Opponent assessment in lizards: examining the effect of aggressive and submissive signals

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During conflict, males often assess their opponent's fighting ability and motivation via dynamic signals. We conducted an interactive video playback study using male Jacky dragons, *Amphibolurus muricatus*, to determine which signalling strategy was the most effective at deterring aggression and eliciting submission. A 3D computer-animated lizard was used to present aggressive signals (push-up displays) and submissive ones (slow arm-waves). This approach reproduced natural display motor patterns precisely while controlling variation in morphology. Treatments all commenced with the stimulus lizard producing bouts of push-ups, but then diverged after the subject lizard's responses, according to predetermined rules. Lizards attacked the stimulus more frequently when it responded to submission with slow arm-waves, revealing that their behavior during a contest is sensitive to social contingencies. Individuals that signal submission without retreating are likely to incur a receiver retaliation cost. In addition, assessment processes are surprisingly sophisticated, involving the monitoring of both an index signal (push-ups) and a conventional one (slow arm-waves) during a single interaction. *Key words:* Amphibolurus, interactive playback, signalling, submissive display, threat display. *[Behav Ecol 19:895–901 (2008)]*

Animals competing for access to limited resources run the risk of receiving an injurious or fatal attack (Clutton-Brock et al. 1979; Enquist and Leimar 1990). Fighting can also entail substantial energy expenditure and increased exposure to predators (Riechert 1988; Hack 1997; Brick 1998). Such costs have driven the evolution of strategies for resolving disputes without resorting to physical combat (Maynard Smith and Price 1973). One widespread strategy is the signalling of fighting ability and aggressive motivation (Adamo and Hanlon 1996; Elwood and Briffa 2001; Kotiaho et al. 2004). It is well established that signal structure can be subject to physical or energetic constraints. Signalling can also involve an element of strategic choice based on individual willingness to bear production costs and/or to risk retaliation by receivers (Hasson 1997; Hurd and Enquist 2005).

Fighting ability and motivation can vary over short time periods. Under these conditions, dynamic signals should be more reliable indicators of an individual's current state than static ones. Our understanding of the relationship between the structure and information content of dynamic signals relies almost exclusively on acoustic playback experiments. A classic example is provided by the relation between the dominant frequency of anuran calls and body size, which provides a potential assessment cue (Davies and Halliday 1978; Arak 1983; Robertson 1986). By varying the dominant frequency of playback calls, it has been shown that this structural property influences the aggressive behavior of rival males (Davies and Halliday 1978; Arak 1983; Robertson 1986; Given 1987; Wagner 1989).

Similarly, insights into the function of strategic signalling come predominantly from acoustic playback involving songbirds. For example, the decision to match a rival's shared song type appears to serve as a graded signal of aggressive intent (Krebs et al. 1981; Beecher et al. 1996). The most compelling evidence for this idea comes from interactive playback experiments in which the pattern of song matching was systematically manipulated (Burt et al. 2001; Molles and Vehrencamp 2001).

Graded signals enable individuals to escalate and deescalate interactions by varying a single parameter. An additional level of sophistication can be achieved by switching between structurally discrete signals. Many species have evolved distinctive submissive signals that provide information about the sender's nonaggressive intentions and function to reduce the likelihood of being attacked. Such signals are widespread among animals that benefit from maintaining close proximity with potential rivals. For example, social primates employ a range of postures, gestures, and facial expressions to appease dominant individuals (de Waal 1986; Liebal et al. 2004; Setchell and Wickings 2005). Despite the importance of such signals in many systems, the influence of submissive strategies on opponent behavior has rarely been tested experimentally.

The visual displays used by iguanian lizards to mediate social interactions have long been the focus of studies into signal function (Ord et al. 2001). Exchanges of aggressive displays between males typically involve vertical head bobs produced by stereotyped movements of the neck and/or limbs (Carpenter 1965; Jenssen 1977). Compared with the extensive literature on iguanian threat displays, evidence for the use of specific signals to communicate submission is limited. Subordinate individuals of 3 *Anolis* species (*Anolis carolinensis, Anolis sagrei,* and *Anolis aeneus*) have been observed performing sets of rapid vertical head movements called multibobs or nods (Stamps and Barlow 1973; Crews 1975; Tokarz 1985). Similarly, Martins and Lacy (2004) have described a pattern of head-bob displays performed by iguanas (*Cyclura carinata*), which is distinctive to an appeasement context.

