviews by Guilford & Dawkins 1991; Pagel 1993; Dawkins & Guilford 1996). Recent studies show that perceptual mechanisms play an important role in evolution. For example, species with warning coloration have morphological attributes that are designed for rapid recognition by potential predators (Rowe & Guilford 1996). The sensory predispositions of receivers have also shaped sexually selected signals such as the calls of frogs (e.g. Ryan & Rand 1993; Ryan 1998) and the visual ornaments of birds (e.g. Andersson 1982) and fish (e.g. Basolo 1990; Rosenthal & Evans 1998). Understanding these phenomena requires experiments designed to characterize receiver preference functions and to identify biases.

Particular progress has been made in studies of acoustic signalling because for over 40 years it has been possible to

conduct playbacks in which a recorded signal and loud-speaker are substituted for a live conspecific (reviews in McGregor 1992; Hopp et al. 1998). The general logic of playback experiments has been extended to explore other modalities, including electrical (Hopkins 1988) and tactile (Parri et al. 1997) signals. In contrast, dynamic visual signals, such as the displays used in courtship and agonistic interactions, have proved relatively recalcitrant to experimental analysis. Traditional methods such as presentation of live conspecifics (Stamps & Tanaka 1981; Cooper & Burns 1987; Decourcy & Jenssen 1994), or the use of models (Ferguson 1966; Gorman 1968; Rowland 2000) or mirrors (Gorman 1968) do not offer a level of control comparable to that which can be achieved in playback experiments. In addition, such techniques provide only limited options for manipulation of signal structure.

Over the last decade, video stimuli have increasingly been used to circumvent these problems. The range of theoretical issues addressed includes social learning (Swartz & Rosenblum 1980; Plimpton et al. 1981; McQuoid & Galef 1993), audience effects (Evans & Marler 1991, 1992), predator recognition (Evans et al. 1993a, b),

Correspondence and present address: T. J. Ord, Department of Biology, Indiana University, 1001 East 3rd Street, Jordan Hall 142, Bloomington, IN 47405, U.S.A. (email: tord@bio.indiana.edu). R. A. Peters, C. S. Evans and A. J. Taylor are at the Department of Psychology, Macquarie University, Sydney, NSW 2109, Australia.

species recognition (Watanabe et al. 1993; Macedonia & Stamps 1994; Macedonia et al. 1994), predatory behaviour (Roster et al. 1995), song learning (Adret 1997; Yamaguchi 1999) and signal timing (Aizawa 1998). There has been particular interest in exploiting this approach to understand mechanisms of male–male competition (Rowland 1995; Bolyard & Rowland 1996) and female mate choice (Clark & Uetz 1992; McDonald et al. 1995; McKinnon 1995; Rowland et al. 1995a, b; Rosenthal et al. 1996; Kodric-Brown & Nicoletto 1997, 2001; Künzler & Bakker 1998; Rosenthal & Evans 1998; Landmann et al. 1999; Nicoletto & Kodric-Brown 1999; Uetz & Smith 1999; Pope 2000). Successful video playback experiments have also been taxonomically diverse: study organisms include arachnids, crustaceans, fish, reptiles, amphibians, birds and primates. Recent technical advances, in particular development of digital video standards that substantially improve image quality, encourage the use of this technique to complement traditional methods for the experimental analysis of visual signals.

However, sensory differences between humans and nonhuman animals suggest that video images are potentially deficient in some contexts (D'earth 1998; Fleishman et al. 1998; Cuthill et al. 2000; Fleishman & Endler 2000). Early experiments addressed this concern by incorporating quantitative comparisons between live and video stimuli to establish whether video playback was appropriate for use with the particular system and behaviour of interest (Clark & Uetz 1990; Evans & Marler 1991). With the steady increase in published research using this approach, there has been a trend to bypass the initial 'calibration' step and move directly into studies addressing biological problems (although see Kodric-Brown & Nicoletto 1997; Landmann et al. 1999; Gonçalves et al. 2000; Trainor & Basolo 2000).

The complex visual displays of lizards invite playback analysis. Following pioneering work by Jenssen (1970), who successfully elicited female responses using 16-mm film loops of a displaying male, recent studies have shown that video sequences are sufficient to evoke male aggressive displays, both in the laboratory (Macedonia & Stamps 1994; Macedonia et al. 1994) and in the field (Clark et al. 1997), and suggest that they also permit species recognition (Macedonia & Stamps 1994; Macedonia et al. 1994). Nevertheless, we know of no quantitative comparison of live and video lizard stimuli comparable to those conducted in arachnids (Clark & Uetz 1990), birds (Evans & Marler 1991) and fish (Kodric-Brown & Nicoletto 1997; Landmann et al. 1999; Gonçalves et al. 2000; Trainor & Basolo 2000).

The Jacky dragon, *Amphibolurus muricatus*, is a semi-arboreal native Australian agamid that relies heavily on visual cues for communication, territorial defence and maintenance of social dominance (Carpenter et al. 1970; Peters et al. 2002). Jacky dragons are sexually size dimorphic (Harlow & Taylor 2000), a trait that typically reflects male–male competition over resources (Stamps 1983). Aggressive displays consist of rapid sequences of stereotyped motor patterns that include tail flicking, push-ups, arm waving and throat extensions (Carpenter et al. 1970).

These behaviours cannot be reproduced by conventional methods.

Our goal in the present study was to determine whether video playback could be used for experimental analyses of visual signalling in *A. muricatus*. We presented adult males with high-resolution digital video sequences depicting a displaying life-sized male conspecific and with the same male confined in a glass tank. Control treatments included an empty tank and the background against which the stimulus lizard had been filmed. Jacky dragons have structurally distinct aggressive and appeasement displays, providing a sensitive assay for changes in signalling behaviour. We measured production of both display types during each test session and also tested for differences in signal structure and in latency to display. In addition, we quantified substrate licking, which reflects olfactory exploration, and changes in the overall level of locomotor activity. We used two exemplars of a displaying male to represent variation in morphology and behaviour. Comparisons between the responses evoked by these video sequences gave us the opportunity to determine whether the lizards could discriminate between individual males.

