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## Efficiency of aggressive and submissive visual displays against environmental motion noise in Jacky dragon (*Amphibolurus muricatus*)

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Despite variations of environmental noise, signals are designed to be effective and conspicuous over an appreciable distance. In particular, visual signals must be perceptible against interference caused by natural elements, such as windblown vegetation. We examined the efficiency of aggressive and submissive displays to elicit behavioural responses from observers in the Jacky dragon (*Amphibolurus muricatus*) across relative environmental noise. Both displays have been reported to play an important role during social interactions in this species. We conducted two video playback experiments that utilised a high-resolution computer-generated lizard animation to produce social displays that were embedded within simulated windblown vegetation. First, we compared the efficiency a full aggressive display action pattern (comprised of a tail-flick, backward-forward arm wave, and push-up body rock) to a slow arm wave submissive display, against identical background of windblown vegetation. Second, we compared the tail-flick (alerting component) to the slow arm wave across three varying natural conditions, in which the vegetation behind the displays acted as simulated noise: calm, typical, and windy. We found that aggressive displays were more efficient to elicit an observer's response than submissive signals. Furthermore, the tail-flick display is more efficient than submissive displays across a range of natural variation in windblown vegetation movement, but both signals remain efficient in the face of environmental motion noise. Our results suggest that constraints from the environmental background scene play may have a critical role in the evolution of signal design used in Jacky dragon communication.

**KEY WORDS:** visual signals, signal efficiency, aggressive, submissive display, wind condition, computer-generated animations, environmental noise, Jacky dragon (*Amphibolurus muricatus*).

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## INTRODUCTION

In animal communication, signals are designed to stimulate the sensory systems of intended receivers (BASOLO 1990; GUILFORD & DAWKINS 1991, 1993; ENDLER 1992; BRADBURY & VEHCAMP 1998; EENDLER & BASOLO 1998). It is assumed that signal structures reflect the action of selective forces and constraints that shape signal characteristics in a way to maximize signal efficiency in its ability to convey information to a receiver by drawing first its attention and by enhancing signal detection, discrimination and processing (CLARK & UETZ 1993; BRADBURY & VEHCAMP 1998). In order to convey information effectively through an ecologically complex environment, animals have to maximize the chance of being detected by social partners (ORD et al. 2002; RYAN & KIME 2003). Since signals are used to mediate social interactions, it is important for receivers to perceive them in an accurate manner to further adopt appropriate behavioural responses (HURD & ENQUIST 2001). Thus, detectability appears to be a critical feature for signal efficiency, which is possibly affected by the properties of the natural background scene in which signals are displayed. When the environment becomes too noisy, it may be difficult to discriminate the signal among levels of interference. A reduction in signal transmission, due to environmental noise, has been described in different sensory capacities, such as auditory (STEPHENS & HARTLEY 1991), seismic (NARINS 1990), chemosensory (ATEMA 1995) to electrical (GABBIANI et al. 1996) modalities. For species that primarily rely on movement-based signals, background motion may strongly influence signal detectability (FLEISHMAN 1986).

Several studies in lizard communication have explored the effect of environmental signalling conditions on signal detection (PETERS & EVANS 2003a; ORD et al. 2007, 2010; PETERS et al. 2007, 2008; PETERS 2008; ORD & STAMPS 2008; WOO et al. 2009), revealing that background visual noise may reduce the efficiency of lizard visual displays. Several lizard species have been found to modify the structure of their visual displays in a way that compensate for the masking effect that arises from movement of windblown vegetation (ORD et al. 2007; PETERS et al. 2007). For instance, when the movement of background vegetation increases, Jacky dragons (*Amphibolurus muricatus*) increase the length of an introductory visual display, named the tail-flick display, which has the principal function to attract receiver's attention (PETERS & EVANS 2003b). Interestingly, it has been reported that *Anolis* spp. also show strategic signalling adjustments, but this time by displaying faster motor patterns rather than longer tail-flicks (ORD et al. 2007), as also seen in *A. muricatus* (PETERS et al. 2007).