The Australian Jacky dragon, *Amphibolurus muricatus*, has a complex display repertoire, making it an ideal subject for investigating the effect of different signalling strategies on opponent behavior. Males perform a highly stereotyped push-up display during interactions with both males and females and in the apparent absence of conspecifics (Carpenter et al. 1970). These displays consist of a backward and forward

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forelimb movement (fast arm-wave) followed by a rapid head raise (push-up) and dip (body-rock) (Peters and Evans 2003). Displays can be modified with postural changes (e.g., lateral compression and gular expansion) and an introductory component (tail-flicks: Peters and Evans 2003). Video playback studies involving males have demonstrated that the distribution of push-up displays over time plays a role in opponent assessment (Ord and Evans 2003; Van Dyk et al. 2007).

Jacky dragons produce 2 other displays: forelimb circumduction (slow arm-waves) and vertical head movements using the neck (slow head-bows). Carpenter et al. (1970) first described these displays in captive lizards and suggested that they serve a submissive function because they were only produced by subordinates. This inference has recently been corroborated by analysis of interactions between males (6 cohorts of 4) in a large (234 m^2) outdoor enclosure (Van Dyk D, unpublished data). Here, subordinate males produced much higher rates of slow arm-waves during intrasexual interactions than dominant males (subordinates: 1.5 slow arm-waves per min; dominants: 0.07 slow arm-waves per min). The behavior of males during video playback further supports this submissive function, with more slow arm-waves being elicited by an opponent which performed high rates of push-up displays compared with one which produced low rates (Ord et al. 2002).

In the present study, we explored the influence of variation in signalling strategy on opponent behavior. Strategies were defined by both the type of signal employed (push-ups and/or slow arm-waves) and the social contingencies governing signal exchange (i.e., responses to aggression and submission). We achieved this by presenting male Jacky dragons with a life-sized digital video conspecific, the behavior of which changed throughout the interaction according to the type of response evoked. In particular, we addressed the question: which signalling strategies are most effective at reducing aggression and increasing submission?

There were 5 interactive video playback treatments. Each of these began with the stimulus lizard performing push-up displays, but they then differed with respect to the rules controlling subsequent display behavior (Table 1). First, we created a "control" treatment in which the simulated opponent responded with chemosensory behavior (substrate licks). The display treatments were inspired by the classic "Hawk," "Dove," and "Retaliator" models of contest strategy (Maynard Smith 1982). We note that this is an inexact parallel because contests were not resolved. "Aggressive" opponents responded to all subject behavior (attacks, push-ups, and slow arm-waves) with push-up displays. We predicted that this treatment would suppress aggressive responses and elevate submissive ones relative to the control treatment. "Submissive" opponents invariably responded with slow arm-waves. We predicted that this would also reduce aggressive responses but differ from the aggressive treatment by reducing submissive responses as well. "Matching" opponents responded to aggression (attacks and push-ups) with push-ups and to sub-

mission (slow arm-waves) with slow arm-waves of their own. The effect of this "mixed" strategy should reflect the more influential social contingency. For example, if responses to submission were predominantly driving the interaction, responses to the matching treatment should mimic those to the submissive treatment. An additional mixed treatment, "opposite," was added to complete the 2 × 2 matrix of logical possibilities. Here, aggression triggered slow arm-waves and submission triggered push-ups. If social contingencies per se are important for determining signalling response, then responses to this treatment should differ from those to the matching treatment.

MATERIALS AND METHODS

Subjects

Subjects were 32 adult male Jacky dragons caught between 2003 and 2005 in bushland around Sydney, Australia (Botany Bay, Lane Cove, and Royal National Parks). Lizards were caught by noosing with nylon monofilament line, a procedure that never resulted in injury. Lizards ranged in length from 75 to 98 mm snout-vent length (SVL) and in weight from 15.5 to 33.5 g.

Indoor housing has recently been described in detail (Van Dyk and Evans 2007). Briefly, it consisted of individual pens (64 cm wide × 75 cm long × 120 cm high) with opaque plastic sheeting on 3 sides to prevent visual contact with neighboring lizards and clear perspex on the remaining side to allow presentation of visual stimuli and recording of responses. Pens had a sand substrate and contained branches and native vegetation. Environmental systems in the rooms were programmed to generate summer conditions with a 14:10 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 behavioral thermoregulation and UV lamps (300 W Osram Ultra-Vitalux) were provided to prevent vitamin deficiency. Lizards were fed twice weekly with live crickets and had access to water ad lib. All lizards were healthy throughout the experiment and either retained for further studies or released at the location of capture.

