

## Assessment of repeated displays: a test of possible mechanisms

Daniel A. Van Dyk<sup>1,\*</sup>, Alan J. Taylor<sup>2</sup> and Christopher S. Evans<sup>1</sup>

<sup>1</sup>Centre for the Integrative Study of Animal Behaviour and <sup>2</sup>Department of Psychology, Macquarie University, Sydney, NSW 2109, Australia

\*Author for correspondence (e-mail: daniel@galliform.bhs.mq.edu.au)

Accepted 20 June 2007

### Summary

Many animals signal their resource holding potential (RHP) to deter competitors from engaging them in potentially costly fights. Studies of this opponent assessment function have generated important insights into signal design and evolution. In the case of sounds, rate of production is often a salient feature. We used digital video playback to conduct analogous experiments exploring the importance of temporal variation in visual signals. Our study focused on the push-up display of male Jacky dragons *Amphibolurus muricatus*, an Australian agamid lizard. This stereotyped movement-based signal is commonly performed during male–male contests. A previous study has shown that Jacky dragons responses are influenced by the overall display rate of a video conspecific. We built upon this finding by investigating the effect of short-term variation in display rate. Each playback

sequence varied systematically across a different combination of display parameters, while keeping the total number of push-ups constant. Other potential cues, such as morphology and the characteristics of individual motor patterns, were precisely controlled. The aggressive signalling and locomotor behaviour of subject males varied significantly between sequences. Most notably, performance of throat expansions, a typical agamid threat posture, was suppressed by video sequences with temporal clumping of displays. These results show that lizards are sensitive to differences in the temporal fine structure of display sequences and suggest that display concentration is an important assessment cue.

Key words: visual signals, opponent assessment, Jacky dragon, *Amphibolurus muricatus*.

### Introduction

Males often come into conflict with each other over access to resources. This has led to the evolution of a variety of strategies for resolving disputes. Although fighting is an option, the associated costs often create pressure to pursue less risky alternatives (Maynard Smith, 1974; Parker, 1974). Under such conditions, competitors may assess suites of cues and/or signals to better estimate their chances of winning fights. If the likelihood of prevailing is low, it is often adaptive to withdraw without incurring further cost.

Much of the research into opponent assessment has focused on establishing links between signals/cues and predictors of fight outcome. The search for predictors typically centres upon an individual's fighting ability and the perceived value of contested resources (Enquist, 1985; Hurd, 2006; Parker, 1974). For assessment to persist as a strategy, signals must reliably correlate with physical or motivational attributes.

Reliability can be maintained through a number of different processes (reviewed in Hurd and Enquist, 2005). Index signals are reliable because their performance is inextricably constrained. Examples of index signals include the acoustic characteristics of anuran calls and of deer roars, both of which correlate with body size (Bee et al., 1999; Davies and Halliday, 1978; Reby et al., 2005). Handicap signals entail production costs (Zahavi and Zahavi, 1997). The willingness of individuals

to incur these costs is bound to components of fighting ability and motivation. Production costs can include investment in badges, energy expenditure during displays, exposure to predation and loss of time. For instance, the temporal structure of shell rapping in hermit crabs suggests that it functions as a signal of stamina (Briffa and Elwood, 2000a; Briffa and Elwood, 2000b). The reliability of conventional signals is enforced by the opponent's response. If a weak individual produces an exaggerated signal, it could be attacked by stronger opponents. The costs of such attacks are thought to make bluffing an unsuccessful strategy, and hence fights occur only when rivals signal at similar levels. Colour patches and song type sharing in birds have been cited as cases of conventional signalling (Molles and Vehrencamp, 2001; Qvarnstrom, 1997; Vehrencamp, 2000).

It is logical to suppose that if a signal is reliably linked to predictors of contest outcome, then it is probably being assessed. This statement represents a hypothesis, which is most unambiguously tested by the controlled manipulation of potential signals. Static visual signals such as colour patches can be altered relatively easily with paints, dyes or filters (Göth and Evans, 2004; Hunt et al., 2001; Olsson, 1994; Veiga, 1993). Dynamic visual signals have presented a more recalcitrant problem. While our understanding of acoustic communication such as deer roars, frog calls and bird song is well advanced due

to historical developments in sound acquisition, manipulation and playback (Clutton-Brock and Albon, 1979; Davies and Halliday, 1978; Falls, 1963), it is only recently that improvements in technology have made dynamic visual signals similarly accessible. In particular, the development of robotic models (Martins et al., 2005; Simpson, 1968) and video playback (Clark and Uetz, 1992; Evans and Marler, 1991; Ord et al., 2002) has made the experimental analysis of movement-based signals possible for the first time.

An opponent observing a sequence of dynamic visual displays has access to four potential sources of information: sender morphology, display motion characteristics, choice of display type and display rate. In relation to display rate, three mechanisms of assessing a single repeated behavioural action have been considered (Payne and Pagel, 1997). First, the assessor may be averaging actions to improve its estimate of signal characteristics. This is equivalent to a single round within the sequential assessment model (Enquist and Leimar, 1983). Here, signals constrained by physical limitations (i.e. index signals) are expected to be transmitted with error. Repetition facilitates the gradual reduction of error levels in a manner analogous to statistical sampling. Second, competitors might be assessing the best action so far and ignoring all previous actions (Payne and Pagel, 1996). In this model, each superior action is, in effect, the signal. Third, the signal might be a cumulative function of all the actions performed (Payne, 1998). This mechanism is most likely to occur when repetition imposes a high time cost, as in displays of endurance. Payne and Pagel described features of contests and signals that could be used to infer the presence of one of these mechanisms (Payne and Pagel, 1997).

Iguanian lizards are an ideal model group for studying mechanisms of opponent assessment. Intense selective pressure to reduce the risks of male–male competition has contributed to a rich diversity of signals (Carpenter, 1965; Ord et al., 2001) designed to exploit the well-developed iguanian visual system. Dynamic signals, involving stereotyped movements of the head and body, are a prime example of this (Carpenter and Ferguson, 1977; Stamps, 1977). Many species have evolved a repertoire of structurally distinct displays, as defined by the cadence of head movements, and much of the work in this field is concerned with quantifying the variation in display choice between different contexts (DeCourcy and Jenssen, 1994; Hover and Jenssen, 1976; Lovern et al., 1999; Macedonia and Clark, 2003; Martins, 1993; McMann, 2000; Orrell and Jenssen, 2003). In captivity, dominant males are often observed displaying more than subordinates, and high display rates in the field have been linked to laboratory measures of endurance and contest success (Carpenter, 1962; Carpenter, 1965; Deslippe et al., 1990; Perry et al., 2004; Prieto and Ryan, 1978). Endurance capacity is also correlated with display behaviour in an anti-predator context (Leal, 1999).

