



## RESEARCH PAPER

# Aggressive Signal Design in the Jacky Dragon (*Amphibolurus muricatus*): Display Duration Affects Efficiency

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**Abstract**

Design characteristics of signals, such as their duration, may have evolved to maximize signal efficiency. It is commonly assumed that constraints on signal design have usually shaped the most optimal display characteristics to improve signal transmission and information transfer of the signaller, and detection by intended receivers. In this study, we tested whether the characteristics (duration, speed and frequency) of an aggressive display, the push-up body rock, exhibited by the Jacky dragon (*Amphibolurus muricatus*) have likely evolved for optimal signal efficiency, as it is able to draw attention to the signaller. We performed two video playback experiments using high-resolution 3D animations testing the effect of variation in push-up body rock structure. In experiment 1, we manipulated push-up body rock display structure. We gradually increased the number of push-ups exhibited by a digitally animated Jacky dragon increasing the overall display duration. In experiment 2, we developed four stimuli based on population-typical push-up body rock display for duration (short and long), and frequency of push-ups (1 or 5 consecutive push-ups) by manipulating push-ups' speed. In both experiments, we measured the probability of an orienting response and response latency of focal lizards when being exposed to the different stimuli. Our results showed that display duration is critically important for signal efficiency in the aggressive push-up body rock display. If we are to understand the design characteristics of signals used in animal communication, then it appears important to consider the possible trade-off between signal efficiency and costs.

**Introduction**

In animal communication, signal design reflects selection for characteristics that maximize signal efficiency in its ability to draw attention to the signaller. It is commonly assumed that signals must be shaped in a way that favours their transmission across the environment with the ultimate aim to stimulate the sensory system of receivers (Endler 1992, 1993; Bradbury & Vehrencamp 1998; Rowe 1999; Ryan & Kime 2003). To convey information effectively in an environment that can be spatially and temporally

heterogeneous, animals should develop specific mechanisms, as signalling behaviour, to enhance signal transmission as well as signal detection (Ord & Stamps 2008; Ord et al. 2010). For instance, free-ranging *Anolis* lizards have been reported to add an alerting signal prior to their visual displays in a visually noisy environment (Ord & Stamps 2008).

Lengthy signals may be particularly effective when transmission occurs across long distances (Morton 1977; Forrest 1994). To date, most studies that examine duration have focused on the necessity for signals to be more conspicuous against background

noise (the Lombard effect: Lane & Tranel 1971). For example, during heavy whale-watcher boat traffic, killer whales (*Orcinus orca*) increase the duration of their calls to compensate for anthropogenic noise (Wieland et al. 2010). Other sources of auditory noise from the environment (Wiley & Richards 1982) may require individuals to increase the length of their signals, such as the case of interference from other conspecific calls (Lengagne et al. 1999), interspecific calls (Schwartz & Wells 1985; Schwartz 1987) or noise generated directly by the surrounding environment, such as wind-blown vegetation (Brumm 2004). More recently, several studies on lizards have considered the impact of wind-blown vegetation on the visual system (Ord et al. 2007; Peters et al. 2007; Ord & Stamps 2008; Ord et al. 2010).

The duration of signals may also reflect selection for an increased signal efficiency to convey information to the receiver by attracting its attention and to enhance signal detection, discrimination and processing (Clark & Uetz 1993; Bradbury & Vehrencamp 1998; Vehrencamp 2000). For instance, duration was found to be the key characteristic (and not the amplitude, sweep area, velocity or acceleration) of a stereotyped tail-flick (TF) display that serves to draw opponent's attention in the Jacky dragon (*Amphibolurus muricatus*); lengthy TFs appeared to be more conspicuous than shorter ones (Peters & Evans 2003b).