Jacky dragons are commonly found in visually complex habitat ranging from coastal heathland, rocky ridges, to sclerophyll forests along central and southeast Australia (HARLOW & TAYLOR 2000). This species exhibits highly stereotyped displays during territoriality and mating confrontation. The Jacky dragon's repertoire consists of an advertising tail-flick (PETERS & EVANS 2003b), a backward-forward arm wave, an aggressive push-up body rock and a submissive slow arm wave displayed during male-male interactions and courtship (CARPENTER et al. 1970; CARPENTER & FERGUSSON 1977; GIBBONS 1979; ORD & EVANS 2002; ORD et al. 2002; PETERS & ORD 2003). In an experiment where male-male interactions have been simulated, VAN DYK & EVANS (2008) reported that Jacky dragons modified their behavioural responses according to the nature of agonistic signals exhibited by a computer-generated lizard animation. Male Jacky dragons initiated or abstained from an attack based on the characteristics of

the opponent behavioural sequences either made of submissive or aggressive displays. Hence, responses to opponents during signal interactions may influence the potential outcome of the contest. As of critical functional importance, it can be assumed that Jacky dragons' submissive or aggressive displays have likely evolved in a way that minimizes the competing masking effect of background visual noise. However, to date this assumption has never been experimentally validated.

We conducted two experiments that examined the efficiency to elicit behavioural responses from observers of submissive and aggressive signals of Jacky dragons when displayed in visual noise. To this aim, we developed a digitally animated Jacky dragon exhibiting both displays and we followed behavioural responses (probability of an orienting response and response latency) of focal lizards when being exposed to these displays. The high-resolution computer-generated animation technique ensured to present standardised visual stimuli to focal individuals limiting then variations in behaviour of demonstrators across the different experimental trials (WOO & RIEUCAU 2011). In the first experiment, we tested the efficiency of submissive (slow arm wave) and aggressive (full display action pattern and tail-flick) signals exhibited by the digitally animated lizard. In the second experiment, we examined the efficiency of these displays over three natural wind conditions (calm, typical, and windy) against three examples of vegetation characterising Jacky dragon natural habitats (*Banksia* spp.). As we examine the interaction between the efficiency of social signals and increasingly complex environments, we may observe one of the following situations: (1) signal efficiency decreases as the complexity of environmental noise increases, (2) both signals remain efficient as environmental noise increases, (3) aggressive signals are more efficient than submissive signals across all environmental conditions or (4) submissive signals are more efficient than aggressive signals across all environmental conditions.

## MATERIALS AND METHODS

### *Subjects*

We collected 20 Jacky dragons (*A. muricatus*) from Lane Cove, La Perouse, and Royal National Parks in Sydney, NSW Australia. Each lizard was wormed with ivermectin or Felex Plus® before they were placed in an individual enclosure that was also visually isolated from other lizards. Each enclosure measured 64 × 75 × 120 cm, and were constructed of three white panels and one clear Perspex® panel (supplied by All Plastics, Chatswood, Sydney, Australia). The clear front panel allowed subjects to see video stimuli and allowed us to record behavioural responses to display stimuli. Each enclosure also included wooden branches and stumps for basking perches, leaf foliage, and a layer of Sydney sand substrate. Lizards were fed live house crickets (*Acheta domesticus*) twice a week (supplied by Pisces Enterprises, Brisbane, Queensland, Australia) and had ad libitum access to fresh water that was provided in small plastic bowls. The crickets were dusted with vitamin supplements (Herptivite with beta carotene and calcium with vitamin D<sub>3</sub>, Rep-Cal Research Labs, Los Gatos, California, USA) before we fed our subjects. Enclosures were sprayed daily with water to ensure adequate moisture and humidity. All experimental subjects were maintained under a 14:10 hr L/D cycle with additional heat lamps (125 w Spotone, Phillips, NSW, Australia) for 10 hr per day. Ultraviolet (UV) lamps (300 w Ultra-Vitalux, Osram, NSW, Australia) were illuminated for half-an-hour in the morning (07:30) to prevent vitamin deficiencies. After the study, all animals were released at their original site of capture, as in accordance to NSW National Parks and Wildlife Services guidelines.

*Computer-generated stimuli*

*Acquisition of the display behaviours.* As we employed a reliable technique for capturing lizard displays on video (see ORD et al. 2002; VAN DYK & EVANS 2007), we compiled a catalogue of aggressive and submissive behavioural sequences which we used as a basis for our animations.