Stimulus sequences

Video playback has now been widely adopted, particularly for studies of dynamic visual signals, but there have been few previous uses of interactive techniques (although see Ord and Evans 2002). Making the simulated opponent responsive to subject behavior introduced several challenges, the most critical of which was the maintenance of continuity between successive video clips (Rosenthal 2000). We overcame this constraint by using laser scanning and 3D computer modelling to construct an artificial lizard, which allowed us to define all aspects of appearance and posture. The model was then animated to match precisely the display behavior of live lizards.

We recorded video footage of lizards performing push-up displays and substrate licks using the procedure detailed by Ord et al. (2002). Briefly, the home pens were modified by inserting a standard wooden perch and a blue cardboard background. Recordings were made with a digital video camcorder (Canon XL1, optical resolution 625 lines, shutter speed 1/250 s, F8) on mini-DV tape (Sony DVM60PRO). Focal length was adjusted to ensure that the lizard appeared life sized on the video monitor subsequently used for playbacks (Sony Trinitron Color Video Monitor PVM-14M2A). Illumination was provided by an 800-W photographic P2/11 tungsten–halogen lamp. A small terrarium containing a male lizard was placed in front of the pen to evoke push-up displays from the lizard being filmed.

Table 1

Interactive rules controlling the behavior of the stimulus lizard

Treatment	Subject response	
	Aggressive (attack or push-up)	Submissive (slow arm-wave)
Control	Substrate lick	Substrate lick
Aggressive	Push-up	Push-up
Submissive	Slow arm-wave	Slow arm-wave
Matching	Push-up	Slow arm-wave
Opposite	Slow arm-wave	Push-up

This procedure effectively generated aggressive behavior, but not submissive displays. To film slow arm-waves, we placed the lizard in a glass aquarium (30 cm wide × 30 cm long × 60 cm high) containing the wooden perch and background used previously. Recordings were made with 2 digital video camcorders (Canon MV650i) trained apart so that usable footage would be obtained whatever the orientation of the lizard. We then played back sequences of a lizard performing aggressive push-up displays on a video monitor (Sony Trinitron Color Video Monitor PVM-14M2A) placed adjacent to the subject.

To animate Jacky dragon displays, we first obtained a taxidermic specimen (102 mm SVL) and then made a 3D laser scan (see Supplementary Material). The resulting polygon mesh was imported into a modelling program (LightWave 3D v8.3, NewTek Inc., San Antonio, TX) running on a Power Mac G5 (Apple Computer Inc., Cupertino, CA). Realistic skin texture was acquired by photographing a live lizard (93 mm SVL) with a digital SLR camera (Canon EOS 300D). We defined the model's range of movement by creating 61 virtual "bones" and fixing each of these to a particular region of the body (see Peters and Evans 2003).

We selected 5 push-up displays from the same lizard to provide the template for the movement of our 3D model. In each display, the lizard was perpendicular to the camera and did not change his orientation. All displays commenced with tail-flicks, followed by a rapid arm-wave and 2 push-up/body-rocks. A different lizard provided the 5 slow arm-wave displays. Each display consisted of a single circumduction of the forelimb, starting with the limb touching the substrate. The 2 substrate lick motor patterns were based on a third lizard. These involved lowering the head to the substrate and raising it again.

Note that our selection of playback models does not involve pseudoreplication because the domain of interest is signalling strategy rather than display structure or other individual characteristics, and each subject received unique playback sequences determined by their response in each treatment. This design maximizes statistical power, although at the cost of not permitting tests for possible interactions between signalling strategy and other opponent attributes. Such questions would be logical extensions but are outside the scope of the present study.