METHODS

Subjects

We captured 21 male Jacky dragons between January and March 1999 in bushland surrounding Botany Bay, south of Sydney, Australia. They ranged in size from 22.0 g, 88 mm SVL (snout–vent length) to 45.0 g, 108 mm SVL and were all sexually mature (minimum size at maturity: 11.2 g, 72 mm SVL; Harlow & Taylor 2000). Each animal was wormed shortly after capture and then held in a glass aquarium (36 × 92 cm and 38 cm high) for a minimum of 4 weeks to habituate to captivity. Aquaria had sand substrates and contained branches and foliage to provide refuges and places for basking. Cardboard sheets were placed between adjacent tanks to screen males from nearby conspecifics. Lizards were maintained on a 14:10 h light:dark cycle (lights on at 0600), corresponding to midsummer. In addition, heat lamps (125W, 240V Philips Spotone) and UV lamps (300W Osram Ultra-Vitalux) were suspended above the aquaria. These allowed behavioural thermoregulation and ensured access to UV light to prevent vitamin deficiency. Room temperature was maintained at approximately 26°C, and there was a temperature gradient from this value to 30–34°C measured on perches directly beneath heat lamps. Jacky dragons are insectivores and will consume only live prey. We fed lizards twice weekly with live crickets dusted with vitamin supplements (RepCal); this also provided environmental enrichment, allowing animals to hunt invertebrates as they would in the wild. Water was available ad libitum in a small bowl and aquaria were lightly sprayed to provide additional moisture when humidity was low. All lizards were healthy at the end of the experiment and were retained for further studies of display structure and function; they will eventually be released at the point of capture. Permission

for the study was obtained from the Animal Care and Ethics Committee of Macquarie University and the NSW National Parks and Wildlife Service.

For experiments, we moved the lizards into large pens (64×150 cm and 120 cm high) which were constructed of aluminium frame and rigid plastic sheeting. The sides and back of each pen were opaque white to reflect light and provide isolation from neighbouring males, while the front was clear Perspex to allow presentation of visual stimuli and videorecording. Pens were arranged in a row along one wall of the room so that interaction with conspecifics could be confined to experimental presentations. Housing arrangements and husbandry routine during experiments were identical to those for animals housed in aquaria, except that each pen was fitted with an additional perch constructed from rough-sawn timber. This was positioned in the centre of the pen, directly below the heat lamp, and provided a level platform 85 cm from the floor. A runway descending from the perch towards the front wall of the pen allowed subjects to approach and inspect experimental stimuli.

Preparation of Video Stimuli

We began by videorecording the response of 12 lizards to another male presented in front of their individual pens for at least 20 min. Lizards typically responded with aggressive displays, often moving about the pen and approaching their opponent. We recorded video sequences with a uniform light blue background and used a fixed camera trained on the artificial perch, where lighting was ideal. This controlled image brightness and the contrast between lizard and background, so that differences in responses later evoked by playback of different video males could be attributed specifically to variation in individual morphology and behaviour. To avoid habituation, we added the constraint that stimuli should be constructed with minimal reuse of video footage. This required creation of a large library of clips. We selected the two male lizards that displayed most reliably and videorecorded them over 12 daily sessions until we had accumulated sufficient material. We created matching control sequences by recording footage of each perch without the lizard present.

Recording and editing procedures

Pens were illuminated by an 800-W photographic P2/11 tungsten-halogen lamp during recording sessions. To encourage lizards to climb on to the perches beneath the heat lamps, we reduced room temperature to 22°C to exaggerate the thermal gradient. Room temperature returned to 26°C as soon as filming was complete.

Videorecordings were made with a Canon XL1 3-CCD digital video camcorder (optical resolution 625 lines) with a shutter speed of 1/250 s at an aperture of F8 on Sony DVM60EX digital tape. We adjusted focal length to ensure that the image of the lizard on the video monitor later used for playback was precisely life sized. This equipment captures images of much higher quality than the analogue camcorders used in most earlier video

playback studies; luminance bandwidth is increased by a factor of three and colour interference artefacts are eliminated by separate processing of red, green and blue signals.

To elicit display behaviour, we positioned a trolley supporting a small glass tank (21×41 cm and 23 cm high) containing a live male conspecific in front of the pen, directly below the lens of the digital camera. We were thus able to obtain footage of lizards displaying directly towards the camera. To minimize potential stress on live stimulus lizards, we used three animals (body size range 20.5–25.0 g, 87–88 mm SVL) in rotation. The back of the trolley was covered with opaque black cloth so that it functioned as a blind, concealing the experimenter and camera. A cardboard screen between the front of the pen and the trolley was initially used to conceal the tank. Once the subject lizard was observed on the perch, we pulled away the screen to reveal the stimulus male. Recording sessions lasted for ca. 20 min (maximum of 30 min) and were conducted between 0800 and 1400 hours.

We transferred raw footage digitally from the camcorder to a DraCo nonlinear video editing workstation (MS MacroSystem Computer GmbH), using an IEEE 1394 'firewire' interface. Our goal was to produce stimulus sequences that reproduced the natural pattern of display behaviour during an aggressive interaction. This required editing because lizards spent only part of each recording session on the perch, climbing down repeatedly to display from branches in the pen and to approach the male in the tank. We used footage from a pilot study, in which lizards had been tracked continuously while interacting with a live conspecific, to create stimulus 'templates' based upon the time intervals between successive display bouts (142 min of footage for male A and 150 min for male B). We then used MovieShop v 5.2 software to edit together sequences of aggressive displays, resting and nondisplay movement, to match these records of spontaneous natural behaviour. Since the editing process was entirely digital, we were able to avoid degradation caused by unnecessary A/D conversion and compression processes. Image quality was thus limited only by the characteristics of PAL DV format (horizontal resolution 550 lines; data rate 3.6 Mb/s).

