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Interactive video playback and opponent assessment in lizards

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Abstract

Video playback has been used to explore many issues in animal communication, but the scope of this work has been constrained by the lack of stimulus–subject interaction. In many natural contexts, each participant's signalling behaviour is dependent from moment-to-moment on that of the other. Analyses of acoustic communication demonstrate the value of reproducing such social contingencies. We assessed the utility of interactive playback for studies of visual signalling by comparing the responses of male Jacky dragons, *Amphibolurus muricatus*, to interactive and non-interactive digital video playbacks of a life-sized conspecific. Displays produced by lizards in the interactive condition had the effect of suppressing the aggressive display of their simulated opponent. Each stimulus sequence generated during an interactive playback was subsequently played to a size-matched control animal. Males that could interact with the video stimulus responded principally with aggressive displays, while those that could not produced a mixture of aggressive and appeasement signals. Adding a degree of receiver responsiveness is hence sufficient to alter the type of signal evoked, even when video stimuli are physically identical. Interactive playback permits the experimental study of a broader range of theoretical topics and can enhance the realism of video stimuli. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

The design of animal signals has been shaped by both environmental factors (e.g. Wiley and Richards, 1982; Endler, 1992) and the sensory properties of receivers (e.g. Andersson, 1982; Basolo, 1990; Ryan and Rand, 1993). Playback experiments have greatly facilitated the exploration of these phenomena in the auditory, electrical and tactile modalities. Visual signals have proved relatively recalcitrant. Morphological cues have been studied by using surgical manipulation (e.g. Møller, 1988; Basolo, 1990), paints or dyes (e.g. Smith, 1966) and optical filters (e.g. Bennett et al., 1996) to alter appearance. However, complex motor patterns such as the displays used in courtship and agonistic interactions cannot be properly controlled when live animals are used as stimuli, nor can they realistically be reproduced with models. Video playback offers a potential solution to this problem, allowing the straightforward

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modification of both movement (Clark and Uetz, 1992; Evans et al., 1993b; Rosenthal et al., 1996) and morphology (Rosenthal and Evans, 1998). Recent technical advances, in particular the development of digital video standards that substantially improve image quality, also encourage the use of this approach for the experimental analysis of visual signals.

Studies conducted over the last decade have used video playback to address a wide range of topics, including social learning (McQuoid and Galef, 1993), audience effects (Evans and Marler, 1991, 1992), predator recognition (Evans et al., 1993a,b), foraging behaviour (Roster et al., 1995), male–male agonistic interactions (Macedonia and Stamps, 1994; Macedonia et al., 1994; Yang et al., 2001), female mate choice (Clark and Uetz, 1992; McKinnon, 1995; Rosenthal and Evans, 1998; Landmann et al., 1999) and motion perception (Lea and Dittrich, 1999). Successful experiments have been conducted with arachnids, crustaceans, fish, reptiles, anuran amphibians, birds and primates. There are clearly potential constraints on the use of video playback arising from sensory differences between humans and non-human animals (D'Eath, 1998; Fleishman et al., 1998), but quantitative comparisons demonstrate that video sequences are indistinguishable from confined conspecifics in several systems and contexts (Clark and Uetz, 1990; Evans and Marler, 1991; Kodric-Brown and Nicoletto, 1997; Landmann et al., 1999; Ord et al., in press). Classic findings first reported using surgically-manipulated live animals (Basolo, 1990) have also been replicated with digital video stimuli (Rosenthal and Evans, 1998).

Communication often relies upon interaction. For example, in territorial disputes, the roles of sender and receiver typically alternate repeatedly between participants, producing a complex series of signal exchanges. For some purposes, abolishing interaction with the subject can be an advantage because it confers additional control and allows the presentation of a standard stimulus (e.g. Plimpton et al., 1981; Evans and Marler, 1991; Kodric-Brown and Nicoletto, 1997). In other circumstances, the lack of a natural moment-to-moment dependency linking the behaviour of the subject with that of a simulated companion can be a deficiency with the potential to reduce or abolish responses (e.g. Pepperberg, 1994; D'Eath and Dawkins, 1996; Trainor and Basolo, 2000). In a revealing study, Kodric-Brown and Nicoletto (1997) showed that female guppies (*Poecilia reticulata*) responded similarly to video sequences and live males presented behind one-way glass, but spent significantly more time with the same males presented behind clear glass. This finding suggests that social interaction can substantially affect responses to a visual signal.