Here, we extended the study of Peters & Evans (2003b) in which the duration of the TF display proved to be the key characteristic of the display efficiency as an introductory component to alert receiver attention in the Jacky dragon, an agamid lizard from eastern Australia found in diverse vegetation habitats. In this study, we examined the display characteristics (duration, speed and frequency) of an aggressive signal exhibited by male Jacky dragons, named the push-up body rock. The push-up body rock display is a short, stereotyped motor pattern that consists of a series of consecutive push-up bouts. This display, which is generally preceded by an initial alerting TF, is recognized by conspecifics as a challenge display but that can be also performed during other social interactions, such as courtship and territoriality (Carpenter et al. 1970). If duration effectively enhances signal efficiency, the push-up body rock display would be more conspicuous when the display is longer. We tested this hypothesis by conducting two experiments where the duration and the speed (i.e. velocity and acceleration) of the aggressive display, as well as the number of push-ups, exhibited by a digitally animated Jacky dragon, were experimentally manipulated and subsequently presented to

focal lizards. In Experiment 1, we gradually increased the number of consecutive push-ups exhibited by a simulated demonstrator lizard increasing the overall display duration. In Experiment 2, we developed four stimuli based on population-typical push-up body rock display for duration (short and long) and frequency of push-ups (1 or 5 consecutive push-ups), and so we manipulated how fast each push-up was executed. Consequently, to evaluate the relative importance of duration, we manipulated the stimuli to incorporate variations in speed, in addition to the overall length. In both experiments, we followed behavioural responses of focal subjects (probability of an orienting response and response latency) when being exposed to different stimuli.

## Methods

### Subjects

Male Jacky dragons were collected from Lane Cove, La Perouse, and Royal National Parks in Sydney, Australia, and were held in captive facilities at Macquarie University. Enclosures measured 64 × 75 × 120 cm and consisted of three adjacent opaque white boards with one side that was a sheet of clear Perspex<sup>®</sup> panel (All Plastics Engineering Pty Ltd, Chatswood, NSW, Australia). The opaque boards provided visual isolation from neighbouring male lizards, while the Perspex<sup>®</sup> allowed for the presentation of stimuli and video recording of behaviour. Each enclosure contained wooden branches and stumps for basking, native leaf litter and Sydney sand substrate. Subjects were fed with live crickets (*Acheta domesticus*; supplied by Pisces Enterprises, Brisbane, Queensland, Australia) twice a week and had access to water *ad libitum*. Lizards were maintained under a 14:10 h L/D cycle with additional heat lamps (125 W Spotone, Phillips, NSW, Australia) for 10 h per day and ultraviolet (UV) lamps (300 W Ultra-Vitalux, Osram, NSW, Australia) that were illuminated for half-an-hour in the morning to prevent vitamin deficiencies. Room temperature was held at approximately 25 ± 2°C with minor fluctuations in relative humidity and temperature. Lizards were maintained in an extended summer schedule of 8 mo between September and June. Once the study was completed, lizards were released near the point of capture.

