DISPLAY RATE AND OPPONENT ASSESSMENT IN THE JACKY DRAGON (AMPHIBOLURUS MURICATUS): AN EXPERIMENTAL ANALYSIS

by

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Summary

Honest signals allow animals to assess an opponent without the injury risk of fighting. Playback experiments have shown that call rate is an important parameter in the acoustic signals of several taxa. Here we describe an analogous study of a visual display. Male Jacky dragons, *Amphibolurus muricatus*, respond to intruding conspecifics with a stereotyped series of motor patterns, including a push-up. These displays are typically given in bouts and there is substantial individual variation in inter-bout interval. In a recent video playback experiment, we found that the display rate depicted in two sequences appeared to influence the type of signal response evoked. The present study was designed to systematically examine the importance of this cue, while controlling opponent morphology and all other aspects of signal structure. Male lizards were presented with five digital video stimuli, each depicting the same male conspecific, but with inter-bout intervals that varied over the full natural range. The duration of aggressive push-up responses changed significantly as a function of stimulus

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properties. Males tracked playback display rate from unusually slow to the population mean, but displayed less to stimuli with unusually fast rates. The interval between display bouts is hence salient to conspecifics, independent of other characteristics. These findings are consistent with the idea that energetically-expensivedynamic visual signals play a role in opponent assessment.

Introduction

In many taxa, there is intense competition over territories, mates, and other resources. When contests degrade into physical combat, the risk of injury can be high. However, most encounters do not escalate to this level (Maynard Smith & Price, 1973; Parker, 1974) because there are mechanisms for opponent assessment that allow animals to avoid fighting when they are unlikely to win (Zahavi, 1977; Clutton-Brock & Albon, 1979).

Physical attributes such as the overall size of an opponent, or the dimensions of weapons such as horns or antlers, can play a role in determining contest outcome. These properties also provide cues for estimating potential fighting ability (*e.g.* Geist, 1987; Johnson, 1988). The structure of some signals similarly facilitates opponent assessment — the inverse relationship between body mass and fundamental frequency is a familiar example (Davies & Halliday, 1978; Arak, 1983; Ryan & Brenowitz, 1985; Robertson, 1986; Given, 1987; Wagner, 1989; Gouzoules & Gouzoules, 1990; Hauser, 1993). In anuran amphibians, potential opponents producing low-frequency calls are more likely to be avoided (Davies & Halliday, 1978; Arak, 1983; Robertson, 1986). Other signals, such as colour patches or badges, can reveal the dominance status of a rival and hence provide an indirect indication of their ability to compete for resources (Rohwer, 1975, 1977; Rohwer & Ewald, 1981; Järvi & Bakken, 1984; Hover, 1985; Møller, 1987; Røskaft & Rohwer, 1987; Höglund & Lundberg, 1989; Thompson & Moore, 1991; Pryke *et al.*, 2001).

Dynamic signals are likely to be particularly useful indicators of fighting ability because they can reveal moment-to-moment variation in condition and motivation. High signal rates have consistently been found to correspond with high levels of aggression (Carpenter, 1961, 1963; Clutton-Brock *et al.*, 1979; Stewart & Rand, 1991; Alberts *et al.*, 1992; Adhikerana & Slater, 1993; Langemann *et al.*, 2000). Signal production is often energetically costly (Rand & Rand, 1976; Clutton-Brock *et al.*, 1979; Bennett *et al.*, 1981; Taigen & Wells, 1985; Marler & Moore, 1988; Vehrencamp *et al.*, 1989; Cherry, 1993), can increase predation risk (Green, 1990; Jakobsson *et al.*, 1995) and reduces time available for other activities such as foraging (Radesäter *et al.*, 1987) or thermoregulation (Rand & Rand, 1976), so only individuals better able to incur such costs can afford to signal at high rates. We therefore expect signal rate to provide honest information about condition. Similar arguments have been proposed to explain strong correlations between signal rate and female mate choice (Gibson & Bradbury, 1985; Gottlander, 1987; Radesäter *et al.*, 1987; Alatalo *et al.*, 1990; Passmore *et al.*, 1992; Cherry, 1993; Collins, 1994; Kodric-Brown & Nicoletto, 1996; Yang & Greenfield, 1996; Gray, 1997).