From our recordings, we recorded 65 slow arm wave (SAW) displays, which yielded an average for duration ( $N = 65$ , mean  $\pm$  SE =  $27 \pm 11.79$  frames) and frequency of displays per bout ( $N = 19$ , mean  $\pm$  SE =  $3.21 \pm 2.04$  frames). We employed a logarithmic transformation to normalise the distribution, then back-transformed the data to acquire average duration and rate. We recorded display lateralization and found no preference in forelimb usage [ $\chi^2(1) = 0.016$ ,  $P = 0.898$ ]. We then sourced aggressive clips (AGG) as tail-flick (TF) and push-up body rock (PUBR) display combinations (see ORD et al. 2002; VAN DYK & EVANS 2007) that constituted individual display action patterns (DAP). A complete DAP sequence consisted of the initial alerting component of a TF that was followed by a backward-forward arm wave, and then completed with a PUBR. From our measurements, we were able to identify a population-typical PUBR based on the mean duration (mean  $\pm$  SE =  $12.66 \pm 2.27$  frames) (WOO & RIEUCAU 2008). We also measured TFs, and acquired a population-typical durations (mean  $\pm$  SE =  $51.61 \pm 33.02$  frames).

We designed 15 animation stimuli to use for all playback sequences. Exemplar models were comprised of five SAW, five AGG, and five control (still lizard) models. We created exemplars to prevent habituation to the stimulus displays. The use of multiple and randomly chosen exemplars allowed us to control for pseudoreplication that may arise from the use of repeated presentations of any unique sequence to focal subjects meant to perform replication instead of using proper independent replicates (ROSENTHAL 1999, 2000; MCGREGOR 2000; WOO & RIEUCAU 2012). Although the duration remained the same, we based the exemplars on different displays from a range of captive individuals.

*Development of the digitally animated Jacky dragon.* Previously, we created the animation with specific design characteristics that allowed us to manipulate and create isolated motor patterns (see WOO 2007; WOO & RIEUCAU 2011, 2012). More specifically for the current study, we matched the stimuli to 15 exemplar animation sequences using the “rotoscoping” technique (GATESY et al. 1999, 2010), which was superimposed onto video footage of population-typical aggressive and submissive displays (WOO 2007; WOO & RIEUCAU 2011), as based on both our indoor and outdoor captive populations. Each exemplar had the animated lizard scaled at a perceptual distance of three metres from the subject (Fig. 1).

For each sequence, we included a background of moving vegetation to simulate a natural environment. The total length of a stimulus clip was 6 min. The first 5-min showed an inactive lizard perched on a branch, which allowed subjects to habituate to the random motion noise. At 5 min, the lizard would produce one of the signal exemplars or remain inactive (control). We embedded an electronic marker tone to signal this transition, which was only audible on the VHS tape. The marker allowed us to identify the habituation period, and signalled the onset of an animated display. After the display, the sequence continued for an additional 60 sec with natural background movement and a standing still animated lizard (Fig. 1). The final sequences were completed using the same technique as in previous studies (see WOO 2007; WOO & RIEUCAU 2011, 2012). We elected to use the same equipment for playback and recording as in WOO & RIEUCAU (2012).

*Environmental noise and vegetation*

For Experiment 1, a 6-min sequence of background moving vegetation was filmed under natural conditions in La Perouse National Park using a Canon digital camcorder (MV650i, Cannon Inc., Japan). A wooden perch was placed 3 m from the camera to facilitate subsequent addition of the 3D lizard to the scene (see PETERS & EVANS 2007).

For Experiment 2, we modified environmental noise. We used a large 1 m diameter commercial cooling pedestal fan (Ebony Fans) with adjustable speed to simulate variation in wind

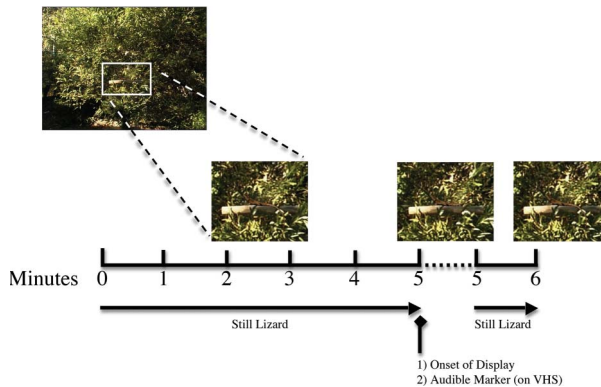


Fig. 1. — Timeline for each trial, which depicts the stimulus at a simulated 3 m in depth, and selectively cropped to illustrate the progression of a single trial. Across the 6-min trial, windblown vegetation maintains a constant speed (calm, typical, or windy). During the first 5 min, a still animated lizard sits on the perch. At 5 min, the animated lizard produces a display (e.g., tail-flick), and then returns to the exact posture prior to the onset of the display. At the 5-min point, an audio marker is recorded onto the VHS tape so we could identify the onset of the display and measure the orientation and latency to respond to the stimulus.