We animated the completed model lizard by "rotoscoping" (Rosenthal 2000; Peters and Evans 2003, 2007). First, we adjusted the position of the virtual camera in LightWave 3D so that it corresponded to the focal length and orientation of the original video camera. Then we inserted a single frame from video footage of a live lizard in the background, manipulated the model lizard's bones to superimpose it precisely over the video lizard, and used a "key frame" to save these adjustments (Figure 1). We then advanced one frame in the animation time line, inserted the next frame in the background, and repeated the process. This procedure produced an animated sequence with the same motion characteristics as the original video lizard (see examples in Supplementary Material). Rapid motor patterns, such as tail-flicks, required a key frame for each video frame (Peters and Evans 2003). Slower motor patterns, such as slow arm-waves, could be reproduced by defining alternate frames and interpolating bone positions between these values.

Prior to rendering a clip, we repositioned the virtual camera so that the animated lizard was the same size as the original taxidermic lizard (102 mm SVL) on the playback monitor and centered on the background frame of an empty perch. The model's postures at the start and finish of each clip were identical. To avoid motion artifacts between clips, we added a standard transition phase (10 s) in which the model moved from its starting posture to the posture in the first frame of the animated motor pattern; a second transition phase at the end
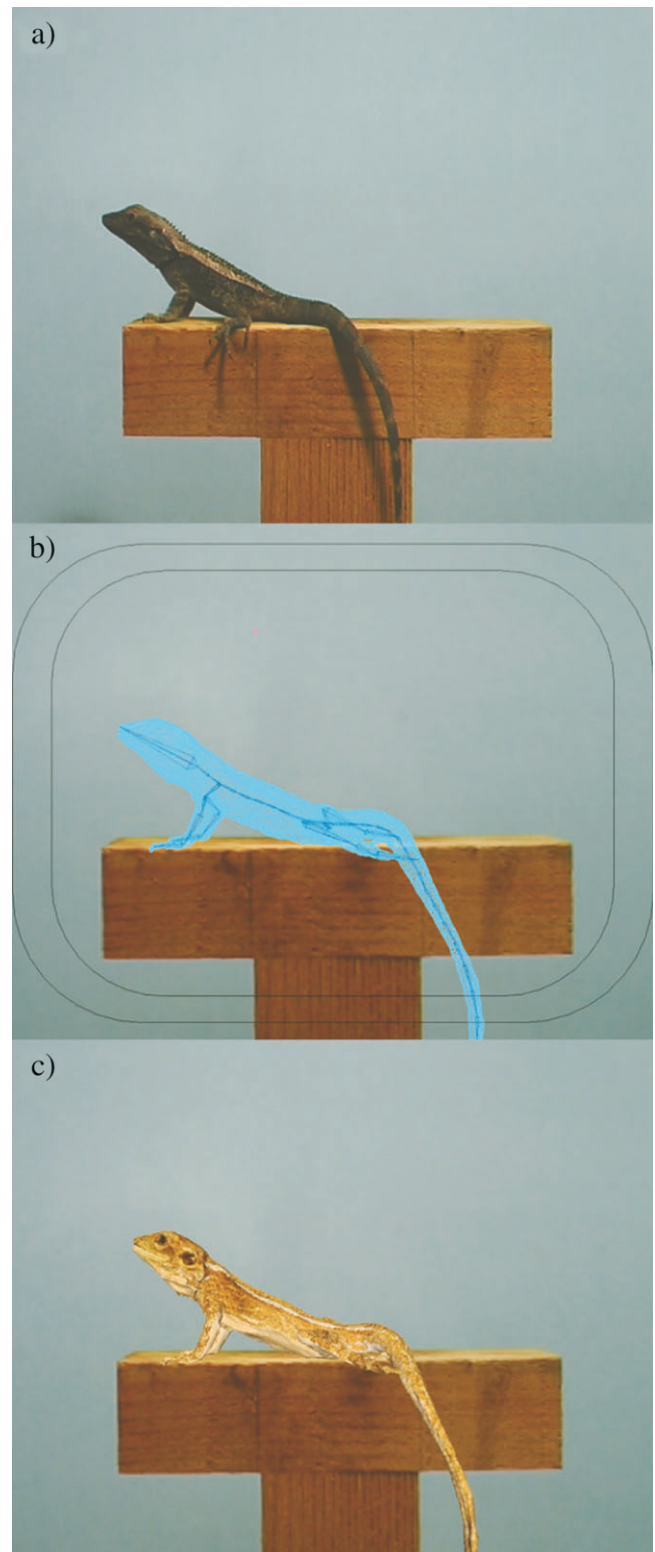