Interactive sound playbacks have been used with increasing frequency since the pioneering work of Petrinovich and Patterson (1980). These techniques have become so sophisticated that experiments are limited only by the ability of researchers to choose the appropriate vocal response to a signalling animal (Dabelsteen and McGregor, 1996). The development of computer-controlled systems that monitor vocal activity, and then respond automatically, has begun to overcome this obstacle (Evans, 1991; Schwartz, 1994). Interactive sound playback has not only allowed the more realistic simulation of acoustic interactions, it has also permitted the experimental analysis of function by systematically perturbing the 'rules' of signal exchange (e.g. McGregor et al., 1992; Dabelsteen et al., 1997; Otter et al., 1999; Peake et al., 2001).

In the present study, we assessed the effects of interactive video playback on the signalling behaviour of an Australian lizard, the Jacky dragon, *Amphibolurus muricatus*. To our knowledge, this is the first application of interactive video playback to the study of visual communication.

The Jacky dragon is a semi-arboreal agamid which relies heavily on visual signals for territorial defence and maintenance of social dominance (Carpenter et al., 1970). Displays consist of rapid sequences of stereotyped motor patterns that include tail-flicking, push-ups, head-bowing and arm-waving (Carpenter et al., 1970; Peters et al., in press). These complex visual signals invite playback analysis.

There have been no studies of the visual physiology of the Jacky dragon, or any of its relatives, so there is no basis for predicting how video stimuli might be perceived in this species.

However, we have previously shown that aggressive responses to a life-sized digital video opponent are indistinguishable from those evoked by a confined live conspecific (Ord et al., in press). The results of these quantitative comparisons provide the necessary empirical basis for a program of video playback experiments designed to explore signalling behaviour. In this earlier study, we also found that Jacky dragons tracked temporal changes in the signalling behaviour of a simulated opponent and altered their display responses accordingly (Ord et al., in press), suggesting that such moment-to-moment variation may be important in natural contests.

We explored the effects of interactive video playback by using a computer-controlled library of digitized sequences to simulate the aggressive behaviour of one lizard engaged in a dyadic signal exchange. Adult males were each tested in two conditions in a within-subject design. In interactive treatments, displays produced by subject lizards had the effect of suppressing the aggressive display of their simulated opponent. Stimuli generated during these trials were subsequently presented to size-matched control animals. Each lizard in the non-interactive control treatment was hence shown a display sequence that was physically identical to that experienced by the paired male in the interactive condition, but they were unable to influence the behaviour of their video opponent. Comparison of the responses evoked in these two conditions allowed us to isolate and measure the effect of interaction in an opponent assessment context.

2. Methods

2.1. Subjects

Subjects were 12 sexually-mature male Jacky dragons. Lizards were wild-caught between January and March 1999 in bushland surrounding Botany Bay, south of Sydney, Australia. They ranged in size from 22.0 g, 85 mm SVL (snout–vent length) to 38.0 g, 100 mm SVL. Each animal was wormed shortly after capture and then held in a glass aquarium (36 × 92 × 38 cm) for a minimum of 4 weeks to habituate to captivity.

Housing was designed to match as closely as possible characteristics of the natural habitat. 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 light regime of 14–10 h light–dark cycle (lights on at 0600), corresponding to midsummer. In addition, heat lamps (125 W Spotone, Philips, NSW, Australia) and ultraviolet (UV) lamps (300 W Ultra-Vitalux, Osram, NSW, Australia) 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 the heat lamps. We fed lizards twice weekly with live crickets dusted with vitamin supplements (RepCal, Vic, Australia); this also provided environmental enrichment, allowing animals to hunt invertebrates as they would in the wild. Water was available ad lib in a small bowl, and the aquaria were lightly sprayed to provide additional moisture when humidity was low.