Here we explore the relationship between short-term changes in display rate and opponent assessment in Jacky dragons *Amphibolurus muricatus* (White 1790). Dynamic visual signals are commonly used by Jacky dragons to mediate social interactions (Carpenter et al., 1970). Males threaten opponents with push-up displays, a highly stereotyped sequence of motor patterns consisting of a rapid arm-wave followed by one or more

push-up/body-rocks (Peters and Ord, 2003). Displays can occur in rapid succession, forming a bout. Lizards often modify their displays by adding introductory tail-flicks (Peters and Evans, 2003), or increasing their profile through lateral compression, gular expansion and nuchal crest erection. Previous video playback experiments found that males were sensitive to ‘moment-to-moment’ variation in the display rate of simulated opponents (Ord et al., 2002) and the social contingencies governing interactions (Ord and Evans, 2002). A follow-up study identified overall display rate as a critical parameter, with males displaying more when the stimulus lizard’s inter-bout interval was population-average than to shorter or longer intervals (Ord and Evans, 2003). These findings suggest that males use the temporal properties of display sequences to assess fighting ability or motivation. Jacky dragons also have two putative submissive signals, the slow arm-wave and slow head-bow. These displays are typically performed by subordinate individuals in both indoor pens and large naturalistic outdoor enclosures (D.V.D., personal observation).

In the present study, we investigated which of the three possible mechanisms (average, ‘best-so-far’ or cumulative) underlies the assessment of display rate. We conducted two video playback experiments, each simulating aggressive intruders engaging residents at close range, but examining different patterns of display behaviour over time. Digital video playback was used to control both the morphology of the simulated opponent and the motion characteristics of individual displays, while allowing precise manipulation of the moment-to-moment changes in display rate. This approach provides a uniquely sensitive test of assessment mechanisms.

## Materials and methods

### Subjects

Subjects were adult male Jacky dragons *Amphibolurus muricatus* (White 1790) caught between 2000 and 2005 in National Parks (NP) around Sydney, Australia (Botany Bay NP, Royal NP and Lane Cove NP). Lizards were caught by noosing with fishing line, a procedure that never resulted in injury. We used the same 29 subjects in both experiments, with an extra three subjects included in Experiment 2. Lizards ranged in length from 75 mm to 102 mm snout–vent length (SVL) and in mass from 15.5 g to 39.0 g. Following capture, subjects were placed in cloth bags and transported by car to large indoor pens (64 cm wide × 75 cm long × 120 cm high). Pens consisted of opaque plastic sheeting on three sides to prevent visual contact with neighbouring lizards and clear Perspex™ on the remaining side to allow presentation of visual stimuli and recording of behaviour. Pens had a sand substrate and contained branches and vegetation to facilitate climbing, basking and hiding. Environmental systems in the rooms were programmed to generate summer conditions with a 14 h:10 h light:dark cycle and a temperature of approximately 26°C. A heat lamp (125 W, 240 V Philips Spotone) was positioned over each pen to enable behavioural thermoregulation and UV lamps (300 W Osram Ultra-Vitalux) were provided to prevent vitamin deficiency. Lizards were fed twice weekly with live crickets dusted with vitamin supplements (RepCal™) and had access to water *ad lib*. Pens were misted with water daily to maintain humidity levels. These husbandry procedures, developed over the last decade,

have been successful in maintaining health and social responsiveness over periods ranging up to several years in captivity. Subjects were either retained for further studies or released at the location of capture.

#### Video stimuli

##### Recording

Video footage of lizards basking and performing push-up displays was recorded according to the procedure detailed elsewhere (Ord et al., 2002). Briefly, pens were modified by covering the floor with a thick layer of foliage and inserting an artificial wooden perch directly under the heat lamp. Room temperature was then lowered to between 18°C and 20°C to exaggerate the thermal gradient within the pens, thereby encouraging the lizards to bask on the perch. A piece of light blue cardboard was placed behind the perch to standardise the contrast between the lizard and the background. Lizards were allowed 1 week to acclimate to these new conditions before filming commenced.

Illumination was provided by an 800-W photographic P2/11 tungsten-halogen lamp, which was angled to place the perch shadow out of camera frame. Recordings were made with a digital video camcorder (Canon XL1; optical resolution 625 lines; shutter speed 1/250 s; aperture F8). Focal length was then adjusted to ensure that the lizard appeared life-sized on the screen subsequently used for playback.

Recording and testing occurred between 08:00 h and 14:00 h, which corresponds to the period of peak activity (Ord, 2001). A small aquarium containing a male lizard was placed on the trolley below the camera and concealed with a black cloth. When the subject lizard was visible on the viewing monitor the tungsten-halogen lamp and video camera were switched on and the black cloth removed. Filming continued until the subject lizard left the perch.

##### Editing

Video footage of one lizard, (SVL 89 mm, mass 27 g), was used in the playback experiment. This allowed us to manipulate the distribution of displays over time without confounding variation in other parameters. Note that this design is not pseudoreplicated because the domain of interest is signalling rate, rather than morphology, display structure or other individual characteristics. Our design hence maximises statistical power by controlling irrelevant variation, although at the cost of not permitting tests for possible interactions between signal rate and other attributes. Such questions are outside the scope of the present study.

Footage was digitally transferred from a video editing program (Final Cut Pro 3.0, Apple Computer, Inc.) and assembled into sequences. Two clips were selected based on their consistent display structure (three push-up/body-rocks per display), giving 30 push-up/body-rocks with which to create playback stimuli. Displays were accompanied by tail-flicks and some gular expansion.

Eight sequences were created. Each was 14 min long and showed an empty perch for the first 2 min, followed by the stimulus lizard inactive on the perch for the next 2 min. The remaining 10 min showed the lizard performing a series of push-up displays, separated by periods of inactivity. Each series contained the same 30 unique push-up/body-rocks in the same order. The only difference between them was the interval between displays, and hence the number of push-up/body-rocks occurring per minute. Displays commenced in the first 5 s of the minute and finished by 20 s. Intervals between push-up/body-rocks in any 1 min fell within the range found in natural bouts, as calculated by Ord and Evans (Ord and Evans, 2003). Thus, the displays within a single minute constituted one bout.

The 'constant', 'initial' and 'spike' sequences showed a display bout in each minute, but differed according to the number of push-up/body-rocks per bout (Table 1; Fig. 1A–C). In the 'constant' sequence, each bout contained 3 push-up/body-rocks, whereas the first bout contained 6 push-up/body-rocks in the 'initial' sequence and the fifth bout contained 9 push-up/body-rocks in the 'spike' sequence. The 'pulsed' and 'block' sequences both contained bouts of 6 push-up/body-rocks (Table 1, Fig. 1D,E). In the 'pulsed' sequence, the bouts occurred in every second minute whereas in the 'block' sequence they occurred every minute over the first 5 min. The escalation sequences consisted of 4 bouts containing 3, 6, 9 and 12 push-up/body-rocks (Table 2, Fig. 1F–H). In the 'slow escalation' sequence, a bout occurred every third minute in increasing order of magnitude. The 'fast escalation' sequence presented the same sequence, but with shorter intervals; bouts occurred every minute over the first 4 min. The 'de-escalation' series was matched for rate of change to 'slow escalation', but in the opposite direction; this presented a display bout every third minute, in decreasing order of magnitude.