### Motor pattern duration

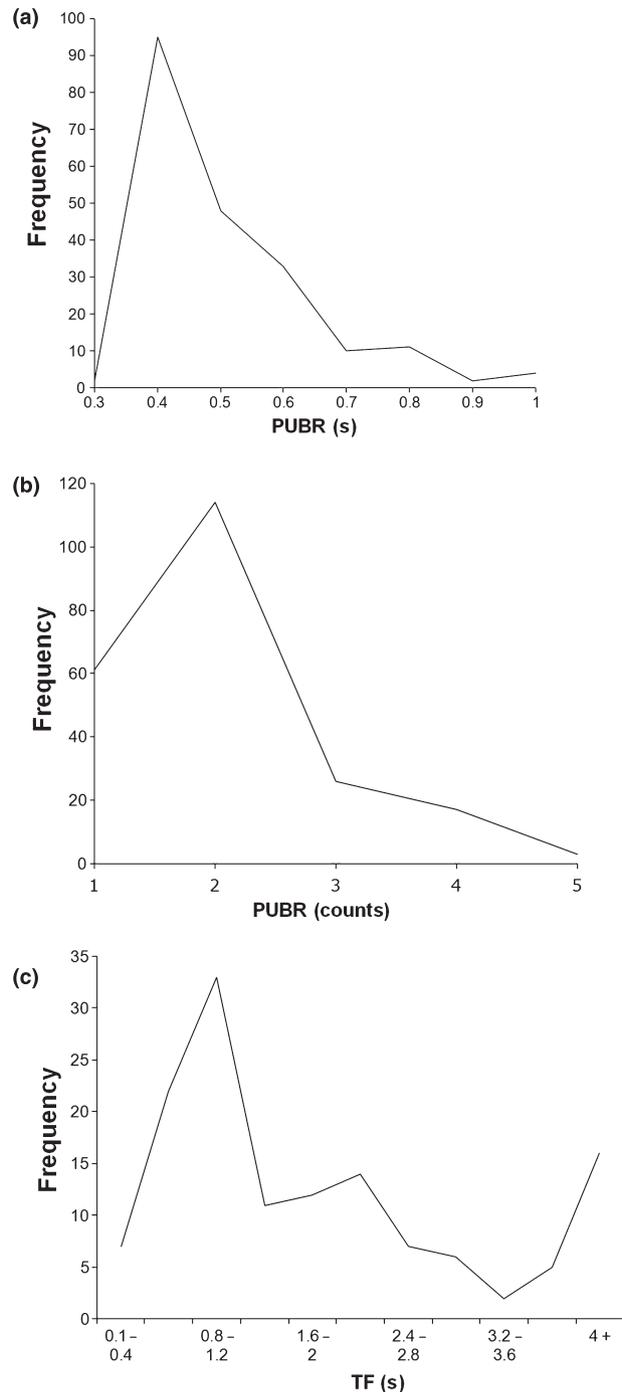
We were able to define a population-typical display by sampling the average duration of displays among

captive individuals. To acquire a population-typical display, we defined duration as the total amount of time (in seconds) it took to complete the entire display per bout. We recorded PUBRs from indoor and outdoor archive footage of male–male interactions (Ord & Evans 2002; Ord et al. 2002a,b; Peters & Ord 2003; Van Dyk & Evans 2007). From our recording, we measured the display durations in seconds (25 frames/s PAL standard) and bouts (consecutive number of PUBRs). We then analysed 30 clips from seven outdoor lizards and 74 clips from five indoor individuals. Because of the lack of displays, three outdoor and one indoor sequences were excluded from our analysis. PUBR display durations (mean  $\pm$  SD = 0.506  $\pm$  0.09 s; Fig. 1a) were averaged across individuals, and then the outdoor and indoor samples, which did not differ appreciably, were combined. Jacky dragon bout length was estimated at mean  $\pm$  SD = 2.19  $\pm$  0.31 PUBRs (Fig. 1b).

Distribution counts for TF displays were also estimated by randomly excluding counts until all subjects had equal number of recorded counts. TF duration was also sampled from the same outdoor and indoor individuals. As not all individuals displayed a TF, we only analysed 25 sequences from four outdoor and 21 sequences from four indoor individuals for TF durations. Estimated population-typical duration was mean  $\pm$  SD = 2.06  $\pm$  1.32 s (Fig. 1c).

### Stimulus animation

We used a taxidermic lizard as a model for our animations (Woo 2007). The model was scanned into a three-dimensional object using a Konica Minolta VI-9i camera (Konica Minolta Holdings, Inc., Tokyo, Japan) by New Dawn<sup>®</sup> (Bexley North, NSW Australia) and processed into a readable digital format for an animation program, Lightwave<sup>®</sup> v7.5 (NewTek Inc., San Antonio, TX, USA). The model object (50 000 polygons) excluded the texture and a tail. The modeller program allowed us to infuse a number 'bones' similar to the skeletal morphology of the lizard. A spinal column including sacral vertebrae for the tail were infused into the object along with four appendages for two front and two hind legs. The incorporation of 'bones' allowed us to manipulate the object within a 3D plane. We then added texture to the body of the object by taking digital photographs (JPEG) of the taxidermic lizard from various positions and angles (i.e. frontal and orthogonal views of head, body and tail). Each body area was cropped and placed adjacent to adjoining body areas using Adobe<sup>®</sup> Photoshop<sup>®</sup> Elements v2.0 (Adobe Systems Incorpo-