Comparative analyses suggest that iguanian lizards have evolved complex visual signals to improve opponent assessment under conditions of high male-male competitive intensity (Ord *et al.*, 2001). The Jacky dragon, *Amphibolurus muricatus*, is a medium sized, semi-arboreal Australian agamid. Communication is primarily visual and involves push-up, arm-wave and tail displays (Carpenter *et al.*, 1970; Peters *et al.*, 2002). The presence of male-biased sexual size dimorphism (Harlow & Taylor, 2000), evidence of territoriality in the field (Harlow & Taylor, 2000) and the formation of dominance hierarchies in captivity (Carpenter *et al.*, 1970) all suggest that opponent assessment is likely to be important.

In a recent video playback study (Ord *et al.*, 2002), male Jacky dragons were shown two sequences depicting male conspecifics, which differed in both body size and aggressive display rate. The video male with the higher display rate elicited significantly more slow arm-waves, which are putative appeasement signals, even though the male depicted was the smaller of the two (Ord *et al.*, 2002). Subjects also tracked stimulus display rate, producing more slow arm-waves when they saw the video opponent display vigorously, and switching to aggressive push-ups when the video lizard displayed less frequently (Ord *et al.*, 2002). These observations imply that Jacky dragons are sensitive to variation in display rate and that this attribute might be important in opponent assessment.

In the present study, we evaluated the importance of display rate directly by using video playback to make precisely-controlled changes in the interval between successive push-up bouts. This approach eliminated variation in other opponent attributes and allowed us to isolate the effects of signalling behaviour. Manipulations were based upon estimates of natural variation in signal behaviour and were scaled in standard deviations of inter-bout interval. We predicted that subjects would attempt to match stimuli with slow or average display rates, but that this would not be possible with the stimuli depicting unusually high display rates.

Methods

Subjects

Subjects were 36 sexually-mature male Jacky dragons. Lizards were wild-caught between March 1999 and November 2000 in urban bushland surrounding Botany Bay, Sydney, Australia. They ranged in size from 18.0 g, 83 mm SVL (snout-vent length) to 46.5 g, 95 mm SVL. Each animal was de-wormed shortly after capture and then held in a glass aquarium (36 cm wide × 92 cm long × 38 cm high) 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 06:00), corresponding to midsummer. In addition, heat lamps (125W 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. Lizards were fed 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 lib* 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 study.

One week prior to experiments, lizards were moved into large pens (64 cm wide × 150 cm long × 120 cm high) 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 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.

Temporal properties of display behaviour

We wished to explore lizard responses to natural variation in display rate. The first step in creating playback stimuli was therefore to measure the intervals between bouts of display during dyadic aggressive interactions. Video footage from two earlier studies (Ord & Evans, 2002; Ord *et al.*, 2002) was analysed to estimate a population mean inter-display interval. Twelve male lizards, ranging in size from 22.0 g, 88 mm SVL to 45.0 g, 108 mm SVL, were individually video-recorded while engaged in signal exchanges with a male confined in a small glass tank positioned in front of their pen (see Ord *et al.*, 2002 for a detailed description of recording procedure). Recording sessions lasted for approximately 20 min and were conducted between 08:00 and 14:00 hours over a period of 17 days.

Data on intervals between push-up displays were collated from the first 20 min of up to four sessions, depending on the number of sessions recorded. Push-up displays typically occur in bouts, and there is considerable individual variation in temporal structure. To measure inter-bout intervals, we required a method for segregating these from the briefer pauses that occur within a single display, or between displays within a bout. This problem was first considered by Schleidt (1974), who demonstrated that signalling behaviour often has a log-normal distribution, such that each of the above classes of temporal interval should be represented by a separate distribution in a frequency histogram. This general approach has recently been adapted to identify natural bouts of feeding behaviour in cattle (Tolkamp & Kyriazakis, 1999). We calculated frequency distributions for $\log_{10}$-transformed intervals between successive push-ups for each male. Figure 1 depicts a representative example. It was then possible to identify, by inspection, individual maximum values for intra-bout intervals (range [back-transformed from logs]: 6.3-12.6 s). Intervals greater than these cut-offs were identified as belonging to an inter-bout distribution and were used to obtain the mean value for each male. These individual means were then averaged to estimate population inter-bout interval (39.8 s ± 11.7 SD).

Video stimuli

We used archival footage from a previous study (Ord *et al.*, 2002) in which we had recorded aggressive displays of a male lizard (24.5 g, 90 mm SVL) on an artificial perch in front of a static blue background, using a Canon XL1 digital video camcorder (optical resolution 625 lines; shutter speed 1/250 s; aperture F8) and Sony DVM60EX digital tape. 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 have previously demonstrated that these video sequences evoke aggressive responses comparable with those elicited by a live opponent (Ord *et al.*, 2002).