conditions. Three wind speeds were selected to represent natural conditions (PETERS et al. 2008): calm (1.40 m/sec), typical (2.72 m/sec), and windy (4.24 m/sec). Wind speed was measured using a Velocicalc<sup>®</sup> anemometer (Model No. 8345/8346, TSI Incorporated Shoreview, MN, USA). The fan blew air at these three speeds across three types of representative natural vegetation with similar foliage composition (*Banksia* spp.). In order to exclude the anemometer from the filmed frames, wind-speed readings were taken at the start and finish of each sequence. These readings were averaged to provide an estimate for each sequence: calm (1.65 m/sec), typical (2.75 m/sec), and windy (4.35 m/sec). A natural log perch was fastened to the top of a wooden platform covered in *Banksia* spp. branches and then placed amongst the vegetation. We filmed sequences of 6 min each on a relatively sunny day with < 0.20 m/sec wind speed from a distance of three metres. Lastly, we converted all vegetation footage to individual image sequences (JPEGs) that were after that included in the background of each display sequence.

### Procedure

We followed focal lizards' behavioural responses when exposed to the different displays exhibited by the digitally animated lizard. We measured the probability of an orienting response and the latency to respond to the presented stimulus (following PETERS & EVANS 2003b's methods). We considered an orienting response as an observable movement of the focal subject's head towards the display (PETERS & EVANS 2003b). We recorded orienting responses when lizard redirected their gaze toward the video monitor and we scored, for each experimental test, whether or not an orienting response occurred. In addition, we measured latency to respond to the stimulus. Response latency is defined as the time (in frames) required to a focal individual to orient its gaze or turned its head to the stimulus from the onset of the animated display.

### Experiment 1

We used 20 focal individuals and exposed them to a total of six treatments over 6 days in a split-plot design. We created 15 stimulus sequences: five SAW, five DAP stimuli, and five control



sequences (still lizard on a perch). During the first three treatments, stimulus presentation was randomised according to the exemplar. On the first treatment, all subjects were individually presented with SAW clips, with each exemplar shown to 10 different lizards. On the second treatment, each lizard saw the control stimulus. On the third treatment, all subjects saw AGG clips, with each exemplar shown to 10 different individual lizards. The design was counterbalanced, such that subjects were first presented with SAW clips for the first treatment now were presented with AGG sequences. Control sequences were still shown to all lizards during the second treatment. Subjects that saw AGG clips during the first treatment were now presented with SAW clips. We randomised stimulus presentation across each block to ensure that the same subject was not presented with the same exemplar twice.

### *Experiment 2*

We used nine animations consisting of three exemplars of TFs (isolated from three DAP clips), three exemplars of SAWs and three exemplars of control (inactive). Each of these exemplars was embedded in a scene depicting the three wind speeds, across three different types of vegetation: calm (1.65 m/sec), typical (2.75 m/sec), and windy (4.35 m/sec). Twenty focal lizards were tested during 18 consecutive days. During the first 9 days, each subject was presented with only one stimulus combination (display  $\times$  wind condition) per day. We then counterbalanced the trials with an additional 9 day period of testing where each subject was presented with the reverse order of sequences.

### *Statistical analysis*

For Experiment 1, we used mixed-model ANOVAs to compare the probability of orientating responses and latency to respond of focal lizards (dependent variables) to aggressive and slow arm wave stimuli (fixed effects). We included focal lizards' identity as a random effect in our mixed-models to control for pseudo-replication.

For Experiment 2, mixed-model ANOVAs were used to compare the probability of orientating responses and response latency for a main effect of display type (two levels: tail-flick and slow arm wave) and wind condition (three levels: calm, typical, and windy), and an interaction between these two factors. We included display type and wind conditions as fixed effects and focal lizards' identity as a random effect in our mix-models. To examine whether the vegetation type affected displays efficiency, we ran mixed-model ANOVAs with the same random effect structure to compare across sites. We analysed the probability of orientating response and response latency to tail-flicks and slow arm waves across wind conditions also using mixed-model ANOVAs. We performed Tukey's post-hoc tests for pairwise comparisons for each display as wind condition increased.