One week prior to experiments, lizards were moved into large pens (64 × 150 × 120 cm) 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 visual isolation from neighbouring males, while the front face was clear perspex to allow presentation of visual stimuli and video-recording. 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 the 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 toward the front wall of the pen allowed subjects to approach and inspect experimental stimuli (Fig. 1).

2.2. Temporal properties of display interaction

We wished to determine the typical temporal relationship between the displays of two males engaged in an exchange of signals. This information would subsequently be used to define parameters of an interactive playback algorithm capable of reproducing the response timing of a real opponent (see below). We presented 12 subject lizards with nine separate stimulus males, each confined in a glass tank (21 × 41 × 23 cm), which was placed in front of their pen. The tank was supported on a trolley, the back of which 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 located within the pen, the screen was pulled away to reveal the stimulus male. We video-recorded the responses of both subject and stimulus lizards. Recording sessions lasted for approximately 20 min (maximum of 30 min) and were conducted

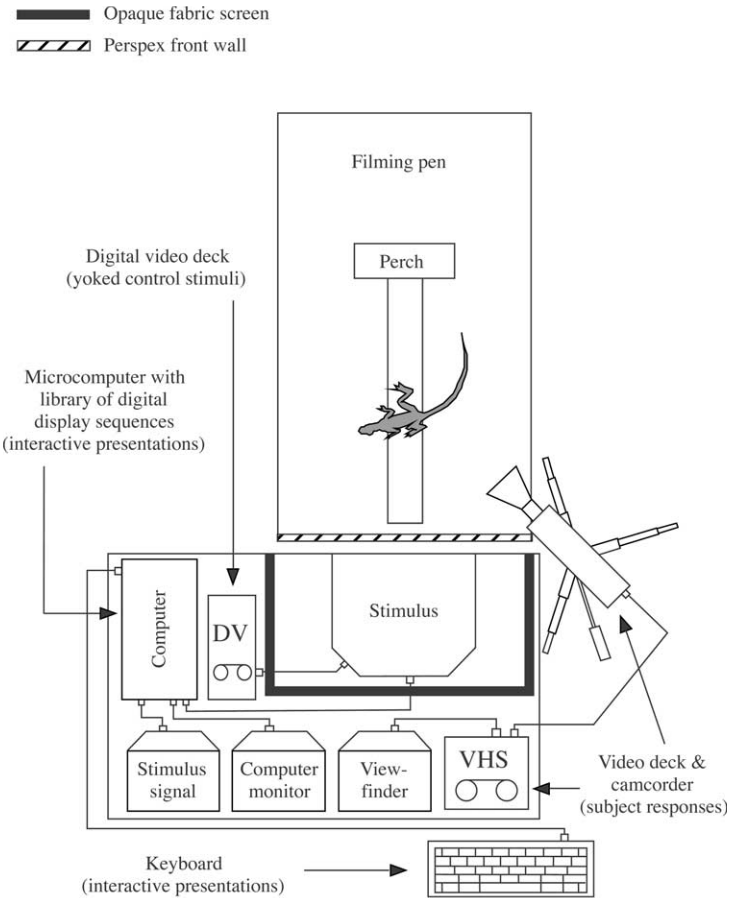

Fig. 1. Plan view of experimental set-up. Equipment was mounted on a trolley to facilitate movement between filming pens. Screening around the stimulus monitor acted as a blind, concealing the experimenter and equipment. Lizard display bouts were signalled by a key press; all other aspects of stimulus presentation were controlled by the interactive playback algorithm. Stimuli for yoked control presentations were recorded digitally to avoid degradation of image quality. Subject responses were video-recorded using a view-finder monitor, which allowed remote manipulation of the camera. Other monitors repeated the stimulus signal being presented and allowed the experimenter to track the status of the interactive playback program.

between 0800 and 1400 h, which is the period of maximum activity (Ord et al., in press), over a period of 17 days.