Raw footage was transferred digitally from the camcorder to a DraCo nonlinear video editing workstation (MS MacroSystems Computer GmbH), using an IEEE 1394 ‘firewire’ interface. MovieShop v5.2 software was then used to edit sequences of aggressive displays, resting and non-display movement, to produce five video stimuli (Table 1). These had inter-bout intervals that varied from two standard deviations shorter than the population mean (highest display rate) to two standard deviations longer than the mean (lowest display rate). We chose to base this series of stimuli on inter-bout interval because this was the parameter originally measured from video footage. The resulting stimulus set varied systematically in display rate, but it is important to note that the increments from one stimulus to the next were not equal on this dimension (Table 1). This phenomenon is an inevitable consequence of

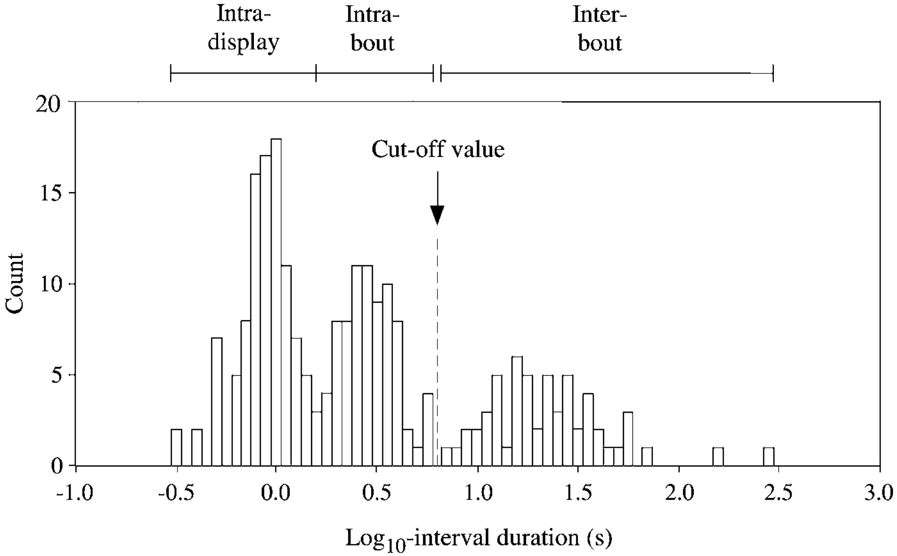

Fig. 1. Frequency distribution of intervals between push-ups for an individual male Jacky dragon. Aggressive displays consist of one or more push-ups, which are produced in rapid succession and typically occur in bouts. Note that intra-display, intra-bout and inter-bout intervals form three distinct populations. We used archival footage from previous studies (Ord & Evans, 2002; Ord *et al.*, 2002) to estimate the minimum interval between bouts for each male (0.8 for this individual) and used only values greater than this to calculate an individual mean. These scores ($N = 12$) were then used to estimate the mean and variance of population inter-display intervals. See text for details.

the inverse transform relating rate and period; it occurs with all temporally-patterned events (Gaioni & Evans, 1984). Enough raw footage was available to ensure that individual clips were not used more than once in completed sequences, avoiding a potential confounding effect of differential habituation. Completed stimuli were digitally transferred to PAL DVCAM tape for playback.

Playback presentations

Individual male lizards were shown each stimulus once. Presentation order was randomised using the 'RandomUniformInteger' option in StatView 5.0 (Abacus Concepts Inc.), with the constraint that no stimulus could occupy the same order position more than 9 times in the completed matrix (*i.e.* 5% of the total number of presentations). To control for potential diel variation in response, subjects received all five playbacks at the same time of day. Test sessions were separated by 24 h.