Figure 1
Representative frames of a (a) video lizard, (b) model lizard showing polygon mesh and virtual "bones," and (c) model lizard with skin texture. (See Supplementary Material for stimulus clips.)

returned the model to its starting posture. The total duration of each clip was set at 25 s. We added a top and front light to mimic the lighting conditions of the original video recording

setup. Clips were rendered in the PAL-DV format (576 lines, 25 frames per s) and saved as JPEGs. These were converted to a DV stream using QuickTime player v7 (Apple Computer Inc.). This video format has been used successfully in a series of digital video playback experiments with Jacky dragons (Ord and Evans 2002, 2003; Ord et al. 2002; Peters and Evans 2003, 2007; Carlile et al. 2006; Van Dyk and Evans 2007; Van Dyk et al. 2007).

Animated displays were assembled into playback sequences using video editing software (Final Cut Pro 3, Apple Computer Inc.). Sequences were 15 min long and organized into 1-min blocks. Each block contained a motor pattern clip (25 s), followed by a clip of the lizard basking motionless on the perch (35 s). Push-up display bouts consisted of 2 identical displays, each containing 2 push-up/body-rocks (average duration 4.0 s) separated by a 2.0-s interval. Slow arm-wave bouts contained 4 identical displays (average duration 1.0 s) with no interval. Bouts of substrate licking depicted 2 identical motor patterns (average duration 0.5 s) separated by a 2.0-s interval. The temporal bout structure of display and nondisplay responses fell within the natural range observed under both laboratory and seminatural conditions (Van Dyk D, unpublished data).

We built 12 playback sequences in total (5 push-up, 5 slow arm-wave, and 2 substrate lick). The push-up and slow arm-wave sequences showed a different display bout every minute for the first 5 min. This order was then repeated twice to produce a 15-min sequence. The order of display bouts within the first sequence was chosen at random. In each subsequent sequence, the order was modified by moving the first display bout to the end of the queue. Each sequence thus began with a different display bout (e.g., ABCDE, BCDEA, CDEAB, DEABC, and EABCD). The 2 substrate lick sequences depicted alternating bouts of substrate licks with each sequence commencing with a different bout.

Each subject was randomly assigned a unique order of treatments. We used a different push-up display sequence in each treatment and paired slow arm-wave sequences and push-up sequences so that switches between display types always occurred between the same 2 sequences. The control treatment was slightly different, as only 2 substrate lick sequences were available. Here, subjects were randomly divided into 2 groups, with each group viewing a different sequence.

Interactive playback experiment

Subjects occupied their pens for at least 3 weeks before testing. Testing commenced between 0900 and 1000 h and ran for approximately 4.5 h. Lizards were tested in the same order to maintain a constant intertest interval. We used 6-day break between treatments to minimize carryover effects.

Some of the test equipment was mounted on a trolley, so that it could be positioned in front of each line of pens with minimal disruption. This included the stimulus presentation monitor (Sony PVM-14M2A; resolution >600 lines, screen size 34 cm measured diagonally), a CCTV camera (Panasonic WV-CP240/G) fitted with a wide-angle lens (Panasonic WV-LA210C3), and a second monitor (Panasonic TC-1470Y) repeating the camera signal to function as a viewfinder. Before testing, we calibrated the presentation monitor using PAL standard pluge bars (Final Cut Pro 3.0, Apple Computer Inc.).

The remaining test equipment was concealed at one end of the room and was linked to the mobile presentation system via cables. Playback sequences were stored in an external drive (LaCie 160GB) and played on a computer (Final Cut Pro 3, iMac G3, Apple Computer Inc.). The playback signal passed through an IEEE 1394 "firewire" cable to a digital video converter (Canopus ADVC110) and was then transmitted to the stimulus presentation monitor via an S-video cable. An

S-VHS deck (Sony DVD player/VCR SLV-D910AZ) recorded the subject's responses and sent a signal to a second viewfinder monitor (Panasonic TC-1470Y).

Subjects were familiarized with the experimental apparatus by presenting a 10-min clip of a blank perch on the day before testing began. Each playback session followed the same protocol. The trolley was moved into position and adjusted so that the entire pen was visible on the viewfinder monitor. We then played a 3-min clip of an empty perch. At the end of this period, a sequence of push-up displays was triggered.