For both experiments, control values were removed from all analyses due to the absence of response during those trials. All analyses were conducted with Statistica 10 (StatSoft, Inc. Tulsa, Oklahoma, USA).

## RESULTS

### *Experiment 1*

The probability of an orienting response significantly differed between the two displays ( $F_{1,19} = 40.04$ ,  $P < 0.0001$ ). DAPs exhibited by the digitally animated Jacky dragon were more efficient to elicit orienting responses of focal lizards than slow arm wave displays (mean probability of an orienting response  $\pm$  SEM: DAP =  $0.85 \pm 0.057$ ,  $N = 40$ ; SAW =  $0.275 \pm 0.071$ ,  $N = 40$ ; Fig. 2a). We also found that response latency

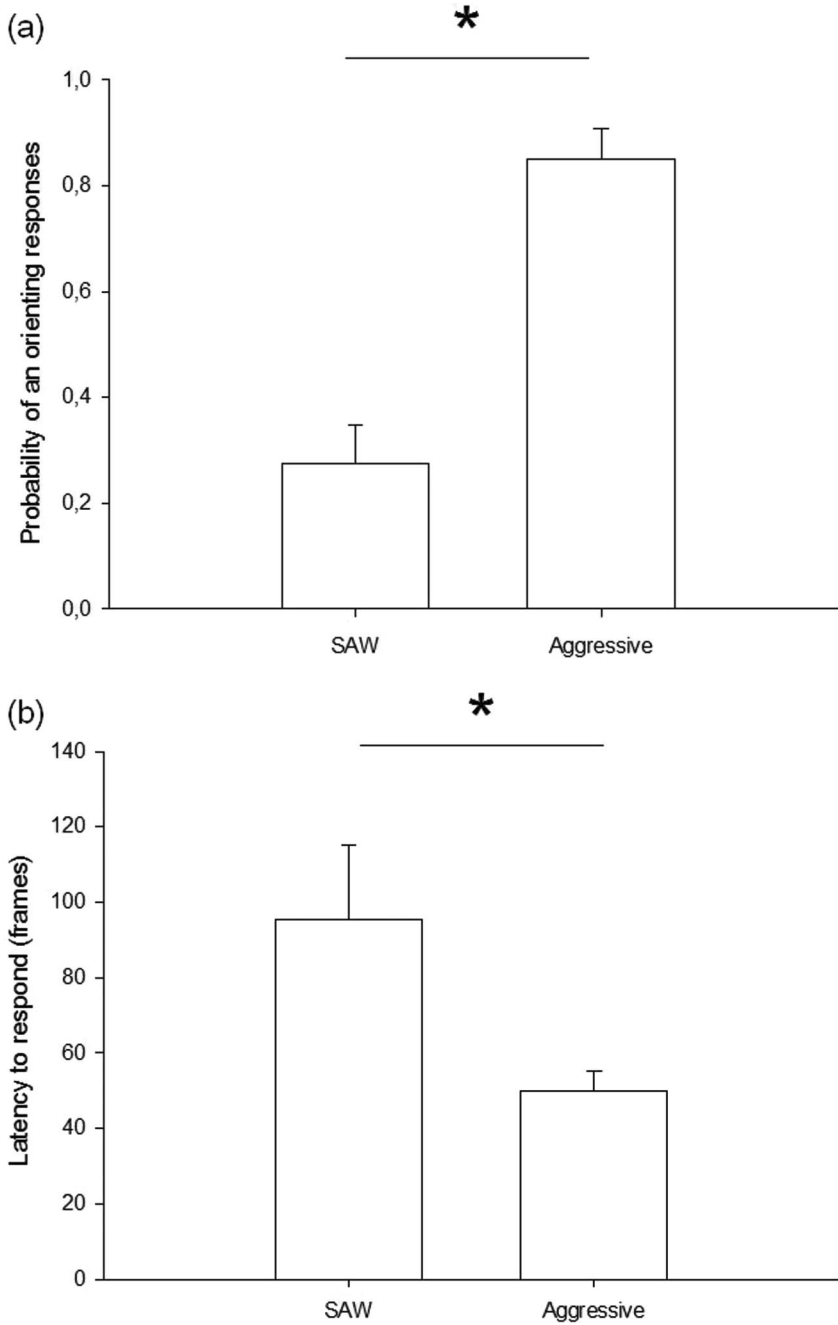


Fig. 2. — Response to display components as seen against natural background: (a) aggressive were significantly more efficient to elicit behavioural responses from observer lizards than slow arm waves, and (b) latency to respond shows a faster orientation to aggressive displays in comparison with the onset of submissive signals. All results are expressed as a mean and its standard error. \*  $P < 0.05$ .