Apparatus and test procedure were based on those used in earlier video playback experiments (Ord & Evans, 2002; Ord *et al.*, 2002). 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. Stimuli were presented using a Sony GV-D300E DVCAM deck connected to

TABLE 1. *Characteristics of stimuli presented to male Jacky dragons*

Stimulus type	Inter-bout interval (s)	Display rate (bouts/min)	Number of bouts	Number of displays	Total duration of display (s)	Playback duration (min)
−2SD	16.4	2.80	56	158	67.1	20
−1SD	28.1	1.85	37	113	54.1	20
Mean	39.8	1.35	27	81	40.7	20
+1SD	51.6	1.10	22	61	33.3	20
+2SD	63.3	0.90	18	53	30.7	20

All stimuli depicted the same video lizard performing aggressive displays. Inter-bout intervals were adjusted in increments of one standard deviation to cover the estimated population range. Corresponding display rates are shown for comparison. Note that, since rate and interval are inversely related, regular increments in one dimension produce non-linear change in the other (see text for details).

the playback monitor. Image quality in this system was limited only by the PAL digital video standard (5 : 1 compression; horizontal resolution 550 lines).

We began each test 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 video camera operated remotely from behind an opaque barrier, and the whole test session was recorded for subsequent analysis.

Data analysis

The structure of Jacky dragon aggressive displays has recently been described (Peters *et al.*, 2002; Peters & Ord, in press). These signals typically begin with repeated tail lashing followed by a rapid backward and forward arm-wave, and then one or more push-ups, in which the anterior portion of the body is raised by flexing the forelimbs.

We scored bouts of push-up display from videotapes using the ‘JWatcher 0.9’ event-recorder program (Blumstein *et al.*, 2000). To compare responses evoked by stimuli, we examined the summed duration of all push-up display bouts performed during stimulus presentations. On preliminary analysis, we found significant variation in response as a function of test day. To remove this potentially obscuring effect, we used a repeated-measures ANCOVA (SPSS 10 for Macintosh, 2000, SPSS Inc) with factors for stimulus and subject and a covariate for day. When a plot of test day and response revealed a curvilinear relationship, we added an additional covariate of day^2. We report results from both a General Linear Model (GLM) and a Quadratic Polynomial Model (QPM).

The latency to respond to each stimulus was also measured. When displays did not occur, subjects were assigned a score equal to the duration of the test session (1200 s). Latency data were $\log_{10}$-transformed to eliminate positive skew. Two individuals failed to display in any treatment and were excluded from analyses. We used an alpha level of 0.05 throughout.

Results

The stimulus series produces a monotonically-increasing function when plotted in terms of total duration to correspond with our response measure (Fig. 2a). Lizard displays (Fig. 2b) tracked stimulus characteristics over the three longest intervals (+2SD to mean), but were progressively reduced at shorter intervals (-1 and -2 SD), corresponding to the highest display rates. This variation in total display duration is reflected in a significant main effect for treatment (GLM: $F_{4,58} = 7.584$, $p = 0.048$; QPM: $F_{1,58} = 4.53$, $p = 0.024$). Response latencies (Fig. 2c) approximately mirror display duration, suggesting that increases in playback display rate, up to the population mean, evoke correspondingly more rapid responses. However, the treatment main effect for this measure fails to achieve statistical significance (GLM: $F_{4,58} = 1.863$, $p = 0.129$; QPM: $F_{1,58} = 3.269$, $p = 0.076$).

Discussion

Playback results demonstrate that male Jacky dragons are sensitive to the display rate of a simulated opponent. This attribute is sufficient to cause changes in signalling behaviour, even when there is no correlated variation in other characteristics, such as body size. In addition, the form of the display response function (Fig. 2b) was successfully predicted by estimates of the mean and variance in population inter-bout intervals. Subjects increased total display duration to match that depicted in stimuli as intervals were reduced from +2SD to the population mean (Fig. 2a, b), but displayed less when shown the same video lizard displaying at rates exceeding the population average (Fig. 2b).

Lizard displays are energetically costly (Rand & Rand, 1978; Bennett *et al.*, 1981; Marler & Moore, 1988). It is thus likely that these signals provide reliable information about fighting ability by revealing correlates such as physical endurance. The effect of our experimental manipulation of display rate has implications for natural agonistic encounters: Jacky dragons that are able to perform rapid sequences of push-ups should inhibit production of corresponding signals by their opponents. High display rates are a characteristic of dominant and aggressive lizards (Alberts *et al.*, 1992; Carpenter, 1961, 1963), which typically occupy territories that are larger (Rand, 1967; Brattstrom, 1974; Ferner, 1974), and of better quality (Fox *et al.*, 1981;