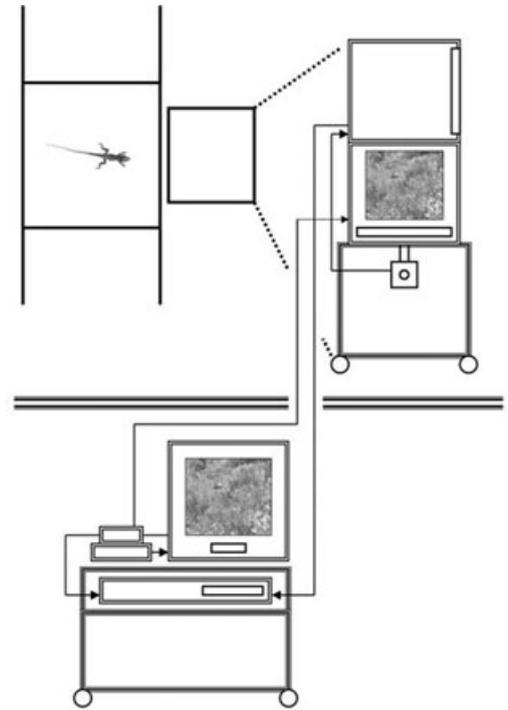


**Fig. 1:** Population-typical display modal distribution were examined from indoor and outdoor video sequences: (a) the duration of a single PUBR was measured from 12 lizards (seven outdoor/30 clips and five indoor/74 clips), (b) the number of consecutive PUBRs was also measured from the same 12 lizards (seven outdoor/30 clips and five indoor/74 clips) and (c) the duration of individual tail-flick (TF) was measured from eight lizards (four indoor/25 clips and four outdoor/21 clips).

rated, San Jose, CA, USA). The JPEG images that highlighted textural areas on the model object were then synchronized to a UV map in the modeller program. The entire object was weight-shaded according to antagonistic movements. This allowed the object movement to be linear without other parts of the object counteracting smooth movement. Lastly, the finished object was transferred to the layout program, which allowed us to design our scenes.

The model lizard movement patterns were then matched to a population-typical sequence using a technique known as 'rotoscoping' (Gatesy et al. 1999; Woo & Rieucau 2008, 2011; see also Gatesy et al. 2010 for a detailed description of the rotoscoping technique). The model clip was exported into individual JPEG frames using Apple QuickTime™ Player v6.0 (Apple Computer Inc., Cupertino, CA, USA). Each frame was then placed in the background of the layout program. The object lizard was then manipulated to match the JPEG lizard frame by frame in each consecutive image. We manipulated the object by rotating one bone and allowing it to pivot against the adjoining point on an adjacent bone. The position of the object's posture was matched to a JPEG on the background of the layout program. When one position was matched, the frame was 'key-framed' to allow the program to map out the sequence of movements. Rotoscoping allowed us to repeat motor pattern displays in a smooth transition that sourcing video playback clips from archive footage does not allow for this transition. We matched the PUBR display to the closest available mean duration sequence from our sourced sequences following Woo's (2007) procedure. The lizard stimulus was then placed at a perceptual distance of 3 m on a perch (Fig. 2). The screen was situated right against the Perspex of the enclosure; however, each individual was allowed to move freely within the enclosure.

Each sequence incorporated natural moving background of wind-blown vegetation that was filmed at La Perouse National Park, so that the motor patterns were viewed in an ecologically relative context (see Peters & Evans 2007). The same vegetation sequence was used as the background for all stimuli and for all trials. The initial 5 min of each sequence had the still animation on a natural perch to allow experimental subjects to habituate to the video playback stimulus. At 5 min, the digitally animated lizard would display one of the five motor patterns or the control (e.g. motionless lizard on a perch). After the display, the digitally animated lizard would return to a stationary position on the perch. Each stimulus sequence totalled 6 min.