significantly differed between the two displays ( $F_{1,15} = 11.15$ ,  $P = 0.0004$ ). Aggressive displays exhibited by the animated lizard elicited faster responses of focal individuals than submissive slow arm waves (mean latency to respond  $\pm$  SEM: DAP = 49.97 frames  $\pm$  5.35,  $N = 34$ ; SAW = 95.54 frames  $\pm$  19.45,  $N = 11$ ; Fig. 2b). The results of Experiment 1 suggest that aggressive displays are more efficient than slow arm wave displays to elicit behavioural responses from observer lizards.

### Experiment 2

A significant effect of the display type exhibited by the digitally animated Jacky dragon on the probability of orienting responses of focal lizard was detected ( $F_{1,19} = 10.95$ ,  $P = 0.003$ ). Tail-flick displays were more efficient to elicit orienting responses than slow arm wave displays (Fig. 3a). Wind condition did not affect the probability of orienting responses ( $F_{2,37} = 1.44$ ,  $P = 0.24$ ). The interaction between wind condition and display type was non-significant ( $F_{2,35} = 0.71$ ,  $P = 0.49$ ). Vegetation type did not affect the efficiency of both displays in eliciting orienting responses across the three wind conditions ( $F_{2,28} = 0.82$ ,  $P = 0.45$ ). We did not detect any significant effect of the vegetation type on the probability of orienting responses for either tail-flicks ( $F_{2,40} = 1.52$ ,  $P = 0.23$ ) or slow arm waves ( $F_{2,40} = 0.10$ ,  $P = 0.90$ ). Our post-hoc analysis did not reveal significant comparisons for both displays as wind speed increased ( $P > 0.05$ ).

Display type significantly affected the latency to focal lizards' responses ( $F_{1,16} = 10.77$ ,  $P = 0.004$ ). Lizards responded faster to tail-flicks displayed by the animated Jacky dragon compared to slow arm waves (Fig. 3b). The effect of wind condition on responses latency just failed to reach statistical significance ( $F_{2,20} = 3.30$ ;  $P = 0.056$ ) with a trend in longer latency to respond when wind speed increased for the two displays (Fig. 3b). The interaction between wind condition and display type was non-significant ( $F_{2,23} = 0.13$ ,  $P = 0.87$ ). No significant effect of the vegetation type on responses latency of local lizards has been found ( $F_{2,14} = 0.74$ ,  $P = 0.49$ ). However, we found a significant difference of response latency to tail-flick displays across wind conditions ( $F_{2,22} = 4.46$ ,  $P = 0.02$ ) with slower responses at high wind speeds when the animated lizard displayed tail-flicks. This effect was not observed for slow arm wave displays ( $F_{2,12} = 0.32$ ,  $P = 0.73$ ). Tukey's post-hoc tests showed a significant difference in response latency for tail-flicks between calm and windy signalling conditions ( $P < 0.05$ ); however, all other comparisons were not significant ( $P < 0.05$ ).

## DISCUSSION

Our results revealed that aggressive and submissive signals in Jacky dragons can overcome the masking effect of vegetation motion noise insuring that signals may be accurately transmitted during social interactions. Although both social signals were salient, we found that submissive slow arm waves were less efficient to elicit behavioural responses from observer lizards than aggressive DAPs across the full range of wind conditions. However, as wind speed increases both signals seemed to remain efficient.