#### Playback experiment

##### Design

Experiment 1 tested for the effect of variation in the display rate/time profile, while keeping the total number of push-up/body-rocks (PUBR) constant. We systematically altered four display series parameters: initial rate, maximum rate,

Table 1. Temporal display series characteristics of stimulus sequences in Experiment 1

Display series characteristics	Stimulus sequences				
	Constant	Initial	Spike	Pulsed	Block
Initial rate (PUBR min <sup>-1</sup> )	3	6	3	6	6
Maximum rate (PUBR min <sup>-1</sup> )	3	6	9	6	6
Overall rate (PUBR min <sup>-1</sup> )	3	3	3	3	3
Average bout size (PUBR bout <sup>-1</sup> )	3	3	3	6	6
Display series duration (min)	10	10	10	9	5

PUBR, push-up/body-rocks. For type of stimulus sequence, see Fig. 1.

concentration of displays within bouts and duration of display behaviour, in five playback sequences (Fig. 1A–E).

Planned pair-wise comparisons between sequences allowed us to gauge the influence of each display series parameter. These were based on *a priori* predictions, as follows. If responses to sequences with an initial display rate of 6 PUBR  $\text{min}^{-1}$  differed from those to sequences with an initial display rate of 3 PUBR  $\text{min}^{-1}$ , this would implicate initial display rate in opponent assessment. Similarly, if maximum display rate were important, then responses to the sequence with a maximum rate of 9 PUBR  $\text{min}^{-1}$  should differ from those to sequences with a maximum rate of 6 PUBR  $\text{min}^{-1}$ , which in turn should differ from those to sequences with a maximum rate of 3 PUBR  $\text{min}^{-1}$ . If opponent assessment were principally dependent upon the relative concentration of displays within bouts, then responses to sequences that averaged 6 PUBR/bout should differ from those to sequences that averaged 3 PUBR/bout. Finally, if the total duration of the display sequences (endurance) were an important factor, then responses to sequences that extended to 10 and 9 min should differ from those to the sequence that lasted only 5 min.

Experiment 2 tested for the effects of more global, monotonic change in display rate. We manipulated three display series parameters: presence of change, rate of change and direction of change, in four playback sequences (Table 2; Fig. 1D,F–H). As in the first experiment, playback sequences were designed to vary with respect to the three parameters, allowing us to assess the influence of each with planned pair-wise comparisons. The total number of push-up/body-rocks was held constant and the time in which displays occurred was kept between 4 and 5 min.

Planned comparisons were as follows. If monotonic rate change affected assessment, then responses to the sequence with no rate change should differ from those to the sequences with this characteristic. If the rate of change were a critical factor, then lizards would be expected to respond differently to the

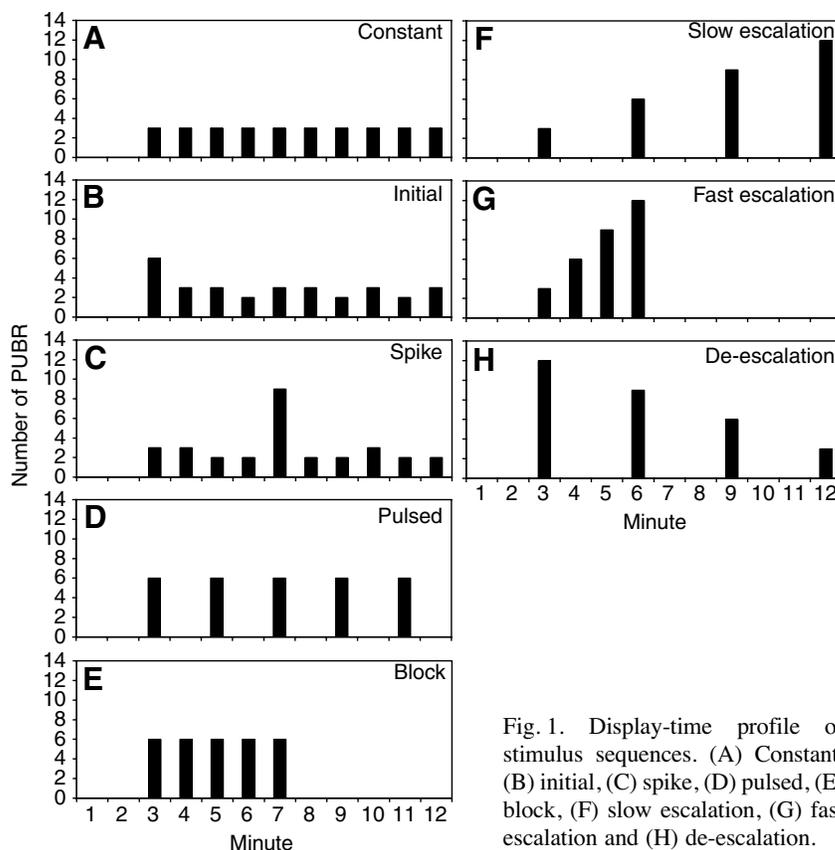


Fig. 1. Display-time profile of stimulus sequences. (A) Constant, (B) initial, (C) spike, (D) pulsed, (E) block, (F) slow escalation, (G) fast escalation and (H) de-escalation.

rapidly escalating sequence, compared to the other sequences. Similarly, if the direction of change were important, then responses to the positively escalating sequences should differ from those to the de-escalating sequence. Treatments also necessarily differed according to some of the parameters predicted in Experiment 1, allowing us to re-test these factors.

In both experiments, lizards viewed one playback sequence per day, with a 2-day break between presentations. This resulted in a 13-day testing period for Experiment 1 and an 11-day testing period for Experiment 2. In Experiment 1, each subject experienced a unique random presentation order. In Experiment 2, the number of subjects exceeded the number of possible combinations, so we ensured that no more than two lizards experienced any particular order of treatments.

Table 2. Temporal display series characteristics of stimulus sequences in Experiment 2

Display series characteristics	Stimulus sequences			
	Pulsed	Slow escalation	Fast escalation	De-escalation
Initial rate (PUBR $\text{min}^{-1}$ )	6	3	3	12
Maximum rate (PUBR $\text{min}^{-1}$ )	6	12	12	12
Overall rate (PUBR $\text{min}^{-1}$ )	3	3	3	3
Average bout size (PUBR bout $^{-1}$ )	6	7.5	7.5	7.5
Display series duration (min)	9	10	4	10
Monotonic change	No	Yes	Yes	Yes
Rate of change (PUBR $\text{min}^{-2}$ )	n/a	1	3	1
Direction of change	n/a	Positive	Positive	Negative

PUBR, push up/body rocks; n/a, not applicable.

### Test procedure

Experiment 1 was carried out in March 2005 and Experiment 2 was conducted in June of the same year. All subjects occupied their experimental pen for at least 1 week prior to testing. Lizards typically exhibited normal thermoregulatory and feeding behaviour within hours of being placed in a pen.