All subjects responded to live stimuli with display behaviour, often moving about the pen and approaching their opponent. However, only two stimulus lizards responded with aggressive displays. Excluding sessions where signal exchanges failed to occur, information was available for 10 subjects. Data were collected from the first 20 min of three sessions for each individual. We measured the time elapsed between each display produced by the stimulus male and the reply from the subject. An average display response time was then determined for each lizard, and these values were used to calculate a group average.

Jacky dragons have both aggressive and appeasement displays (Carpenter et al., 1970). Aggressive displays typically begin with repeated tail-flicks, in which the tail is swept rapidly from side to side. This is commonly followed by a rapid backward and forward arm-wave and one or more push-ups, in which the anterior portion of the body is raised by flexing the forelimbs. Appeasement displays are characterised by head-bowing or arm-waving movements that are qualitatively slower than those observed in aggressive displays. Push-up displays by subject lizards occurred 15.4 ± 8.5 s (mean ± SD) after the start of their opponents' aggressive display bout and 19.1 ± 16.4 s (mean ± SD) after the start of an appeasement signal. As there was no significant difference between these two intervals (Wilcoxon signed rank test: $Z = -0.41$, $N = 5$, $P = 0.69$), we used the overall mean latency value (17.3 s) for the timing of responses during interactive playbacks.

2.3. Design

Experiments were conducted in two identical rooms housing six filming pens each. Lizards were first paired by body weight and then randomly assigned to pens, with the constraint that pair-members occupy corresponding positions in each room. We used a within-subject design in which each animal experienced both interactive and non-interactive playbacks. Interactive playbacks involved the presentation of a video male conspecific whose display rate was controlled from moment-to-moment by the subject lizard's own display behaviour. The video stimulus sequences presented during interactive sessions were digitally recorded for subsequent non-interactive presentation to the paired control lizard. This treatment hence measured responses to video stimuli that were identical in every way to those experienced in interactive presentations, but which had no reliable relationship to the subjects' display behaviour. Following traditional usage in experimental psychology (Reynolds, 1968), we refer to animals in this condition as 'yoked' controls.

Aggressive lizards tend to be larger and to have higher display rates (Carpenter, 1961, 1963; Alberts et al., 1992). To account for possible body size effects on display behaviour, each member of a size-matched pair was used to generate a non-interactive stimulus sequence for the other. To control possible test order effects, half of the lizards (evenly distributed across both rooms) received interactive followed by yoked control presentations, while the other half received the reverse order. The two tests for each animal were conducted on successive days and at approximately the same time of day (±20 min) to control diel variation in response.

2.4. Video stimuli

2.4.1. Recording and editing procedures

We recorded aggressive displays from a male lizard (45.0 g, 108 mm SVL) housed in a filming pen lit by an 800 W photographic P2/11 tungsten–halogen lamp, using a Canon XL1 digital video camcorder (optical resolution 625 lines; shutter speed 1/250 s; aperture F8) and Sony DVM60EX digital tape (see Ord et al., in press). The camera was trained on the artificial perch in the centre of the pen and remained static to avoid changes in the background. Focal length was adjusted to ensure that the image of the lizard on the video monitor later used for playback was precisely life-sized.

We then selected the longest sequence of raw display footage, which lasted 93 s and included five display bouts (mean duration 3.33 s), and transferred it digitally from the camcorder to a DraCo nonlinear video editing workstation (MS Macro-

Systems Computer GmbH, Wetter, Germany), using an IEEE 1394 ‘firewire’ interface. MOVIESHOP V5.2 software was then used to edit this sequence into discrete clips containing either a single aggressive display bout, or footage depicting a stationary lizard with only breathing movements apparent. The start and endpoint of each breathing sequence were selected so that the clip could be ‘looped’ to vary the inter-display interval during playback with no accompanying change in the appearance of the stimulus image. Edited clips were then transferred to a Commodore Amiga 4000 computer using PAR V2.55 hardware/software (Digital Processing Systems, Inc, Kentucky, USA; 50 fields/s, 752 × 576 pixels resolution). This digital video system provided a library of sequences that could be played back in real time under computer control (see below).