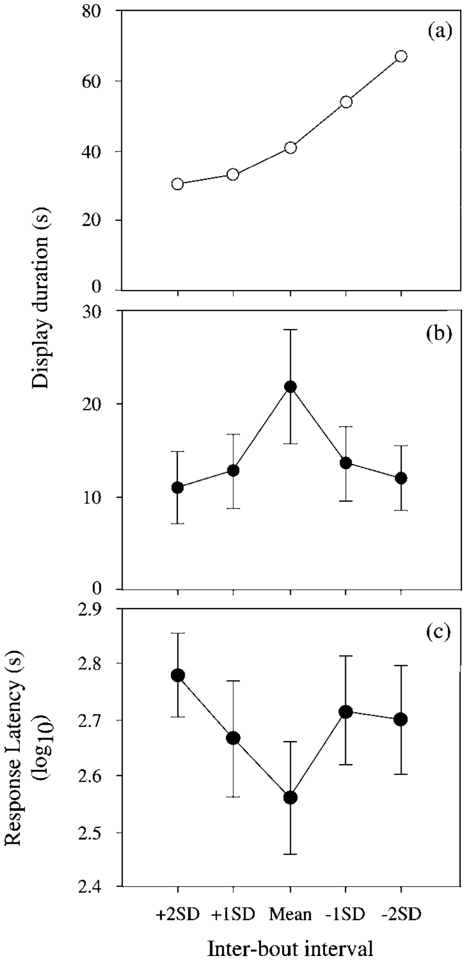

Fig. 2. Stimulus properties and lizard display responses. (a) Total duration of display in each of five stimulus sequences. Successive stimuli differ by one standard deviation of inter-bout interval and are depicted from slow (+2SD) to fast (−2SD) rate. See Table 1 for stimulus characteristics. (b) Mean (± SE) total duration of display evoked. (c) Mean (± SE) latency to first display.

Fox, 1983; Stamps & Eason, 1989). Such animals are likely to have greater reproductive success (Trivers, 1976; Dugan, 1982). Aggressive display rate may hence predict ability to compete for resources that influence fitness.

The response of Jacky dragons to variation in opponent signal rate is similar to that described by Clutton-Brock & Albon (1979) in their classic paper on roaring contests in male red deer, *Cervus elaphus*, which is frequently cited as an example of honest signalling. Temporal changes in the roaring rate of stags are associated with differences in fighting ability. Playback experiments simulating a male roaring at an escalating rate showed that resident stags initially matched the recording, but broke off the aggressive interaction upon hearing the highest roaring rate (Clutton-Brock & Albon, 1979). These results establish that signal rate is important, but leave open the question of how this cue is assessed.

Mechanisms of signal rate assessment

Payne & Pagel (1997) discuss three alternative models of the way in which animals might measure signal rate. When information is transferred with error, assessment based on the average magnitude of all signals performed so far provides the greatest accuracy in evaluating fighting ability (the 'sequential assessment game' — Enquist & Leimer (1983)). In this model, signal repetition functions to confirm the message of previous displays; signal rate consequently remains relatively constant throughout an interaction. However, in many systems, signal rate escalates as an interaction progresses (*e.g.* red deer — Clutton-Brock & Albon (1979); Siamese fighting fish — Simpson (1968); Evans (1985); Jacky dragons — Ord & Evans (2002); Ord *et al.* (2002)). If transmission error is relatively low, assessment might instead be based on the 'best attempt' so far, with each consecutive signal replacing the estimate obtained from the previous one. For such a process, the energy invested in previous signals is effectively wasted. When signals incur significant costs (*e.g.* from fatigue), assessment is more likely to be based on a cumulative measure of all displays performed. In this scenario, successive signals function to augment, rather than confirm or replace, the message of previous displays. Payne & Pagel (1997) conclude that the most likely mechanism for assessment of roaring rate by red deer stags is a cumulative function rule, together with a threshold that varies according to individual condition. Most recently, Taylor & Elwood (2003) have shown that contest duration can successfully be predicted by a quite different model that considers only the condition of the weaker participant.

These theoretical models generate predictions suitable for experimental testing in playback experiments, and lizard displays provide an opportunity to extend such analyses into the visual domain. By presenting stimuli that vary in signal rate over the course of a simulated encounter, it should be possible to establish the mechanisms used for opponent assessment. For example, it would be revealing to compare stimuli in which display rate was held constant, escalated, or concentrated during irregular bouts of intense signal activity over the course of the presentation period. Planned comparisons could then test whether Jacky dragons are assessing signal rate using a recent average, 'best-so-far', or cumulative rule.

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