We mounted some of the test equipment on a trolley, so that it could be positioned in front of each pen with minimal disruption to subjects. This included the stimulus presentation monitor (Sony PVM-14M2A; resolution >600 lines, screen size 34 cm measured diagonally), a CCTV camera (Panasonic WV-CP240) fitted with a wide-angle lens (Panasonic WV-LA210CSE) and a second monitor (Panasonic TC-1470Y) repeating the camera signal, to function as a viewfinder. Prior to testing, we calibrated the presentation monitor using PAL standard pluge bars (Final Cut Pro 3.0, Apple Computer).

The remaining test equipment remained static at one end of the room, allowing the experimenter to remain concealed behind the end wall of the lizard pens. This was linked by cables to the presentation system and included an S-VHS deck (Sony DVD Player/VCR SLV-D910) for recording subject responses and a computer (iMac G3) with a large external drive (LaCie 160GB) containing stimuli. Playback sequences were presented using Final Cut Pro 3.0 and transcoded back to S-video using a digital video converter (Canopus ADVC110).

### Statistical analyses

Behavioural responses to the stimulus lizard were scored from test-session video recordings. We measured the frequency of the following responses: push-up/body-rocks, slow arm-waves, gular expansions, bouts of general locomotion and 'attacks', in which subjects touched the Perspex™ panel in an apparent attempt to approach the stimulus. Gular expansion was often sustained for many seconds; we therefore recorded duration to the nearest second. Lizards that did not perform a social response (all behaviours except general locomotion), during at least two stimulus presentations were excluded. This criterion resulted in the removal from analyses of six animals in Experiment 1 and five animals in Experiment 2. Another animal was excluded from the analyses due to its extreme submissive behaviour.

Preliminary examination of the data revealed skewed distributions caused by a high proportion of zero-counts. The resulting variances were greater than their means (overdispersed). The most appropriate method for analysing data with these characteristics is negative binomial regression, a generalisation of Poisson regression, which accounts for overdispersion (Gardner et al., 1995; Ridout et al., 1998). We used the statistical software package Stata (StataCorp LP, College Station, TX, USA), which calculates negative binomial regression with a modified variance estimate to account for within-subject correlations.

Playback type was entered as a dummy-coded explanatory variable in the model to directly examine the effects of varying the temporal properties of display sequences. We included the order of stimulus presentation as a second explanatory variable (also dummy-coded) to account for the potentially obscuring effects of habituation and sensitisation. Size is often an

important determinant of agonistic behaviour. To control for this, we added individual SVL to the model.

The regression coefficients for the dummy codes and for the SVL variables are interpreted as incidence-rate ratios (IRR), which are similar to the odds-ratios of logistic regression. For example, an IRR of 0.5 for a particular category means that response rates are 50% lower than those in the reference category. The significance of the IRRs was examined using Z-tests with *P*-values adjusted to control the proportion of Type I errors across multiple comparisons (false discovery rate) (Benjamini and Hochberg, 1995). This method is preferable to traditional Bonferroni-type procedures because it retains statistical power and avoids Type II errors (Garcia, 2004; Nakagawa, 2004; Verhoeven et al., 2005). We assessed the overall influence of the explanatory variables using the Wald test (Sokal and Rohlf, 1995).

## Results

### Experiment 1

There was significant overall variation in lizard responses across the set of playback stimuli (Table 3). This was reflected in rates of locomotion and push-up/body-rock displays, and in the duration of gular expansion. Pair-wise comparisons between treatments revealed that the rate of locomotion in the 'pulsed' sequence was higher than that in the 'initial' sequence, although this difference just failed to achieve significance once corrected for multiple comparisons (Z-test: pulsed: initial  $Z=2.74$ ,  $N=22$ ,  $P=0.006$ , critical  $P$ -value=0.005, Fig. 2A).

The rate of push-up/body-rocks in the 'pulsed' sequence was significantly less than the rate in both the 'constant' and the 'spike' sequences (pulsed:constant  $Z=-2.76$ ,  $N=22$ ,  $P=0.006$ ; pulsed:spike  $Z=-2.68$ ,  $N=22$ ,  $P=0.007$ , critical  $P$ -value=0.01, Fig. 2B). The 'block' sequence also suppressed the rate of push-up/body-rocks compared to the 'constant' and 'spike' sequence; however, these differences failed to reach statistical significance (block:constant  $Z=-2.19$ ,  $N=22$ ,  $P=0.028$ ; block:spike  $Z=-2.30$ ,  $N=22$ ,  $P=0.022$ ).

Duration of gular expansion seemed to be a particularly sensitive response assay, yielding several significant differences between treatments. The duration of gular expansion in the 'initial', 'pulsed' and 'block' sequences was significantly less than that in the 'constant' sequence (initial:constant  $Z=-2.75$ ,  $N=22$ ,  $P=0.006$ ; pulsed:constant  $Z=-3.74$ ,  $N=22$ ,  $P<0.001$ ; pulsed:spike  $Z=-3.07$ ,  $N=22$ ,  $P=0.002$ , critical  $P$ -value=0.025, Fig. 2C). Similarly, the duration of gular expansion in the

Table 3. Experiment 1: negative binomial regression on response rates in relation to playback treatment and presentation order

Response	Playback treatment		Presentation order	
	Wald $\chi^2_4$	<i>P</i>	Wald $\chi^2_4$	<i>P</i>
Locomotion	12.17	0.016*	18.27	0.001*
Push-up/body-rock	12.10	0.017*	33.90	<0.001*
Gular expansion	25.66	<0.001*	6.76	0.150
Attack	2.26	0.688	15.87	0.003*
Slow arm-wave	0.91	0.923	22.34	<0.001*

\* $P \leq 0.05$ .

'pulsed' and 'block' sequences was significantly less than that in the 'spike' sequence (block:constant  $Z=-3.87$ ,  $N=22$ ,  $P<0.001$ ; block:spike  $Z=-3.22$ ,  $N=22$ ,  $P=0.001$ , Fig. 2C).

Consistent with assessment of the simulated opponent, there was a significant positive relationship between the subject's size and the rate of both slow arm-waves ( $Z=3.32$ ,  $N=22$ ,  $P=0.001$ ) and gular expansion ( $Z=2.09$ ,  $N=22$ ,  $P=0.037$ ). Presentation order was a significant factor in all behavioural responses except gular expansion (Table 3). The relationship between test day and response levels was generally curvilinear, with a peak over the middle days.

### Experiment 2

Overall frequency of attacks and duration of gular expansion were significantly influenced by playback treatment (Table 4). Subsequent pair-wise comparisons revealed significant differences, with subjects attacking the stimulus at a lower rate in the 'pulsed sequence compared to the 'slow escalation' sequence (pulsed:slow escalation  $Z=-3.02$ ,  $N=26$ ,  $P=0.003$ , critical  $P$ -value=0.008, Fig. 3A). Subjects also attacked at a lower rate in the 'fast escalation' sequence compared to the

Table 4. Experiment 2: negative binomial regression on response rates in relation to playback treatment and presentation order

Response	Playback treatment		Presentation order	
	Wald $\chi^2_3$	$P$	Wald $\chi^2_3$	$P$
Locomotion	5.74	0.125	0.18	0.980
Push-up/body-rock	3.53	0.317	2.69	0.442
Gular expansion	11.6	0.009*	7.51	0.057
Attack	10.47	0.015*	7.2	0.066
Slow arm-wave	5.28	0.153	3.54	0.316

\* $P\leq 0.05$ .