Our results suggest that slow arm waves were less efficient to elicit observer responses than aggressive displays (DAPs) and tail-flicks. One possible explanation dwells on the intrinsic design characteristic of the slow arm wave display. Unlike aggressive signals, the signal characteristics of the slow arm wave movement are subtle. A rapid signal with a greater sweep area, such as the tail-flick, is designed to attract

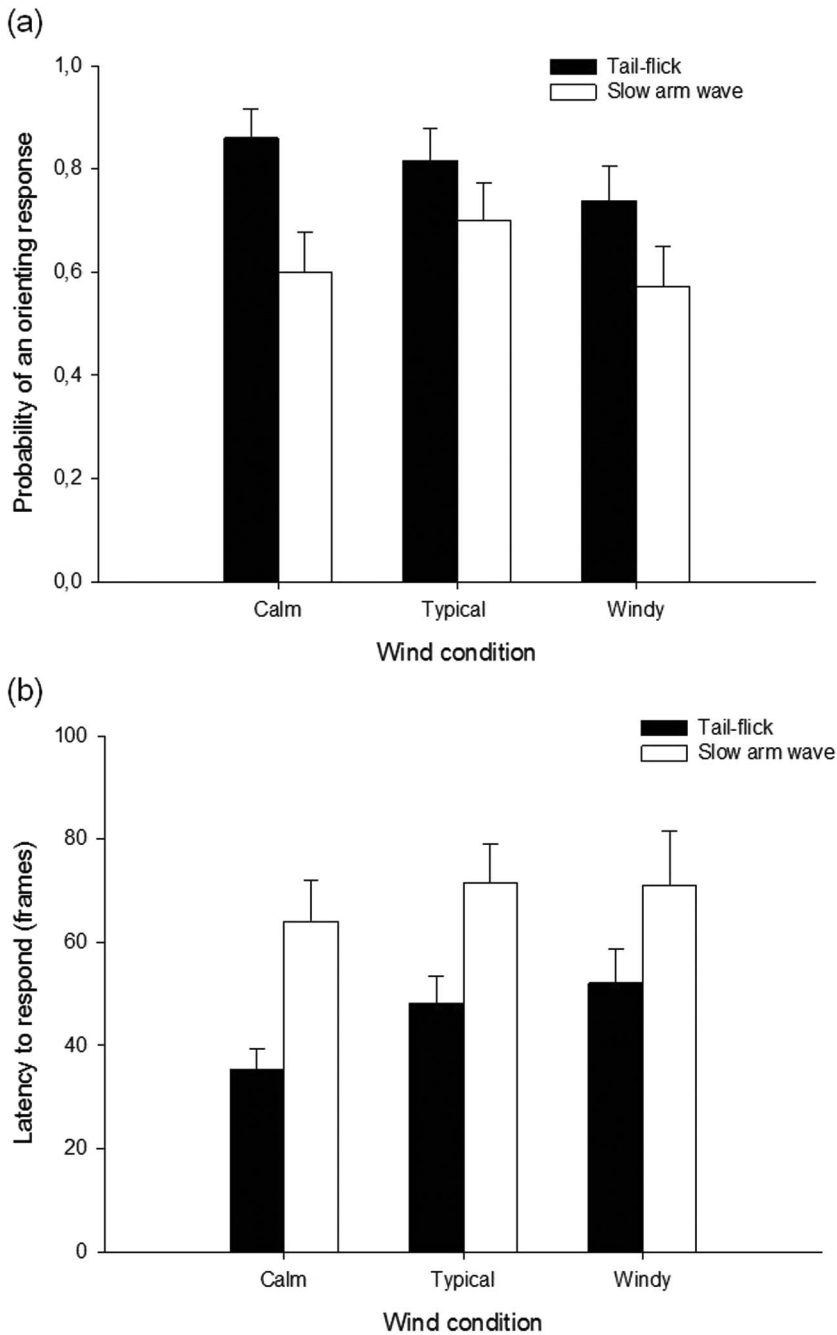


Fig. 3. — Response to display components across three wind conditions (m/sec): calm (1.65), typical (2.75), and windy (4.35). (a) No significant decrease was found for the probability of orientating responses despite a graduate decline from calm to windy signaling condition. (b) A significant increase in latency response was found for tail-flicks as wind condition speed rose, but this effect was no longer found for latency responses to slow arm wave displays. All results are expressed as a mean and its standard error.

immediate receiver's attention (PETERS & EVANS 2003b). In comparison, a submissive slow arm wave has a significantly smaller sweep area (WOO & RIEUCAU 2008). The slow arm wave is considerably slower than other social signals in the Jacky dragon's repertoire (WOO et al. 2009). WOO et al. (2009) also reported that Jacky dragons are most sensitive to high-speed movements than slower ones. In natural conditions, Jacky lizards often display a series of consecutive slow arm waves, making this display longer in comparison to the typical duration of a push-up body rock, but remaining shorter than a tail-flick display (WOO & RIEUCAU 2012). In addition, it has been highlighted that the overall display duration is critically important for aggressive and advertising signal efficiency in this agamid species (PETERS & EVANS 2003a; PETERS 2008; WOO & RIEUCAU 2012).