2.5. *Playback presentations*

2.5.1. *Test apparatus and procedure*

The experimental apparatus (Fig. 1) was based on that used for recording display interactions. A Sony PVM-14M2A colour monitor (resolution $>$ 600 lines; screen size 34 cm measured diagonally) was placed on the shelf at the front of the trolley. Interactive stimuli were presented using the Amiga/PAR system, which was connected directly to the playback monitor (Fig. 1). The video signal from each of these trials was also recorded, using a Sony DSR-20P digital video deck, for subsequent presentation to the paired yoked control lizard.

We began test sessions by recording a 5 min baseline period with the monitor hidden behind a cardboard screen. This was then removed to reveal the stimulus, which was displayed for 20 min. The subject lizard was tracked continuously by the experimenter, using a digital video camera, the signal from which was recorded on a VHS deck.

2.5.2. *Interactive algorithm*

Our model was loosely based on a program used by Evans (1991) to study the effects of interactive call playback in ducklings. We used SCALA MM400 (SCALA AS, Oslo, Norway) to run a simple algorithm controlling selection and timing of video clips displayed by the PAR system. This was designed to simulate the response of one participant in a male–male display interaction. A prose description of the program logic would be as follows: ‘begin an aggressive display bout if no subject display has been detected within the last X s, where X is the estimated mean latency to respond to a conspecific display.’ The experimenter's only role in the process was to indicate with a key press each time the subject began either an aggressive or an appeasement display (Fig. 1). At the beginning of an interactive playback session, the program began playing a looped breathing sequence while polling for a key press (Fig. 2). If none was detected after 17.3 s (mean response time), the program would play the first display bout, then move onto the following breathing sequence and resume polling the keyboard. Each key press caused the program to reset the display interval clock and extend the breathing sequence for another 17.3 s (Fig. 2). Subject lizards were thus able to inhibit aggressive displays by the video male. Fig. 2 presents a representative section of the interaction between one lizard and this computer system. Once the program exhausted the available video sequences (five display bouts), it looped back and began replaying them in the same way.

2.6. *Data analysis*

We scored bouts of aggressive push-ups and appeasement slow arm-waving displays from test session videotapes using ‘THE OBSERVER’ event-recorder program (Noldus Inc., Wageningen, The Netherlands). The difference between the frequency of aggressive and appeasement displays was then calculated for each subject and time interval. The resulting score provides a summary measure, taking into account both the type of display performed and its relative rate. This provided better control of Type I error rate than the alternative approach of analysing each response separately and also ensured that all subject animals contributed to the analysis. A repeated-measures ANOVA with factors for treatment and time was used to compare variation in response over the course of the test session (SPSS 10 FOR MACINTOSH, 2000, SPSS Inc, Illinois, USA). Three