**Fig. 2:** Lizard stimulus situated at a simulated distance of 3 m and embedded in natural background vegetation. Box identifies the location of the lizard animation presented to focal subjects.

All sequences were rendered using Render Farm Commander v2.9 (Bruce Rayne®, Lalor Park, NSW, Australia). Render Farm Commander (RFC) allows all computers that are linked through a network to increase rendering time by distributing tasks. RFC produced a series of JPEGs that were imported as an image sequence into Quicktime™. Image sequences were exported as a digital video (DV) stream file and rendered using Final Cut Pro HD (Apple Computer Inc.). All stimuli were created for PAL-DV standard (5:1 compression; horizontal resolution 575 lines;

25 frames/s). To date, studies have used this technique to successfully elicit behavioural responses from conspecifics (Peters & Evans 2003a,b, 2007; Van Dyk & Evans 2007).

### Procedure

In both experiments, we followed focal lizards' behavioural responses when they were exposed to video sequences of a digitally animated lizard. We measured the probability of an orienting response and the latency to respond to the presented stimulus following Peters & Evans (2003a,b) methods. We considered an orienting response as an observable movement of the focal subject's head towards the digitally animated lizard (Peters & Evans 2003b). We recorded orienting responses when lizards redirected their gaze towards the video monitor and we scored, for each experimental test, whether or not an orienting response occurred. Latency to respond to the stimulus was measured as the time (in seconds) it took for a focal lizard to orient its gaze or turned its head to the stimulus from the onset of the animated display.

### Experiment 1

We tested 20 focal lizards over 14 consecutive days. In this experiment, we manipulated the number of consecutive push-ups exhibited by a digitally animated lizard. Each focal lizard was shown one of seven stimulus sequences: the control had a motionless demonstrator lizard on a perch, while the five other stimuli had a graded series of PUBRs (1–5 PUBRs; see Table 1), and one TF to match population-typical. Each subject saw a different stimulus each testing day. We used a randomized-block design where the presentation order was random-

ized. Playback sequences were repeated for an additional 7 d, in which the stimuli were shown to each lizard, but in reverse order to counterbalance order effects. Each subject hence saw each stimulus twice for a total of 280 stimulus presentations.

### Experiment 2

We tested the same 20 subjects over another test period of 10 consecutive days. Each subject was shown one of five stimulus sequences. One sequence represented a control stimulus with a lizard sitting motionless on a natural perch.

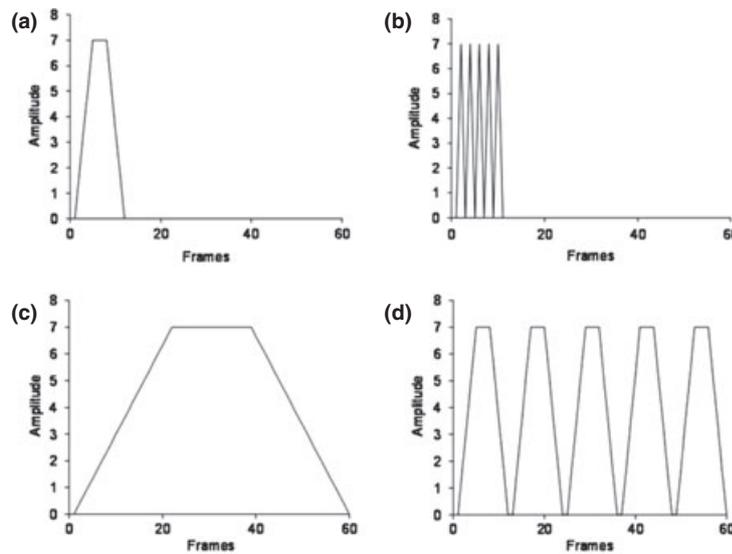
Here, we created four stimuli (see Fig. 3) to test the relative importance of changes in duration (two levels: Long and Short) and PUBRs frequency (two levels: 1 PUBR and five consecutive PUBRs) to elicit behavioural responses from receivers. In addition to manipulating the number of consecutive PUBRs for display duration, we also modified the speed of each PUBR (Fig. 3). We formulated four predictions based on the receiver behavioural responses: the probability of an orienting response and response latency (Fig. 3). (1) If duration is the most salient signal feature, we should expect the combined response to the two shorter duration stimuli (Short-1 and Short-5) to be less conspicuous than the combination of the two lengthier video sequences (Long-1 and Long-5). (2) If conspecific recognition is the most important feature, we should then expect to observe a greater combined response effort towards the two most natural stimuli (Short-1 and Long-5) compared with the combined response to the two unnatural sequences (Short-5 and Long-1). (3) If both duration and speed are important, we should expect a greater response to the stimuli with both design characteristics (Short-5 and Long-5), but at a similar level. As a consequence, behavioural response to Short-1 and Long-1 stimuli would also be similar, but less than the Short-5 and Long-5 sequences. (4) Lastly, if speed (velocity and acceleration) is the critical design component, our focal lizards would respond more to the fastest sequence (Short-5), followed by equivalent responses to the most natural displays (Short-1 and Long-5). The least salient would thus be Long-1, with slowest velocity traits.