We observed subject behavior on the viewfinder monitor and responded to aggressive (attacks and push-up displays) or submissive (slow arm-waves) acts by either advancing to the next clip in the current sequence or switching to a clip in a different sequence according to the social contingency defined by the treatment (Table 1; see examples in Figure 2). Interventions took approximately 1 s, with no break in video signal. Responses were ignored if they occurred within 10 s of a manipulation, thus preventing subjects from completely inhibiting the stimulus lizard's behavior (Ord and Evans 2002). Responses were also ignored if they occurred while the stimulus lizard was performing a display or substrate lick, as a change at this point would have produced unnatural movement. Playback ended after 15 min.

Data analysis

We scored behavioral responses to the stimulus lizard from test session video recordings. The following brief responses were scored as events: push-up/body-rocks, slow arm-waves, bouts of general locomotion, substrate licks, and attacks (attempts to approach the stimulus). We calculated the frequency of each of these behaviors over the 15 min during which the stimulus lizard was visible. Gular expansion could be held for many seconds and was therefore treated as a state; we recorded its duration. Lizards that did not perform a social response (attack, push-up display, and slow arm-wave) in the majority of
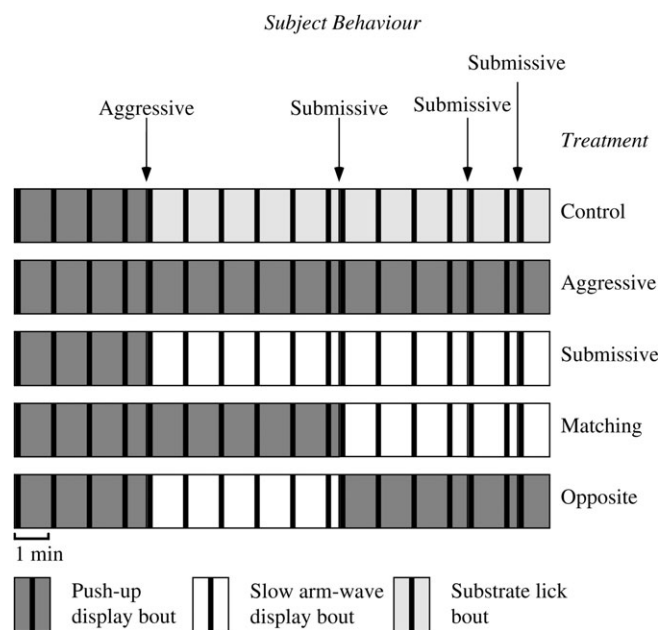

Figure 2
Schematic illustrating the effects of experimentally controlled social contingencies. In this example, the video sequence is that triggered by a subject responding with one aggressive behavior followed by 3 submissive behaviors.

Table 2

Negative binomial regression on response rates in relation to playback treatment and presentation order

Response	Playback treatment		Presentation order	
	Wald χ^2_4	P	Wald χ^2_4	P
Locomotion	11.86	0.0185[*]	45.87	<0.0001[*]
Attack	19.17	0.0007[*]	15.44	0.0039[*]
Gular expansion	3.95	0.4122	5.49	0.2406
Slow arm-wave	3.33	0.50	0.63	0.9596
Substrate lick	4.15	0.3864	25.61	<0.0001[*]

[*] $P \leq 0.05$.

treatments were removed from the analysis. This criterion resulted in 10 subjects being excluded.

Preliminary examination of the data revealed skewed distributions caused by a high proportion of zero counts. The resulting variances were greater than the corresponding means (i.e., overdispersed). An appropriate method for analyzing data with these characteristics is negative binomial regression, a generalization of Poisson regression which accounts for overdispersion (Gardner et al. 1995; Ridout et al. 1998). We used the statistical software package Stata, which calculates negative binomial regression with a modified variance estimate to account for within-subject correlations (StataCorp 2001).

Playback treatment was entered as a dummy-coded explanatory variable in the model to directly examine the effects of varying the rules governing the stimulus lizard's responses. Order of presentation was included as a second explanatory variable (also dummy coded) to account for the potentially obscuring effects of habituation and sensitization. Size is often an important determinant of agonistic behavior. To allow for this, we also added the subject's SVL to the model.