Stimulus characteristics

The two video exemplars differed in both morphology and behaviour (Fig. 1b). Male A was large (45.0 g and 108 mm SVL), but relatively slow to begin displaying (4 min 32 s) and had a low overall display rate (2.15 push-up displays/min). Male B was more gracile (24.5 g and 90 mm SVL) but had a short latency to first display (2 min 38 s) and a high display rate (5.15 push-up displays/min).

Playback Experiment

We wished to present live and videorecorded lizard stimuli when subjects were most active and hence likely to encounter intruding male conspecifics in the field. As there are no published accounts of circadian rhythm

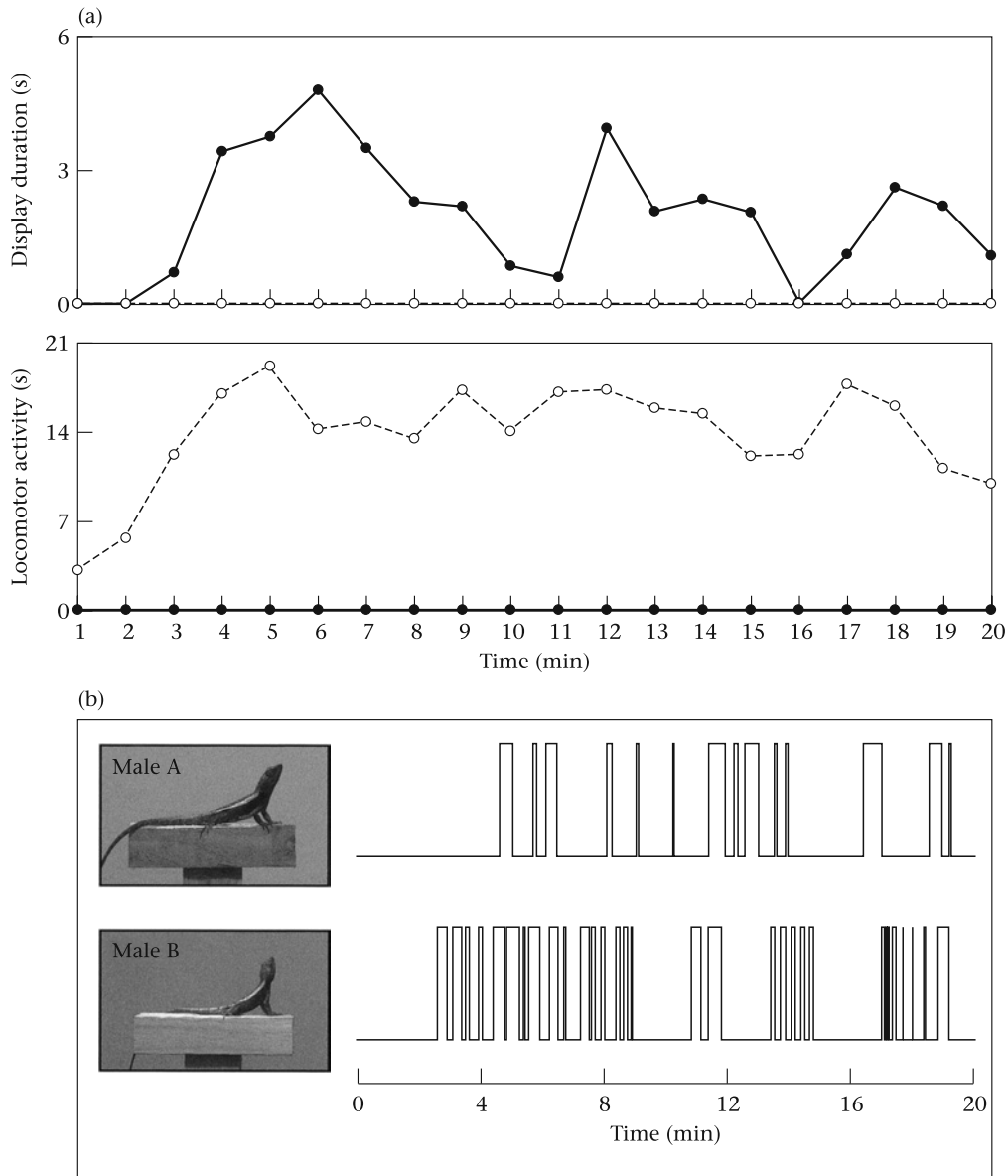


Figure 1. (a) Display duration and locomotor activity in live (\circ) and video (\bullet) lizards. (b) Characteristics of the two video exemplars. Traces adjacent to each still frame depict the timing of display bouts.

in *A. muricatus*, we made timelapse recordings and examined footage for time spent visible on perches and runways. Lizards in these locations could easily see stimuli presented at the front of their pens. They first became active when the heat lamps switched on, ca. 45 min after the room lights. The number of animals visible then increased markedly over the next 2 h, peaking between 0830 and 1030 hours. From ca. 1400 hours onwards, the lizards sheltered in vegetation and were rarely seen moving about their pens. We conducted all behavioural tests between 0800 and 1200 hours to correspond with the period of maximum activity.