'slow escalation' sequence; however, this difference did not reach statistical significance (fast escalation:slow escalation  $Z=-2.15$ ,  $N=26$ ,  $P=0.031$ ).

The duration of gular expansion in both the 'fast escalation' and 'de-escalation' sequences was significantly less than that in the 'pulsed' sequence (fast escalation:pulsed  $Z=-2.72$ ,  $N=26$ ,  $P=0.007$ ; de-escalation:pulsed  $Z=-2.87$ ,  $N=26$ ,  $P=0.004$ , critical  $P$ -value=0.017, Fig. 3B).

Locomotion and slow arm-waving exhibited a significant positive relationship with subject size (locomotion  $Z=2.79$ ,  $N=26$ ,  $P=0.005$ ; slow arm-wave  $Z=2.11$ ,  $N=26$ ,  $P=0.035$ ), whereas push-ups showed a significant negative relationship

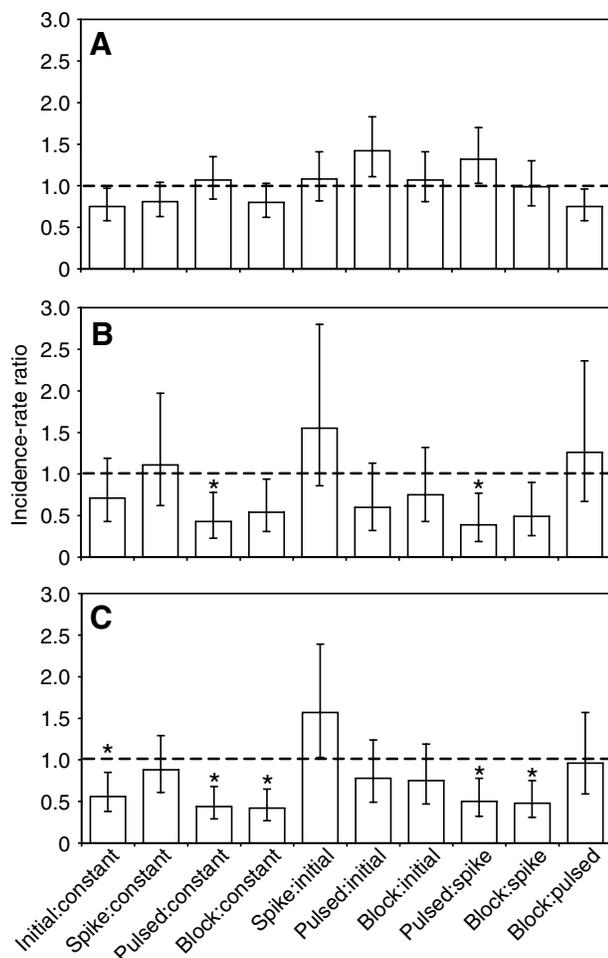


Fig. 2. Experiment 1. Incidence-rate ratios ( $\pm 95\%$  confidence interval) of pair-wise comparisons between treatments. (A) Locomotion (critical  $P$ -value=0.005), (B) push-up/body-rock (critical  $P$ -value=0.01) and (C) gular expansion (critical  $P$ -value=0.025). \*Significant difference between the responses for the two treatments in each pair.

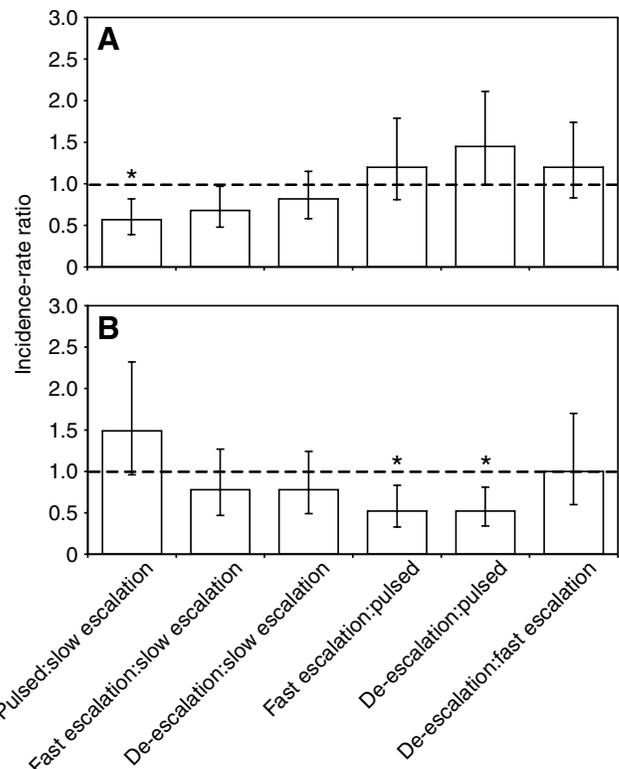


Fig. 3. Experiment 2. Incidence-rate ratios ( $\pm 95\%$  confidence interval) of pair-wise comparisons between treatments. (A) Attack (critical  $P$ -value=0.008) and (B) gular expansion (critical  $P$ -value=0.017). \*Significant difference between the responses for the two treatments in each pair.

( $Z=-2.81$ ,  $N=26$ ,  $P=0.005$ ). In this experiment, which had fewer treatments, we did not detect effects for presentation order on any of our response measures, although gular expansion and attack approached significance (Table 4).

### Discussion

When confronted with a simulated competitor, male Jacky dragons selected their response intensity based on moment-to-moment variation in display rate. Hence the results demonstrate that the timing of push-up/body-rocks within a series is used to assess opponents, independent of any other cues or signals. Aggressive and exploratory responses were particularly sensitive to this aspect of display behaviour; gular expansion, push-up/body-rocks, attacks and locomotion all varied significantly between treatments.

In Experiment 1 the two aggressive displays (gular expansion and push-up/body-rocks), provide the clearest response pattern with which to compare our predictions. The 'pulsed', 'block' and 'initial' sequences suppressed the overall rate of aggressive displays, relative to the 'constant' and 'spike' sequences. In the case of gular expansion, all of these differences were highly significant, whereas for push-up/body-rocks, two differences were significant and another two approached significance (Fig. 2B,C). The most obvious distinction between these stimuli is the 'concentration' (i.e. temporal clumping) of push-up/body-rocks. In the 'pulsed' and 'block' sequences, displays were arranged in fewer bouts, each containing more push-up/body-rocks (5 bouts with 6 PUBR/bout). In contrast, displays were more dispersed in the 'constant' and 'spike' sequences (10 bouts with 3 PUBR/bout).