When the displays were presented across a range of wind conditions, tail-flicks were still more efficient to elicit behavioural responses for observers than slow arm wave displays. Although we did not detect a significant effect of wind condition on the probability of orientating responses from observer lizards, we found that focal lizards had slower responses to tail-flicks displayed by the animated lizards when wind speed increased, an effect that was not observed when the animation displayed slow arm waves. This suggests a differential sensitivity between the two displays to wind condition during signalling, in which the tail-flick display appears more sensitive to the masking effect of environmental motion noise than the slow arm wave display. Given the comparative design characteristics of slow arm waves, an escalation in environmental visual noise increases the time to detect a tail-flick due to receiver's sensory limitations (PETERS 2008). Previous studies have explored how tail-flicks can remain salient in windy conditions arguing that the switch from a continuous to an intermittent display (PETERS et al. 2007) or the rapid change of movement direction of the tail that may enhance detection against a noisy background (PETERS 2008).

Despite potentially sub-optimal signalling conditions, Jacky lizards must still display signals across a range of environmental conditions. In Experiment 2, we measured the efficiency of signals in three natural conditions in which the vegetation behind the displaying lizard moved due to simulated wind. In this study, we did not directly examine whether focal lizards make any behavioural adjustments to the signal structure in response to environmental noise, however previous empirical evidence showed that Jacky dragons can modify their display strategy when confronted to windy conditions (PETERS et al. 2007; PETERS 2008). Jacky lizards lengthen signalling duration when motion noise increased, which further suggests that they are able to recognise and assess vegetation displacement, and change tail-flick display duration to maintain signal efficiency against environmental noise (PETERS et al. 2007). In contrast, *Anolis* lizards have been reported to increase the speed of their push-up, and not the length, when the intensity of wind condition speeds up the movement of vegetation (ORD et al. 2007).

In the visual modality, *Anolis* lizards perceive critical motion characteristics through the complexity of environmental noise, such as the movement of windblown vegetation (FLEISHMAN 1986). A study on four sympatric *Anolis* lizards has shown that individuals moved from a less environmentally noisy habitat to one that is more complex were unable to discriminate dewlap displays in these different conditions (PERSONS et al. 1999). It has been suggested that habitat conditions and the response properties of lizard species visual system have constrained the evolution of design, thus suggesting that environmental selection pressures have shaped visual displays to be habitat-dependent (FLEISHMAN 1988a, 1988b, 1992; FLEISHMAN & PERSONS 2001).

Signalling during extreme windy conditions may be relatively rare. In anuran amphibians, complex acoustic habitats have selectively influenced the detection of competing male calls by females (SCHWARTZ et al. 2001). Females were found to no longer reliably discriminate between the calls of chorusing males during extreme levels of environmental noise (WOLLERMAN 1999). For Jacky lizards, displaying signals during intense windy periods may also be ineffective because conspecifics may not present themselves on visible perches due to dangers of high wind conditions. Signalling in calmer wind conditions may indeed recruit the greatest audience, increase the success of signalling, and reduce energetic expenditure in displaying against wind force by maximizing the potential reception of the signal (FLEISHMAN 1992).

Several studies have explored the physical characteristic of lizard visual stimuli and the influence of environmental signaling conditions (FLEISHMAN 1992; ORD et al. 2007, 2010; ORD & STAMPS 2008; PETERS et al. 2008) and have investigated display design differences at the population and species level (MARTINS et al. 1998; LEAL & FLEISHMAN 2004; ORD & MARTINS 2006; ORD et al. 2007). Our findings therefore contribute to strengthen the growing evidence that constraints from the environmental background scene may play an important role in the evolution of movement-based signalisation in the Jacky dragon. Despite functional and structural discrepancies between the aggressive and submissive displays, we demonstrate that both displays are efficient to elicit behavioural responses from observer lizards across a range of wind conditions. This suggests that the design of signals used in the Jacky dragon communication may have been shaped by dynamic complexity in the natural habitat.

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