Similarly to experiment 1, we used a randomized design where playback presentation was randomized. Each subject saw each of the five sequences within the first five consecutive days. Playback was repeated for an additional 5 d, and the stimulus order presentation was again reversed to counterbalance order effects. Each individual was

**Table 1:** Stimuli used in playback

Stimulus	Number of Consecutive PUBRs	Duration (in seconds)
Control	Still Lizard	0
PUBR1	1 PUBR	0.48
PUBR2	2 PUBRs	0.96
PUBR3	3 PUBRs	1.44
PUBR4	4 PUBRs	1.92
PUBR5	5 PUBRs	2.4
TF	1 TF	1.92

Duration replicated population typical mean values for push-up body rocks (PUBRs) and tail-flick (TF) motor patterns.



Stimulus characteristics				Predictions	
Display	Corresponding figure	Duration	PUBRs	Design component	Response to stimulus
Short-1	a	12 frames 0.48 s	1	Duration	$(\text{Short-1} - \text{Short-5}) < (\text{Long-1} - \text{Long-5})$
Short-5	b	12 frames 0.48 s	5	Recognition	$(\text{Short-1} - \text{Long-5}) > (\text{Short-5} - \text{Long-1})$
Long-1	c	60 frames 2.4 s	1	Interaction	$(\text{Short-5} = \text{Long-5}) > (\text{Short-1} = \text{Long-1})$
Long-5	d	60 frames 2.4 s	5	Speed (velocity)	$\text{Short-5} > \text{Short-1} = \text{Long-5} > \text{Long-1}$

**Fig. 3:** Experiments 2: Push-up body rock characteristics displayed by the digitally animated lizard and predictions for the effects of variation in duration and speed of push-up body rock. (a) Short-1 (one PUBR at normal speed), (b) Short-5 (matched duration, each of the 5 PUBRs at 5x speed), and (c) Long-1 (one PUBR at 1/5 speed) and (d) Long-5 (5 PUBRs at natural speed). Display durations exhibited by the animated lizard were initially set in frames (25 frames/s PAL standard); corresponding display durations in seconds are also presented.

presented with each stimulus twice, for a total of 200 stimulus presentations across all experimental subjects.

**Statistical analysis**

In Experiment 1, we used a univariate ANOVA to investigate the effect of display duration on the probability of orienting responses of our focal lizards. We employed Tukey's *post hoc* tests to check for differences across all treatments (1-5 PUBRs, 1TF and the control treatment).

Latency data were log transformed to normalize the distribution. We conducted a univariate ANOVA

to examine the overall main effect of duration on latency to respond. We also used Tukey's *post hoc* analyses to identify differences between display stimuli for response latency.