Design

We showed subjects four stimuli in separate test sessions: (1) a live lizard housed in a glass tank with a

sand substrate; (2) the glass tank alone; (3) a digital video sequence depicting the same lizard on a standard wooden perch (Fig. 1b); and (4) a digital video of the filming perch and background. This design provided a direct comparison between the responses to live and video lizards and also allowed us to assess whether these stimuli differed from their respective controls (empty tank and perch video). We used a randomized block design in which each animal experienced all four conditions. There were two exemplars of each type, creating two stimulus sets. Lizards were first assigned one of these: 10 males were shown the set containing male A and 11 the set containing male B. There was no significant difference in either mean body size (SVL; $t_{19}=0.21$, $P=0.84$) or mean weight ($t_{19}=0.35$, $P=0.73$) between these two cohorts. Next, we randomly selected the initial stimulus type (live or video)

and finally the sequence of treatments (control–lizard or lizard–control). Trials with live and video stimuli were run as blocks on consecutive days. To control for potential diel variation in response, we gave subjects all four tests at the same time of day (mean intertest interval 24.0 h).

Test procedure

We used the same apparatus as for recording stimulus sequences. For live presentations, we placed a glass tank on the shelf at the front of the trolley. For video playbacks, we substituted a Sony PVM-14M2A colour monitor (resolution >600 lines; screen size 34 cm measured diagonally) connected to a Sony GV-D300E Digital Video Walkman. The tank and the video monitor were fitted with identical baffles with a centre aperture matched to the dimensions of the video screen, so that they appeared as similar as possible. We began test sessions by recording a 5-min baseline period with the tank or monitor hidden behind a cardboard screen. We then removed this to reveal the stimulus, which was displayed for 20 min. The experimenter tracked the subject lizard continuously, using the digital video camera. Behaviour of live stimulus lizards was also recorded, with a second video camera (Panasonic NV-MS4A) trained through the end wall of the tank.

Data Analysis

Jacky dragons have both aggressive and appeasement displays (Carpenter et al. 1970). Aggressive displays typically begin with repeated tail flicking, in which the tail is swept rapidly from side to side. This is commonly followed by a brief backward and forward arm-wave and one or more push-ups, in which the lizard raises the anterior portion of the body by flexing the forelimbs. Display sequences are often accompanied by lateral body compression, an engorged throat and/or raised nuchal and dorsal crests (Carpenter et al. 1970). Appeasement displays are characterized by arm-waving movements that are qualitatively slower than those observed in aggressive displays. Lizards may also lick the substrate more frequently during social interactions (Duvall 1979).

We scored tail flicking, 'push-up' displays (consisting of both rapid arm-waves and push-ups) and appeasement displays (slow arm waving). To quantify behavioural responses that did not involve signalling, we also measured changes in substrate licking and locomotor activity. We scored behaviour in real time from videotapes, using 'The Observer' event-recorder program (Noldus Inc., Wageningen, The Netherlands).

We pooled data obtained with the two stimulus sets to maximize statistical power in comparisons of live and video stimulus conditions. Repeated measures ANOVAs were used to compare changes in each of five response variables over the test session (SPSS 10 for Macintosh, 2000, SPSS Inc).

As the data were not normally distributed, we re-examined effects that were significant in the ANOVA analyses with randomization tests (NPFact; May et al.

1993). These were also used to perform tests of simple effects following significant interactions. Further information is given in Edgington (1987) and in Adams & Anthony (1996), who discussed the use of randomization tests in studies of animal behaviour. Randomization tests confirmed results in all cases; we report those obtained from repeated measures ANOVAs only.

In instances with no significant differences between live and video stimuli, we conducted power analyses with Pass 2000 (Hintze 2000) to confirm that these results were not due to inadequate sample size. We also compared latency to respond for each measure.

To test whether the displays elicited by live and video lizards might have subtle differences in structure, we also examined the mean duration of the tail-flick and push-up sequences for each stimulus type. Finally, we compared the responses evoked by the two video males to determine whether subject lizards were sensitive to the depicted individual variation in morphology and behaviour (Fig. 1). An alpha level of 0.05 was used throughout. All tests are twotailed.

RESULTS

Lizards oriented towards the front of the pen when the cardboard screen was removed at the beginning of each stimulus presentation. In both live and video lizard conditions, they typically began tail flicking shortly after the appearance of the stimulus male (Fig. 2a) and then produced bouts of push-up displays (Fig. 2c) throughout the rest of the test session. The video lizard also elicited slow arm-waves (Fig. 2e), accompanied by marked increases in substrate licking (Fig. 2g) and locomotor activity (Fig. 2i), which continued as long as the stimulus was visible. These responses closely tracked the display rate of the video lizard (Fig. 2). No spontaneous changes in behaviour were apparent in the control conditions (Fig. 2b, d, f, h, j).

We first compared lizard behaviour in all four test conditions, using a three-way repeated measures ANOVA with factors for treatment (lizard or control), stimulus type (live or video) and time. Differences in subject behaviour between lizard and control tests are reflected in robust treatment factor main effects for all five response measures (Table 1). These comparisons reveal that presentation of a conspecific (either live or simulated) caused reliable changes in behaviour, which included production of visual signals and exploratory responses.

Comparison of Live and Video Stimuli

The overall three-way ANOVA reveals that aggressive responses (tail-flicks and push-up displays; Fig. 2a, c) did not differ significantly with stimulus type (live versus video; Table 1). Power analyses confirmed that this was not due to small sample size (tail-flicks: effect size=0.34, sample size needed to detect a significant difference, $N=72$; push-up displays: effect size =0.19, sample size needed to detect a significant difference, $N=212$). The stimulus type \times time and treatment \times stimulus \times time