The regression coefficients for the dummy codes and for the SVL variable are interpreted as incidence rate ratios (IRRs), which are similar to the odds ratios of logistic regression. For example, an IRR of 0.5 for a particular comparison means that response rates in the first treatment are 50% lower than those in the second. 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 error (Garcia 2004; Nakagawa 2004; Verhoeven et al. 2005). The overall influence of the explanatory variables was assessed using the Wald test (Sokal and Rohlf 1995).

RESULTS

Playback treatment significantly influenced the overall rates of both locomotion and attack (Table 2). Subjects performed significantly fewer bouts of locomotion in the opposite treatment compared with the submissive and matching treatments (Z-test—opposite: submissive $Z = -3.0$, $N = 22$, $P = 0.003$; opposite: matching $Z = -3.1$, $N = 22$, $P = 0.002$; critical P value = 0.01; Figure 3a). Locomotion was also suppressed in the opposite treatment compared with the aggressive treatment; however, this difference failed to reach statistical significance (opposite: aggressive $Z = -2.22$, $N = 22$, $P = 0.026$; critical P value = 0.01).

The control, aggressive, and opposite treatments all elicited significantly lower rates of attack than the submissive treatment (control: submissive $Z = -2.25$, $N = 22$, $P = 0.024$; aggressive: submissive $Z = -3.19$, $N = 22$, $P = 0.001$; opposite: submissive
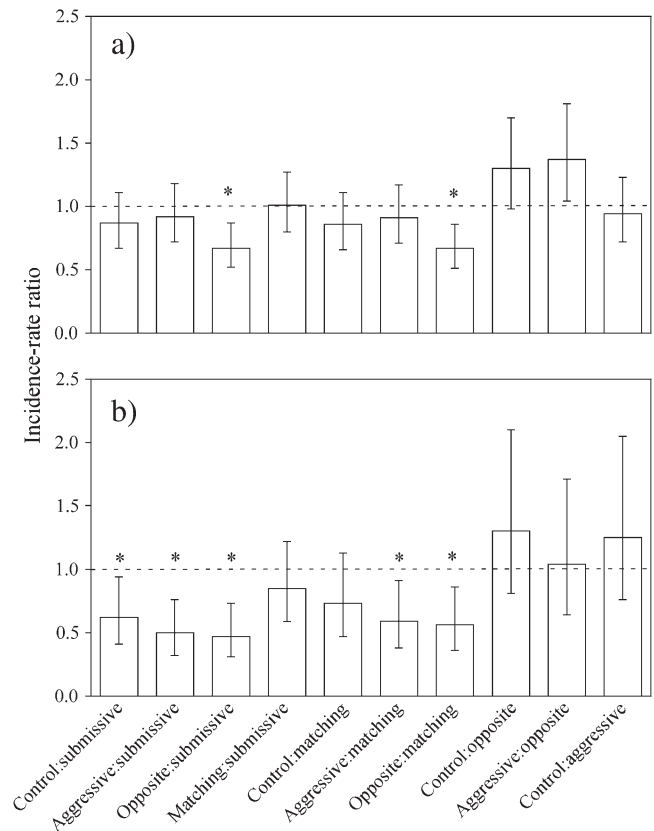

Figure 3
IRRs (±95% CI) of pairwise comparisons between treatments. (a) Locomotion (critical P value = 0.01) and (b) attack (critical P value = 0.025). * Denotes significant difference between the responses for the 2 treatments in each pair.

$Z = -3.44$, $N = 22$, $P = 0.001$; critical P value = 0.025; Figure 3b). Attack rates in the aggressive and opposite treatments were also significantly lower than in the matching treatment (aggressive: matching $Z = -2.4$, $N = 22$, $P = 0.016$; opposite: matching $Z = -2.63$, $N = 22$, $P = 0.008$; critical P value = 0.025).

There was a significant positive relationship between the subject lizard's size and the probability of aggressive response. Both the rate of attack (IRR = 1.04, 95% confidence interval [CI]: 1.0–1.08, $Z = 1.96$, $N = 22$, $P = 0.05$) and the duration of gular expansion covaried with SVL (IRR = 1.16, 95% CI: 1.05–1.29, $Z = 2.87$, $N = 22$, $P = 0.004$). Finally, presentation order had a significant effect on all behavioral responses except gular expansion and slow arm-waves (Table 2).