These results are consistent with the idea that lizards were averaging the number of push-up/body-rocks per bout, such that highly concentrated sequences were perceived as more threatening. Note that the significant main effects for sequence type (Table 2) immediately exclude the cumulative assessment of push-up/body-rocks as a possibility; if subjects had simply been counting displays, then there would be no differences among the treatments. Similarly, responses were not influenced by the maximum number of push-up/body-rocks in any single bout. This allows us also to reject a 'best-so-far' mechanism.

Our model of assessment processes can be further refined by examining the period in which a decision was made. The 'block' sequence only showed displays in the first 5 min, yet responses differed from those to several other sequences (Fig. 3C). This implicates the first half of the display series as a likely assessment window. In addition, the 'initial' sequence, which averaged 3.4 PUBR/bout over this period, triggered significantly lower levels of gular expansion than the 'constant' treatment. This pattern of responses is precisely that which would be expected if opponent assessment were based upon the concentration of displays within the first few minutes of an interaction.

Results obtained in Experiment 2 lend qualified support to the idea of rapid assessment. Here, the rate of gular expansion was significantly lower in both the 'fast escalation' and 'de-escalation' treatments than in the 'pulsed' treatment. Again, the concentration of displays in the first half of the sequence provides the key to understanding these differences. Push-up/body-rocks were highly concentrated in the first 5 min of the

'fast escalation' and 'de-escalation' sequences (7.5 and 10.5 PUBR/bout, respectively). In contrast, the 'pulsed' sequence had a much lower level of display concentration during this period (6 PUBR/bout). The only anomaly in the pattern of responses is the lack of similar differences between the 'slow-escalation' sequence and the 'fast-escalation' and 'de-escalation' sequences. It is possible that effect of the initially low display concentration (4.5 PUBR/bout) was eclipsed by subsequent increases in concentration.

The brief assessment window suggested by both experiments may in part reflect characteristics of the simulated interaction. Resident males viewed an intruder that was close, well lit and unobscured by vegetation. Errors associated with signal perception will hence have been minimised, relative to a natural signal exchange. Such conditions are optimal for rapid assessment. Playback studies in which signal perception was complicated by having the stimulus conspecific obscured to varying degrees and presented at greater distances would provide a direct test of the extent to which increased error rate prolongs assessment.

The pattern of results obtained in the present study implies an averaging mechanism. As has already been argued (Payne and Pagel, 1997), the averaging of actions to better estimate signal characteristics is evidence of sequential assessment (Enquist and Leimar, 1983). This model is based on the idea that information transfer is inherently error-prone, such that repeated actions provide a more accurate estimate of fighting ability. Models of the relation between relative fighting ability, contest structure and the probability of winning necessarily fall outside of the scope of the present study, because the behaviour of one contestant was controlled and the interaction was unresolved. Note, however, that most lizard contest studies designed to evaluate such models have provided support for them (Earley et al., 2002; Jenssen et al., 2005; Lopez and Martin, 2001; Molina-Borja et al., 1998; Olsson, 1992).

Of particular relevance to our findings is the assumption that sequential assessment requires signal reliability to be enforced by physical constraints (Enquist and Leimar, 1983). A commonly used illustration of this type of signalling is the display behaviour of cichlid fish (Enquist and Leimar, 1983). A competitor's size is revealed by lateral displays, its weight by tail beating, and its strength by mouth wrestling. Small, light, weak, fish simply cannot perform these signals at the same level as large, heavy, strong ones (Hurd and Enquist, 2005). The responses of Jacky dragons were consistent with the sequential assessment model, so we anticipate that the same logic is likely to apply to push-up display sequences: only a subset of individuals within the population should be capable of consistently performing highly concentrated display bouts. Short-term temporal structure of display sequences might thus reflect individual variation in a physical attribute such as strength. Assessing an opponent's strength is likely to be important, as muscle capacity (i.e. bite force) has been found to predict fight outcome in several lizard species (Husak et al., 2006; Huyghe et al., 2005; Lailvaux et al., 2004).

Current knowledge of lizard displays is not sufficient to identify the physical constraints on short-term display rate, as this signalling parameter has not been examined in physiological studies. The relationship between overall display

rate in a contest situation and endurance is not strong, at least in the iguanian lizard species that have been tested in laboratory studies (Brandt, 2003; Osborne, 2005). For example, halving the endurance capacity of male side-blotched lizards *Uta stansburiana* significantly reduced the duration of lateral compression, but not the number of push-ups (Brandt, 2003). If this is a lineage-wide phenomenon, it may help to explain why the Jacky dragons in our study did not rely on the cumulative number of displays for opponent assessment. Perry et al. (Perry et al., 2004) did report that field counts of 'broadcast' displays performed by male crested anoles *Anolis cristatellus* predicted both success in staged fights and endurance levels. Broadcast displays are performed spontaneously, in the absence of a visible opponent, and are therefore probably designed to communicate over longer distances (DeCourcy and Janssen, 1994). Hence it is possible that assessment strategies might be distance-dependent, in such a way that intra-bout characteristics only function as a useful predictor of fighting ability in close-range encounters.

Most of the behavioural responses in Experiment 1 varied in a curvilinear fashion over successive test days. This pattern, which was also observed in a previous video playback study involving Jacky dragons (Ord and Evans, 2003), probably reflects the competing forces of sensitisation and habituation. Interactions necessarily ended with the intruder disappearing and the residents remaining in their familiar pen. The perceived threat posed by the video lizard may have therefore decreased over time, resulting in elevated response levels. Conversely, each stimulus sequence depicted the same individual, performing the same displays in the same order. The potential for responses to decrease due to habituation was hence probably quite high (Van Dyk and Evans, 2007). Order effects are a common feature of video playback studies (Burford et al., 2000) and of the repeated presentation of stimuli more generally (Peeke and Peeke, 1973). Experimenters should use caution when determining presentation order, so as to avoid systematic biases (Rosenthal, 1999). We selected presentation order at random and included it as a factor in our analyses to prevent it from obscuring our results (see Materials and methods).

Competing animals of many taxa are sensitive to the temporal characteristics of repeated aggressive signals (see Introduction). Although there has been much previous work with staged contests and signal playback (Adhikerana and Slater, 1993; Briffa and Elwood, 2000a; Briffa and Elwood, 2000b; Burmeister et al., 2002; Clutton-Brock and Albon, 1979; Ord and Evans, 2003), we believe that the present study is the first experimental characterisation of the mechanism underlying the assessment of a repeated threat display in any modality. Understanding the way in which receivers perceive signals and integrate information over time provides a new insight into the 'rules' governing aggressive interactions and the processes that constrain signal reliability.