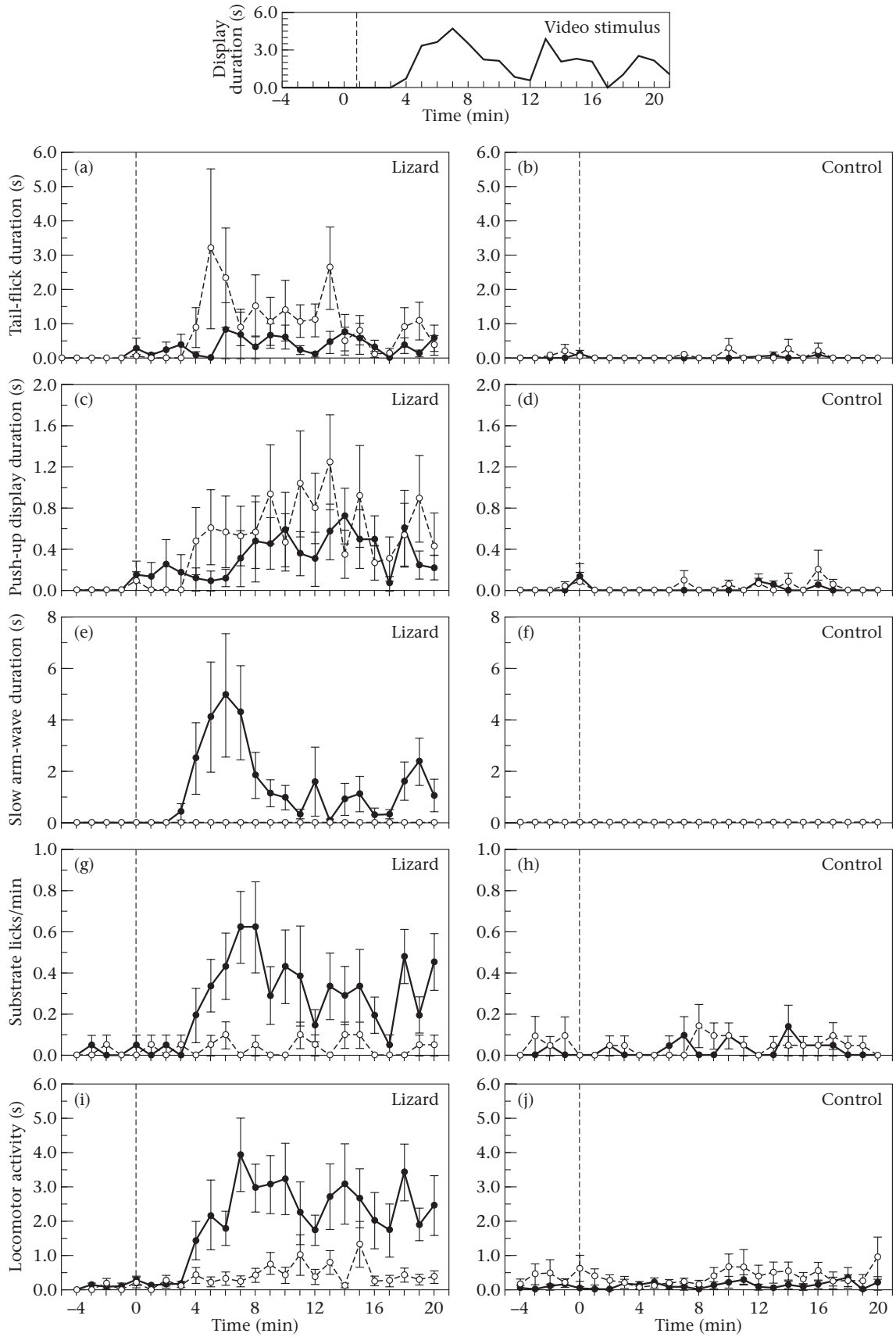


Table 1. Overall three-way repeated measures ANOVAs

Response	Treatment (lizard/control)		Stimulus type (live/video)		Time		Treatment×time		Stimulus×time		Treatment×stimulus×time	
	$F_{1,20}$	P	$F_{1,20}$	P	$F_{19,380}$	P	$F_{19,380}$	P	$F_{19,380}$	P	$F_{19,380}$	P
Tail-flicks	6.321	0.021	2.552	0.126	1.000	0.512	1.000	0.512	1.000	0.512	1.000	0.512
Push-up displays	12.115	0.002	0.888	0.357	1.000	0.512	1.000	0.512	1.000	0.512	1.000	0.512
Slow arm-waves	5.579	0.028	2.261	0.148	1.000	0.512	1.000	0.512	1.000	0.512	1.000	0.512
Substrate licks	17.677	<0.0001	23.285	<0.0001	1.660	0.442	0.579	0.796	1.822	0.413	0.790	0.695
Locomotor activity	11.089	0.003	12.197	0.002	9.569	0.099	1.189	0.553	45.016	0.022	17.898	0.054

Results are reported for five response measures, with factors for treatment (lizard or tank/background control), stimulus type (digital video sequence or live conspecific) and time (20 successive 60-s intervals). See text for details of design and planned comparisons.

interactions for these measures were also nonsignificant (Table 1).

Lizards were seen to perform slow arm-waves only to video stimuli (Fig. 2e). This observation suggested that the distribution of appeasement displays over time might be different in response to live and video lizards. We therefore conducted separate two-way repeated measures ANOVAs for the lizard and control treatments, with stimulus type (live or video) and time factors (Table 2). Analyses comparing the lizard treatments reveal a significant main effect for stimulus type, but not for time (Table 2). This result confirms that the video lizards evoked significantly more slow arm-waves from subjects than the live conspecifics.

The video lizard footage contained a series of aggressive displays, while none was produced by the same males when they served as live stimuli (Fig. 1a). However, the live stimulus males moved about the tank consistently during test sessions (Fig. 1a). Comparisons between video and live stimuli hence test the level of response to a stationary displaying male against that evoked by an active, but nondisplaying male. Pairwise comparisons of aggressive response to live and video lizards reveal no significant differences (Table 2). No differences were apparent in the comparison of video and live control conditions (Table 2).