DISCUSSION

When interacting with a simulated opponent, Jacky dragons modify their behavior in response to different types of agonistic signals (aggressive and submissive) and to the social contingencies governing their production. In particular, the probability of both locomotion and attack varied significantly among treatments. Interactive playback experiments conducted over the last decade have provided strong evidence for such effects in bird song and other systems of acoustic signals (see in the Introduction). We believe this to be the first analogous demonstration for any system of dynamic visual signals.

Although our general prediction that responses to the aggressive and submissive treatments should differ was upheld, our expectation regarding the nature of this difference was not. Specifically, the aggressive treatment failed to suppress

attacks relative to the nonsignalling control treatment, whereas the submissive treatment triggered significantly higher rates of attack. Conversely, the rate of submissive behavior did not vary significantly between these treatments. Our second general prediction was also supported, with subjects responding differently to the matching and opposite treatments. Here, responses to the matching treatment paralleled those to the submissive treatment and responses to the opposite treatment mirrored those to the aggressive treatment. This pattern indicates that the way in which a stimulus male reacted to submissive signals markedly influenced the subsequent aggressive behavior of his live opponent: persisting with push-up displays effectively reduced the rate of attacks compared with switching to slow arm-waves.

The rule governing the stimulus lizard's response to slow arm-waves had a greater impact on subject male behavior than the rule governing responses to attacks and push-ups. This implies that submissive males continued to monitor the behavior of their opponent and were willing to escalate the interaction if his rate of aggressive signalling declined. In the submissive and matching treatments, the stimulus lizard initiated the interaction with aggressive signals but immediately switched to submissive signals at the first occurrence of a submissive response. However, this sudden switch was not accompanied by other typical submissive behavior such as hiding or retreating. It is hence likely that the simulated opponent continued to threaten subjects simply by maintaining his position. Consistent with this, chemosensory behavior in the control treatment was sufficient to evoke aggressive responses. The discrepancy between the video male's highly submissive signals and his continued close proximity may hence have simulated a deceptive use of slow arm-waves. If so, the relative ineffectiveness of the submissive and matching strategies at deterring attacks would be attributable to opponents probing a potentially deceptive rival.

To our knowledge, the possibility that honesty in submissive displays is enforced by receiver retaliation has not previously been raised. The potential benefits of deceptive submission are not as obvious as those obtained from bluffed threats; however, individuals might gain a competitive advantage by continuing to assess their opponent without the cost of aggressive signalling or from launching a surprise attack. Further, experiments in which the signalling strategy of a stimulus lizard is varied independently from approach and retreat behavior would be valuable. Advances in the development of robotic lizards (Martins et al. 2005) offer an approach that might be particularly suitable for such work.

Models of conventional signalling rely on the opponent's response as a stabilizing cost, as the relationship between signal form and content is arbitrary (Enquist 1985; Hurd and Enquist 1998, 2005). Jacky dragon slow arm-waves have properties consistent with membership in this class of signals. There is no intrinsic connection between the rotation of a forelimb and submissive intent. Similarly, although there is interindividual variation in the rate of movement and choice of forelimb, it is not clear that such factors should be affected either by production cost or by level of vulnerability. Indeed, no published playback study has reported systematic variation in the rate of slow arm-wave responses (Ord and Evans 2003; Van Dyk et al. 2007). The structural characteristics of slow arm-waves, together with the results of our experimental manipulations, suggest that this signal is principally constrained by social costs.

In contrast, the aggressive push-up display is unlikely to be a conventional signal. Recall that this sequence of motor patterns involves raising the whole body clear of the substrate (see Figure 3 in Peters and Ord 2003). Movements of this kind are likely to be strenuous, particularly when rapidly repeated in

bouts. They should hence be constrained by physiological factors such as strength or anaerobic capacity, as has been shown for lateral compression in the side-blotched lizard, *Uta stansburiana* (Brandt 2003). Recent playback experiments demonstrate that moment-to-moment variation in push-up display rate is important for opponent assessment (Van Dyk et al. 2007), which is consistent with the idea that this is a physically constrained signal.

Nevertheless, the results of the present study reveal that social contingencies are also important. We conclude that multiple mechanisms operate concurrently and that signal expression stabilized by one mechanism (i.e., physical constraints) need not preclude the employment of signals operating under a different mechanism (i.e., receiver retaliation). These findings reveal a surprising level of complexity in lizard signalling interactions.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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