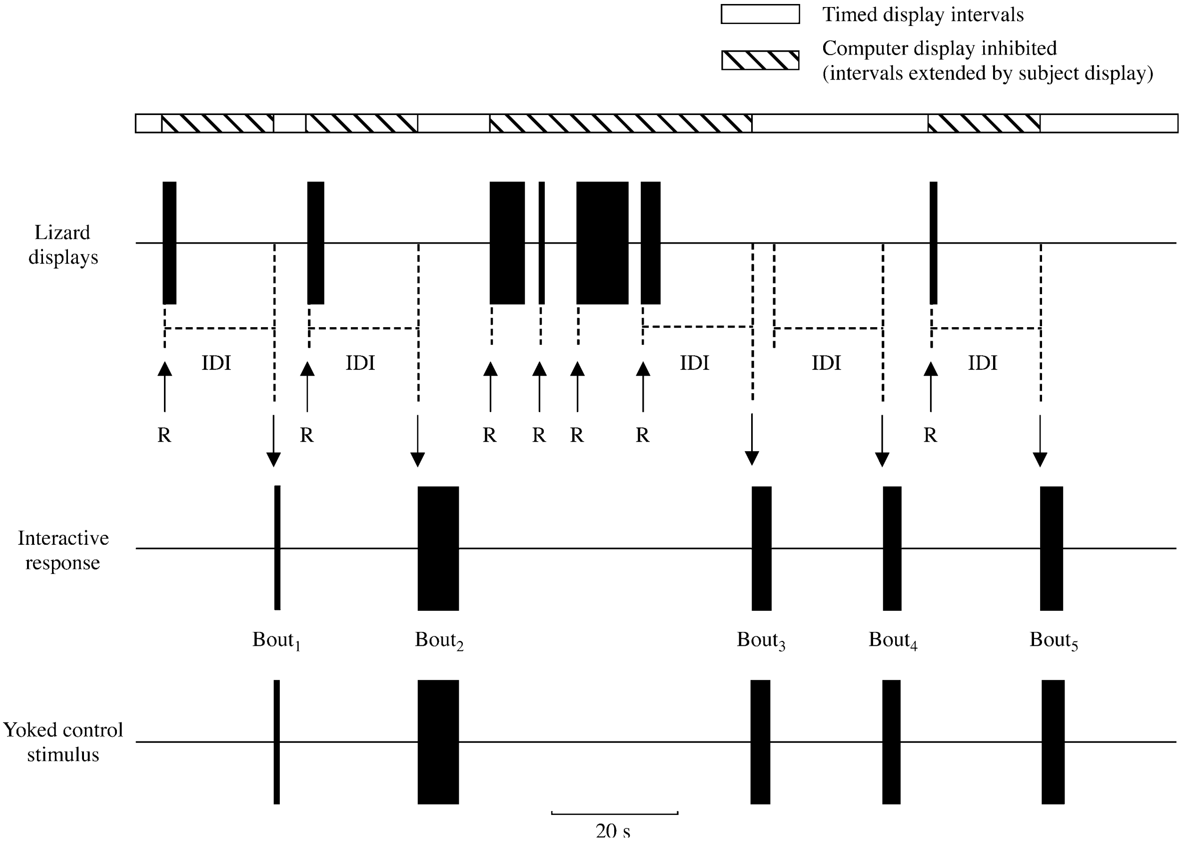

Fig. 2. Timeline from a representative test session, illustrating the operation of the interactive playback algorithm. IDI, interactive display interval—stimulus aggressive displays were initiated 17.3 s after the beginning of the last display observed from a lizard. R, reset of IDI clock—video stimulus display bouts$_n$ (push-ups) were inhibited by a key press from the experimenter each time lizards began a display.

individuals failed to display in either treatment and were excluded from analyses.

In acoustic playback experiments, interactive playbacks consistently evoke stronger aggressive responses than non-interactive or 'looped' stimuli (e.g. Dabelsteen and Pedersen, 1990; Otter et al., 1994; Dabelsteen et al., 1997). We therefore anticipated that lizards whose displays could suppress those of their simulated opponent would be more aggressive than controls. The test for a treatment effect based upon this a priori prediction was one-tailed; tests of other factors were two-tailed.

3. Results

The initial response of lizards in both treatments was appeasement slow arm-wave displays (Fig. 3). In non-interactive treatments, these continued throughout the test session. In interactive treatments, however, the relative frequency of aggressive push-up displays increased steadily over time (Fig. 3). Scores were $\log_{10}(X+1)$ transformed to eliminate positive skew. Analysis of variance reveals significant main effects for both treatment ($F=4.179$, d.f. $=1.8$, $P=0.038$) and time ($F=2.171$, d.f. $=19.152$, $P=0.005$), together with a non-significant interaction ($F = 0.964$, d.f. = 19.152, $P = 0.506$).