The frequency of substrate licking (Fig. 2g, h) and the level of locomotor activity (Fig. 2i, j) were also different in live and video trials, producing significant main effects for treatment and stimulus type for both measures, together with a stimulus type × time interaction for locomotor activity in the three-way ANOVA (Table 1). Subsequent two-way ANOVAs show that each of these responses were evoked more effectively by the video lizards than by live conspecifics (Table 2). Comparisons between control conditions revealed no differences in either substrate licking or activity (Table 2).

Latency to respond

We compared the time interval between removal of the cardboard screen and the first response of each type in all

four conditions. When the behaviour of interest did not occur, subjects were assigned a latency score equal to the duration of the test session (1200 s). Raw latency scores were $\log(x)$ transformed to eliminate positive skew. These analyses reveal patterns consistent with those obtained in ANOVAs comparing behaviour over the whole test session. There was no significant difference in latency to the first tail-flick ($t_{20} = -0.031$, $P = 0.976$) or push-up display ($t_{20} = -0.318$, $P = 0.754$) between live and video lizards. Latencies for appeasement display ($t_{20} = 3.55$, $P = 0.002$), movement ($t_{20} = 2.464$, $P = 0.023$) and substrate licking ($t_{20} = 2.192$, $P = 0.04$) were all significantly shorter for the video lizard, reflecting the generally low frequency of these responses in tests with the live lizard stimulus.

Display structure

We also tested for more subtle differences between the effects of live and video stimuli by comparing the duration of components in the aggressive displays evoked. These reveal no significant differences in either tail flicking (paired t test: $t_{20} = -1.52$, $P = 0.15$) or push-up display (paired t test: $t_{20} = -0.08$, $P = 0.39$) as a function of stimulus type.

In summary, systematic comparisons of responses to live and videorecorded males reveal no differences in aggressive behaviour, whether this is measured as display activity over time (Fig. 2a, c), latency to display, or signal structure. However, video stimuli evoked higher rates of appeasement display (Fig. 2e), substrate licking (Fig. 2g) and increased activity (Fig. 2i) than a confined live conspecific. Latency scores for each of these three measures were also reliably lower for the video stimulus.

Response to Individual Video Exemplars

We observed a clear temporal correspondence between the type of response evoked and the display rate of simulated opponents. Aggressive push-ups tended to be performed during periods in which stimulus displays

Figure 2. Responses ($\bar{X} \pm SE$) to live (○) and video (●) lizard stimuli and controls in successive 1-min intervals. (a, b) Duration of aggressive tail flicking, (c, d) total duration of push-up displays, (e, f) total duration of slow arm-wave appeasement displays, (g, h) frequency of substrate licking and (i, j) overall level of locomotor activity. Top panel shows mean push-up display duration for the two video lizards.

Table 2. Direct comparisons between live and video stimuli: two-way repeated measures ANOVAs with factors for stimulus type and time

Response	Stimulus (live/video)		Time		Stimulus×time	
	$F_{1,19}$	P	$F_{19,380}$	P	$F_{19,380}$	P
Lizards						
Tail-flicks	2.369	0.139	1.000	0.512	1.000	0.512
Push-up displays	0.783	0.387	1.000	0.512	1.000	0.512
Slow arm-waves	6.873	0.016	1.000	0.504	1.000	0.504
Substrate licks	26.039	<0.0001	0.930	0.638	0.477	0.850
Locomotor activity	19.941	<0.0001	0.690	0.740	5.721	0.159
Controls						
Tail-flicks	1.000	0.329	1.000	0.329	1.000	0.329
Push-up displays	0.651	0.429	1.000	0.386	1.000	0.386
Slow arm-waves	—	—	—	—	—	—
Substrate licks	0.630	0.437	1.069	0.439	1.219	0.361
Locomotor activity	3.339	0.083	1.110	0.515	1.236	0.464

Response measures are the same as in Table 1.

were relatively infrequent (Fig. 2c). As stimulus display rate increased, subjects were more likely to respond with slow arm-waves (Fig. 2e), substrate licking (Fig. 2g) and increased activity (Fig. 2i).

There was an obvious difference between our two video exemplars in the level of display depicted, reflecting natural differences in the behaviour of the two males (Fig. 1). This allowed us to assess whether subject lizards were sensitive to individual differences in the morphology and behaviour of video opponents. We calculated the difference between the frequency of aggressive (push-up) and appeasement (slow arm-wave) displays for each subject, for each time interval. The resulting summary score represented moment-to-moment variation in response type (Fig. 3). Male A tended to elicit push-up display responses, while male B typically evoked slow arm-waves. A repeated measures ANOVA with factors for exemplar (A or B) and time reveals significant main effects for exemplar ($F_{1,18}=7.264$, $P=0.014$) and time ($F_{19,342}=2.587$, $P=0.0004$), together with a nonsignificant interaction ($F_{19,342}=1.13$, $P=0.319$). This result shows that subject lizards were sensitive to individual differences between the two video males.

DISCUSSION

Responses to Live and Video Stimuli

Both live and videorecorded conspecifics evoked aggressive displays including tail flicking and push-ups (Fig. 2). The duration of these signals increased significantly relative to the corresponding control conditions (empty tank and video perch; Table 1), but direct comparisons reveal no differences between the levels of response evoked by live and video lizard stimuli (Table 2). We were also unable to detect differences in latency to first display, or in two measures of display structure.

In contrast, videorecorded sequences depicting displaying male conspecifics evoked significantly higher levels of other social behaviour than confined lizards (Table 2).

Subjects responded to the video lizard with appeasement signals (Fig. 2e), which were not evoked by the live conspecific. The frequency of substrate licking and the level of locomotor activity were also significantly greater to video stimuli (Fig. 2). These last two effects are consistent with increased olfactory exploration. While communication in lizards depends principally upon visual signals, olfactory cues also play a role (Duvall 1979; Alberts et al. 1992). Substrate licking potentially provides additional information about an 'intruding' conspecific (Duvall 1979; Alberts & Werner 1993), together with location cues from scent marks within a territory (Alberts & Werner 1993). Activity levels may also reflect changes in general arousal.