We thank K. Woo for assistance with animal capture and husbandry, and W. McTegg for additional support in animal care. We also thank two anonymous reviewers who provided valuable feedback on a draft of this manuscript. This study was approved by the Macquarie University Animal Ethics

Committee (approval no. 2003/014). Collection and housing of animals complied with NSW National Parks and Wildlife Service guidelines under permit S11024. D.V.D. was supported by a Research Award in Areas and Centres of Excellence from Macquarie University. C.S.E. was supported by grants from the Australian Research Council and Macquarie University. Research was conducted in partial fulfilment of the requirements for a doctoral thesis for D.V.D. at Macquarie University.

## References

- Adhikerana, A. S. and Slater, P. J. B. (1993). Singing interactions in coal tits, *Parus ater*: an experimental approach. *Anim. Behav.* **46**, 1205-1211.
- Bee, M. A., Perrill, S. A. and Owen, P. C. (1999). Size assessment in simulated territorial encounters between male green frogs (*Rana clamitans*). *Behav. Ecol. Sociobiol.* **45**, 177-184.
- Benjamini, Y. and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B* **57**, 289-300.
- Brandt, Y. (2003). Lizard threat display handicaps endurance. *Proc. R. Soc. Lond. B Biol. Sci.* **270**, 1061-1068.
- Briffa, M. and Elwood, R. W. (2000a). Analysis of the finescale timing of repeated signals: does shell rapping in hermit crabs signal stamina? *Anim. Behav.* **59**, 159-165.
- Briffa, M. and Elwood, R. W. (2000b). Cumulative or sequential assessment during hermit crab shell fights: effects of oxygen on decision rules. *Proc. R. Soc. Lond. B Biol. Sci.* **267**, 2445-2452.
- Burford, F. R. L., McGregor, P. K. and Oliveira, R. F. (2000). Response of fiddler crabs (*Uca tangeri*) to video playback in the field. *Acta Ethol.* **3**, 55-59.
- Burmeister, S. S., Ophir, A. G., Ryan, M. J. and Wilczynski, W. (2002). Information transfer during cricket frog contests. *Anim. Behav.* **64**, 715-725.
- Carpenter, C. C. (1962). Patterns of behavior in two Oklahoma lizards. *Am. Midl. Nat.* **67**, 132-151.
- Carpenter, C. C. (1965). Aggression and social structure in iguanid lizards. In *Lizard Ecology: A Symposium* (ed. W. W. Milstead), pp. 87-105. Columbia: University of Missouri Press.
- Carpenter, C. C. and Ferguson, G. W. (1977). Variation and evolution of stereotyped behavior in reptiles. In *Biology of the Reptilia (Ecology and Behavior A, Vol. 7)* (ed. C. Gans and D. W. Tinkle), pp. 335-554. London: Academic Press.
- Carpenter, C. C., Badham, J. A. and Kimble, B. (1970). Behavior patterns of three species of *Amphibolurus* (Agamidae). *Copeia* **1970**, 497-505.
- Clark, D. L. and Uetz, G. W. (1992). Morph-independent mate selection in a dimorphic jumping spider: demonstration of movement bias in female choice using video-controlled courtship behaviour. *Anim. Behav.* **43**, 247-254.
- Clutton-Brock, T. and Albon, S. D. (1979). The roaring of red deer and the evolution of honest advertisement. *Behaviour* **69**, 145-169.
- Davies, N. B. and Halliday, T. R. (1978). Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature* **274**, 683-685.
- DeCourcy, K. R. and Janssen, T. A. (1994). Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. *Anim. Behav.* **47**, 251-262.
- Deslippe, R. J., M'Closkey, R. T., Dajczak, S. P. and Szpak, C. P. (1990). A quantitative study of the social behavior of tree lizards, *Urosaurus ornatus*. *J. Herpetol.* **24**, 337-341.
- Earley, R. L., Attum, O. and Eason, P. (2002). Varanid combat: perspectives from game theory. *Amphib. Reptil.* **23**, 469-485.
- Enquist, M. (1985). Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Anim. Behav.* **33**, 1152-1161.
- Enquist, M. and Leimar, O. (1983). Evolution of fighting behaviour: decision rules and assessment of relative strength. *J. Theor. Biol.* **102**, 387-410.
- Evans, C. S. and Marler, P. (1991). On the use of video images as social stimuli in birds: audience effects on alarm calling. *Anim. Behav.* **41**, 17-26.
- Falls, J. B. (1963). Properties of birdsong eliciting responses from territorial males. *Proc. Int. Ornithol. Cong.* **13**, 259-273.
- Garcia, L. V. (2004). Escaping the Bonferroni iron claw in ecological studies. *Oikos* **105**, 657-663.
- Gardner, W., Mulvey, E. P. and Shaw, E. C. (1995). Regression analyses of counts and rates: poisson, overdispersed poisson, and negative binomial models. *Psychol. Bull.* **118**, 392-404.
- Göth, A. and Evans, C. S. (2004). Social responses without early experience:

- Australian brush-turkey chicks use specific visual cues to aggregate with conspecifics. *J. Exp. Biol.* **207**, 2199-2208.
- Hover, E. L. and Janssen, T. A.** (1976). Descriptive analysis and social correlates of agonistic displays of *Anolis limifrons* (Sauria, Iguanidae). *Behaviour* **58**, 173-191.
- Hunt, S., Cuthill, I. C., Bennett, A. T. D., Church, S. C. and Partridge, J. C.** (2001). Is the ultraviolet waveband a special communication channel in avian mate choice? *J. Exp. Biol.* **204**, 2499-2507.
- Hurd, P. L.** (2006). Resource holding potential, subjective resource value, and game theoretical models of aggressiveness signalling. *J. Theor. Biol.* **241**, 639-648.
- Hurd, P. L. and Enquist, M.** (2005). A strategic taxonomy of biological communication. *Anim. Behav.* **70**, 1155-1170.
- Husak, J. F., Lappin, A. K., Fox, S. F. and Lemos-Espinal, J. A.** (2006). Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus*). *Copeia* **2006**, 301-306.
- Huyghe, K. B., Vanhooydonck, H., Scheers, M., Molina-Borja, M. and Van Damme, R.** (2005). Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Funct. Ecol.* **19**, 800-807.
- Janssen, T. A., DeCourcy, K. R. and Congdon, J. D.** (2005). Assessment in contests of male lizards (*Anolis carolinensis*): how should smaller males respond when size matters? *Anim. Behav.* **69**, 1325-1336.
- Lailvaux, S. P., Herrel, A., Vanhooydonck, B., Meyers, J. J. and Irschick, D. J.** (2004). Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proc. R. Soc. Lond. B Biol. Sci.* **271**, 2501-2508.
- Leal, M.** (1999). Honest signalling during prey-predator interactions in the lizard *Anolis cristatellus*. *Anim. Behav.* **58**, 521-526.
- Lopez, P. and Martin, J.** (2001). Fighting rules and rival recognition reduce costs of aggression in male lizards, *Podarcis hispanica*. *Behav. Ecol. Sociobiol.* **49**, 111-116.
- Lovern, M. B., Janssen, T. A., Orrell, K. S. and Tuchak, T.** (1999). Comparisons of temporal display structure across contexts and populations in male *Anolis carolinensis*: signal stability or lability? *Herpetologica* **55**, 222-234.
- Macedonia, J. M. and Clark, D. L.** (2003). Headbob display structure in the naturalized *Anolis* lizards of Bermuda: sex, context and population effects. *J. Herpetol.* **37**, 266-276.
- Martins, E. P.** (1993). Contextual use of the push-up display by the sagebrush lizard, *Sceloporus graciosus*. *Anim. Behav.* **45**, 25-36.
- Martins, E. P., Ord, T. J. and Davenport, S. W.** (2005). Combining motions into complex displays: playback with a robotic lizard. *Behav. Ecol. Sociobiol.* **58**, 351-360.
- Maynard Smith, J.** (1974). The theory of games and the evolution of animal conflict. *J. Theor. Biol.* **47**, 209-221.
- McMann, S.** (2000). Effects of residence time on displays during territory establishment in a lizard. *Anim. Behav.* **59**, 513-522.
- Molina-Borja, M., Padron-Fumero, M. and Alfonso-Martin, T.** (1998). Morphological and behavioural traits affecting the intensity and outcomes of male contests in *Gallotia galloti galloti* (Family Lacertidae). *Ethology* **104**, 314-322.
- Molles, L. E. and Vehrencamp, S. L.** (2001). Songbird cheaters pay a retaliation cost: evidence for auditory conventional signals. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 2013-2019.
- Nakagawa, S.** (2004). A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behav. Ecol.* **15**, 1044-1045.
- Olsson, M.** (1992). Contest success in relation to size and residency in male sand lizards, *Lacerta agilis*. *Anim. Behav.* **44**, 386-388.
- Olsson, M.** (1994). Nuptial coloration in the sand lizard, *Lacerta agilis*: an intrasexually selected cue to fighting ability. *Anim. Behav.* **48**, 607-613.
- Ord, T. J.** (2001). The evolution and function of visual communication in lizards. PhD thesis, Macquarie University, Sydney, Australia.
- Ord, T. J. and Evans, C. S.** (2002). Interactive video playback and opponent assessment in lizards. *Behav. Proc.* **59**, 55-65.
- Ord, T. J. and Evans, C. S.** (2003). Display rate and opponent assessment in the Jacky dragon (*Amphibolurus muricatus*): an experimental analysis. *Behaviour* **140**, 1495-1508.
- Ord, T. J., Blumstein, D. T. and Evans, C. S.** (2001). Intrasexual selection predicts the evolution of signal complexity in lizards. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 737-744.
- Ord, T. J., Peters, R. A., Evans, C. S. and Taylor, A. J.** (2002). Digital video playback and visual communication in lizards. *Anim. Behav.* **63**, 879-890.
- Orrell, K. S. and Janssen, T. A.** (2003). Heterosexual signalling by the lizard *Anolis carolinensis*, with intersexual comparisons across contexts. *Behaviour* **140**, 603-634.
- Osborne, L.** (2005). Information content of male agonistic displays in the territorial tawny dragon (*Ctenophorus decresii*). *J. Ethol.* **23**, 189-197.
- Parker, G. A.** (1974). Assessment strategy and the evolution of fighting behaviour. *J. Theor. Biol.* **47**, 223-243.
- Payne, R. J. H.** (1998). Gradually escalating fights and displays: the cumulative assessment model. *Anim. Behav.* **56**, 651-662.
- Payne, R. J. H. and Pagel, M.** (1996). When is false modesty a false economy? An optimality model of escalating signals. *Proc. R. Soc. Lond. B Biol. Sci.* **263**, 1545-1550.
- Payne, R. J. H. and Pagel, M.** (1997). Why do animals repeat displays? *Anim. Behav.* **54**, 109-119.
- Peeke, H. V. S. and Peeke, S. C.** (1973). Habituation in fish with special reference to intraspecific aggressive behaviour. In *Habituation*. Vol. I (ed. H. S. V. Peeke and M. J. Herz), pp. 59-83. New York: Academic Press.
- Perry, G., LeVering, K., Girard, I. and Garland, T.** (2004). Locomotor performance and social dominance in male *Anolis cristatellus*. *Anim. Behav.* **67**, 37-47.
- Peters, R. A. and Evans, C. S.** (2003). Introductory tail-flick of the Jacky dragon visual display: signal efficacy depends upon duration. *J. Exp. Biol.* **206**, 4293-4307.
- Peters, R. A. and Ord, T. J.** (2003). Display response of the Jacky dragon, *Amphibolurus muricatus* (Lacertilia: Agamidae), to intruders: a semi-markovian process. *Aust. Ecol.* **28**, 499-506.
- Prieto, A. A. and Ryan, M. J.** (1978). Some observations of the social behavior of the Arizona chuckwalla, *Sauromalus obesus tumidus* (Reptilia, Lacertilia, Iguanidae). *J. Herpetol.* **12**, 327-336.
- Qvarnstrom, A.** (1997). Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher. *Proc. R. Soc. Lond. B Biol. Sci.* **264**, 1225-1231.
- Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W. T. and Clutton-Brock, T.** (2005). Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proc. R. Soc. Lond. B Biol. Sci.* **272**, 941-947.
- Ridout, M., Demetrio, C. G. B. and Hinde, J.** (1998). Models for count data with many zeros. In *Proceedings of the XIXth International Biometric Conference*, pp. 179-192.
- Rosenthal, G. G.** (1999). Using video playback to study sexual communication. *Environ. Biol. Fishes* **56**, 307-316.
- Simpson, M. J. A.** (1968). The display of the Siamese fighting fish (*Betta splendens*). *Anim. Behav. Monogr.* **1**, 1-73.
- Sokal, R. R. and Rohlf, F. J.** (1995). *Biometry*. New York: W. H. Freeman.
- Stamps, J. A.** (1977). Social behavior and spacing patterns in lizards. In *Biology of the Reptilia (Ecology and Behavior A, Vol. 7)* (ed. C. Gans and D. W. Tinkle), pp. 265-334. London: Academic Press.
- Van Dyk, D. A. and Evans, C. S.** (2007). Familiar-unfamiliar discrimination based on visual cues in the jacky dragon, *Amphibolurus muricatus*. *Anim. Behav.* **74**, 33-44.
- Vehrencamp, S. L.** (2000). Handicap, index, and conventional signal elements of bird song. In *Animal Signals: Signalling and Signal Design in Animal Communication* (ed. Y. Espmark, T. Amundsen and G. Rosenqvist), pp. 277-300. Trondheim: Tapir Academic Press.
- Veiga, J. P.** (1993). Badge size, phenotypic quality, and reproductive success in the House sparrow: a study on honest advertisement. *Evolution* **47**, 1161-1170.
- Verhoeven, K. J. F., Simonsen, K. L. and McIntyre, L. M.** (2005). Implementing false discovery rate control: increasing your power. *Oikos* **108**, 643-647.
- Zahavi, A. and Zahavi, A.** (1997). *The Handicap Principle. A Missing Piece of Darwin's Puzzle*. New York: Oxford University Press.