4. Discussion

The results of this experiment provide the first evidence that the ability to interact with a digital video sequence can affect the type of response evoked, even when there is no variation in the physical properties of the stimulus. Lizards that could inhibit the display of a simulated opponent produced a higher proportion of aggressive responses than when confronted with a yoked control stimulus that was unresponsive to their behaviour (Fig. 3).

The signalling strategies adopted by lizards during agonistic encounters may similarly be influenced by the moment-to-moment relationship between an opponent's behaviour and their own. High display rates are characteristic of dominant and aggressive lizards (Carpenter, 1961, 1963; Alberts et al., 1992) and typically elicit appeasement responses (Ord et al., in press). However, such signal properties may not be sufficient to determine outcome. We suggest that the responsiveness of receivers may also play a role. Signalling that reduces the frequency of aggressive displays from an opponent will result in one lizard effectively controlling an interaction, and this asymmetry is likely to have implications for successful defence/acquisition of territories and other resources.

Several authors have discussed the lack of interaction in conventional video playback techniques as an issue of stimulus realism, identifying it as a factor that may be responsible for reduced responses evoked by video sequences, relative to live conspecifics (e.g. Pepperberg, 1994; Rowland et al., 1995; D'Eath and Dawkins, 1996; Trainor and Basolo, 2000). The results of the present study are consistent with these predictions and suggest that interactivity is likely to enhance the effectiveness of video stimuli, at least when these simulate social companions.

The large recent literature on interactive sound playback demonstrates that this approach offers additional benefits for the exploration of signal function. For example, experiments simulating an interacting male conspecific have shown that large repertoires enable resident birds to better match the songs of rivals and thus enhance their ability to repel territorial intruders (McGregor et al., 1992; Otter et al., 1994). Interactive playback has also

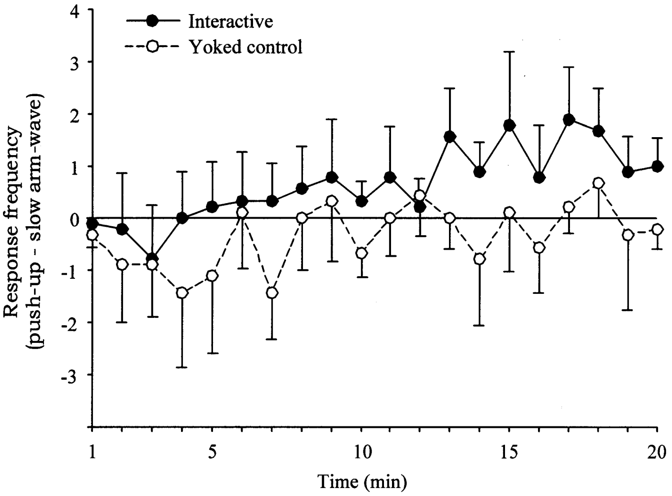

Fig. 3. Comparison of the type of display responses evoked by interactive and non-interactive video stimuli. Values are frequency of aggressive push-up displays minus frequency of slow arm-wave appeasal responses. Positive scores for this measure represent a preponderance of aggressive responses, while negative scores reflect a preponderance of appeasement signals. Scores are mean ± SE.

revealed the importance of vocal interactions such as ‘overlapping’ and ‘alternating’ (Evans, 1991; Dabelsteen et al., 1997), the use of song types to signal aggressive intent (Dabelsteen and Pedersen, 1990; Smith and Smith, 1992, 1996a,b; Nielsen and Vehrencamp, 1995) or advertise male quality (Naguib, 1999) and the influence of eavesdropping on subsequent behaviour in both males and females (Otter et al., 1999; Peake et al., 2001). Studies of male–male competition and female mate choice in anuran amphibians have also benefited from the realistic simulation of natural signal interactions (Schwartz, 1987, 1991, 1994). In summary, interactive sound playbacks have allowed the experimental study of several phenomena that would otherwise have remained inaccessible. We anticipate that interactive video playbacks will prove similarly valuable for the study of visual communication.

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