Sensitivity to Variation in Video Sequences

Changes in the duration and frequency of social responses over the course of test trials suggest that subject lizards were able to track moment-to-moment variation in the behaviour depicted by a video stimulus. Appeasement signals were principally produced when the simulated opponent was displaying vigorously (Fig. 2e). The frequency of substrate licking similarly increased when stimulus display rates were high and fell when they were low (Fig. 2g).

Comparisons of the type of display evoked over the course of each 20-min playback show that lizards could extract sufficient information from the video sequences to discriminate between the two exemplars of displaying male conspecifics (Fig. 3). Despite relatively low statistical power caused by splitting our subject population, the pattern of responses evoked was reliably different. Male B, which had the higher display rate, elicited a larger proportion of appeasement signals, even though he was the smaller of the two (Fig. 1). Static cues such as body size clearly influence the outcome of social encounters in lizards (Blanc & Carpenter 1969; Trivers 1976; Stamps 1984; Tokarz 1985; Stamps & Krishnan 1994), but our results hint that display rate may be more important, at

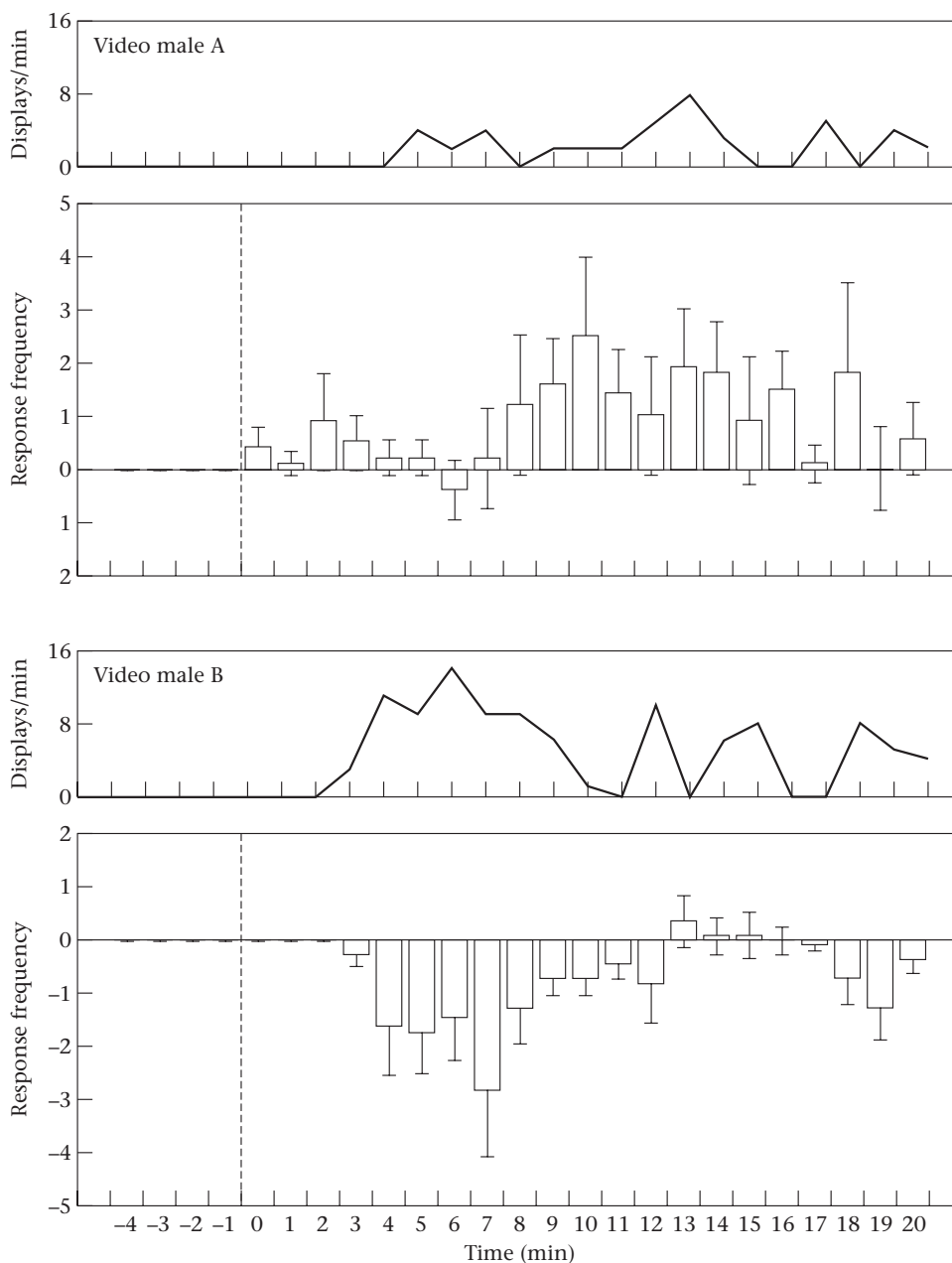


Figure 3. Comparison of the type of display responses ($\bar{x} \pm SE$) evoked by the two video lizard exemplars. Values are frequency of aggressive push-up displays minus frequency of slow arm-wave appeasement signals. Positive scores for this measure represent a preponderance of aggressive responses, and negative scores a preponderance of appeasement signals. Push-up display frequency for each video lizard sequence is provided for comparison.

least in *A. muricatus*. Aggressive displays are energetically costly (Bennett et al. 1981; Marler & Moore 1988) and may hence function as honest signals (Zahavi 1977; Clutton-Brock & Albon 1979) revealing current physical condition. We plan to use video playback experiments to evaluate the importance of display rate in opponent assessment, by systematically manipulating signal production, while holding morphology constant. Our present results are sufficient to establish that lizards could discriminate individual differences between video sequences and vary their display responses accordingly, just as would be expected during natural social encounters.

Strategies for the Experimental Study of Visual Signals

Our results highlight a particular problem for the experimental study of dynamic visual signals: it can be difficult to ensure that an animal used as a stimulus will spontaneously produce the behaviour of interest. The locomotor activity of a confined conspecific seems to have been sufficient to elicit aggressive display (Fig. 1a, 2a, c), but other comparisons suggest that live opponents were deficient stimuli, relative to video sequences (Fig. 2e, g, i, Table 2). We attribute these differences to the lack of display from the live lizards.

Our goal is to understand the design and function of visual signals and video playback is an attractive technique because of the ease with which stimulus characteristics can be defined and manipulated. The potential advantages of this approach have been widely recognized (e.g. Clark & Uetz 1990; Evans & Marler 1991; Rosenthal et al. 1996; Künzler & Bakker 1998; Lea & Dittrich 1999) and it has been used in studies addressing a variety of theoretical questions across a broad taxonomic range (see introduction), but video playback has also attracted criticism, which centres on the fact that cameras and monitors have been designed for the human visual system (D'Eath 1998; Fleishman et al. 1998). Video sequences may consequently be perceived quite differently by nonhuman animals. Problems may arise from differences in critical flicker-fusion frequency (D'Eath 1998; Fleishman & Endler 2000) or spectral sensitivity (Fleishman et al. 1998; Cuthill et al. 2000), the absence of some depth cues (D'Eath & Dawkins 1996; Zeil 2000), and the lack of interaction between subject and stimulus (Pepperberg 1994; Rowland et al. 1995a; D'Eath & Dawkins 1996; Kodric-Brown & Nicoletto 1997; Trainor & Basolo 2000).

To our knowledge, there have been no studies of the visual physiology of the Jacky dragon or any of its relatives. It has, in any case, proved difficult to predict the effectiveness of video playback by considering only the sensory properties of potential subjects. The most sophisticated analysis to date is the work of Fleishman et al. (1998), which used data on the peak absorption frequencies of guppy, *Poecilia reticulata*, retinal cones, together with fluorescence frequencies of video monitors, to develop a mathematical model of the way in which females might perceive a video image. This generated the clear prediction that video stimuli should be deficient relative to live males because of differences between guppies and humans in spectral sensitivity. But experiments conducted with one-way glass to eliminate the confound of interaction between stimulus males and female subjects show that sexual responses to live and video stimuli are indistinguishable (Kodric-Brown & Nicoletto 1997). It is likely that the sensory model (Fleishman et al. 1998) was unsuccessful because females attend principally to courtship displays, rather than static morphological cues (Kodric-Brown & Nicoletto 1997). Theoretical arguments based upon differences between the visual systems of birds (Cuthill et al. 2000) or crustaceans (Zeil 2000) and those of humans have similarly failed to account for the substantial number of successful experiments using video playback in these systems (e.g. birds: Evans & Marler 1991, 1992; Evans et al. 1993a, b; McQuoid & Galef 1993; Watanabe et al. 1993; Adret 1997; Yamaguchi 1999; Clarke & Jones 2001; crabs: Aizawa 1988; Burford et al. 2000; Pope 2000). These examples reinforce the recommendation that empirical tests evaluating the behavioural response to video stimuli should be the first step in any programme of playback experiments (Clark & Uetz 1990; Evans & Marler 1991; Kodric-Brown & Nicoletto 1997; Landmann et al. 1999; Gonçalves et al. 2000; Trainor & Basolo 2000).

It is instructive to compare the potential shortcomings of video playback with those of other currently available techniques for the experimental study of morphology and visual signals. Studies using paints or dyes to change the appearance of animals are vulnerable to criticism on the grounds that subjects may not perceive such alterations as we do (Bennett et al. 1994), an argument that clearly parallels the concerns raised about video manipulations of 'colour' (Fleishman et al. 1998). The alternative approach of presenting live conspecifics behind filters (e.g. Bennett et al. 1996, 1997) has the advantage of allowing the precise manipulation of spectral cues, but at the cost of relinquishing control over behaviour. Since the glass barriers used in such studies were not one-way, this technique has only established that changes in the spectrum of reflected light (e.g. removal of the UV component) have some effect upon social interaction. Surgical manipulation of morphology (e.g. Basolo 1990) raises ethical concerns (Trainor & Basolo 2000) and might also produce confounding changes in behaviour. The use of models is familiar from classical ethology (Tinbergen 1969) and this technique continues to play a role in current studies (e.g. Rowland 2000), but accurate reproduction of colour raises the problems described above. In addition, it is difficult to simulate the complex motor patterns important in many visual displays (Simpson 1968). Mirror stimulation provides dynamic cues, but in an uncontrolled way, and may change the feedback experienced by subjects so that it is systematically different from that in natural interactions (Evans 1985).

We suggest that no currently available technique can reasonably be viewed as a panacea. Each has strengths and weaknesses, and in several cases these are complementary. The challenge for researchers is to identify the approach that has characteristics optimal for their system and for the theoretical question being addressed. In some cases, it might be necessary to use more than one technique, so that potential deficiencies in one are counterbalanced by the strengths of another. Video playback is a useful addition to this armament.

For our specific application, video stimuli were equivalent to confined live conspecifics with some response measures, and superior with others. Planned studies to explore signal design in *A. muricatus* will require precise control over display motor patterns, together with presentation of biologically impossible stimuli. Video playback techniques are uniquely appropriate for studies of this kind (Clark & Uetz 1992; Evans et al. 1993b; Rosenthal et al. 1996; Rosenthal & Evans 1998; Nicoletto & Kodric-Brown 1999).

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