In Experiment 2, we conducted a univariate ANOVA to examine the overall main effect of duration (levels: Short and Long), PUBRs frequency (two levels: 1 PUBR and 5 consecutive PUBRs) and the interaction between these factors for both probability of an orienting response and response latency compared with the control sequence. Similarly to Experiment 1, latency data were log transformed. We used Tukey's *post hoc* tests to identify differences between display stimuli.

All analyses were conducted with SPSS 15 (SPSS Inc., Chicago, IL, USA) for Windows, and thereafter, all results are expressed as a mean and its standard error.

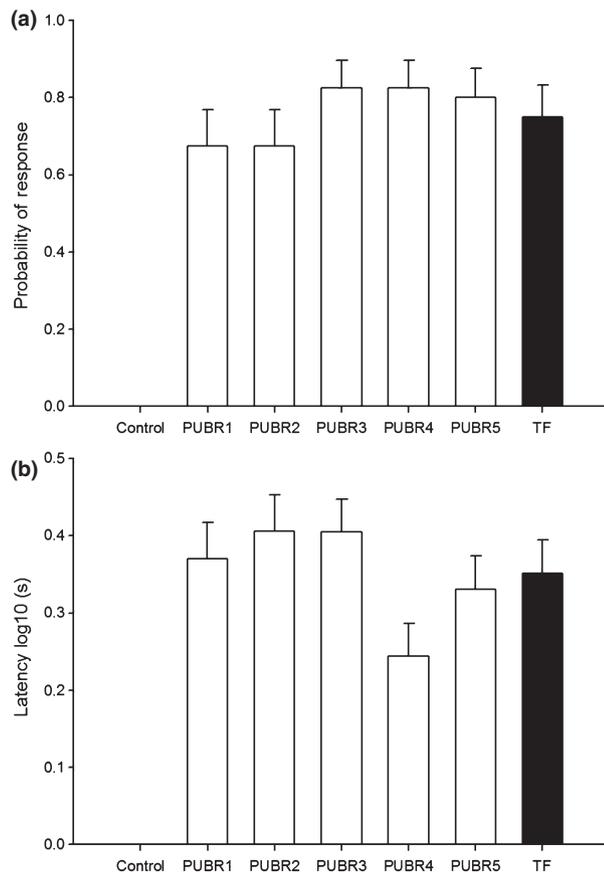
## Results

### Experiment 1

Even though a significant effect of display duration on the probability of an orienting response of focal lizards has been detected ( $F_{6,273} = 21.90$ ,  $p < 0.001$ ) (Fig. 4a), we suspected that this effect was mostly because of the absence of behavioural responses of the focal lizards to the control sequences. When removing all control treatment data from the analysis, the significant effect was no longer detected ( $F_{5,234} = 1.07$ ,  $p = 0.38$ ). In addition, our Tukey's *post hoc* analysis did not reveal any significant differ-

ences between the experimental treatments. This suggests that an increase in the length of the display from 1 PUBR to six consecutive PUBRS did not affect the probability of an orienting response from a receiver.

Despite the absence of an overall significant effect of duration on focal lizards response latency ( $F_{5,176} = 1.97$ ,  $p = 0.08$ ), we found significant differences in response latency between one (PUBR1) and three (PUBR4) push-up body rocks (Tukey's *post hoc* test:  $p = 0.04$ ), two (PUBR2) and four (PUBR4) push-up body rocks (Tukey's *post hoc* test:  $p = 0.01$ ), and between three (PUBR3) and four (PUBR4) push-up body rocks (Tukey's *post hoc* test:  $p < 0.008$ ) (Fig. 4b, see also Table 2 for untransformed data). Four consecutive PUBR displays exhibited by the digitally animated lizard were more effective in eliciting faster responses than one, two or three consecutive PUBRs. We did not detect any other significant difference in any other combinations, suggesting no difference in display conspicuousness greater than four PUBRs.



**Fig. 4:** Experiment 1: (a) probability of an orienting response (mean  $\pm$  SEM) shows no difference in orientation to all stimuli and (b) variation of latency response as a function of the number of PUBRs exhibited (mean  $\pm$  SEM), longer duration reduces subject latency.

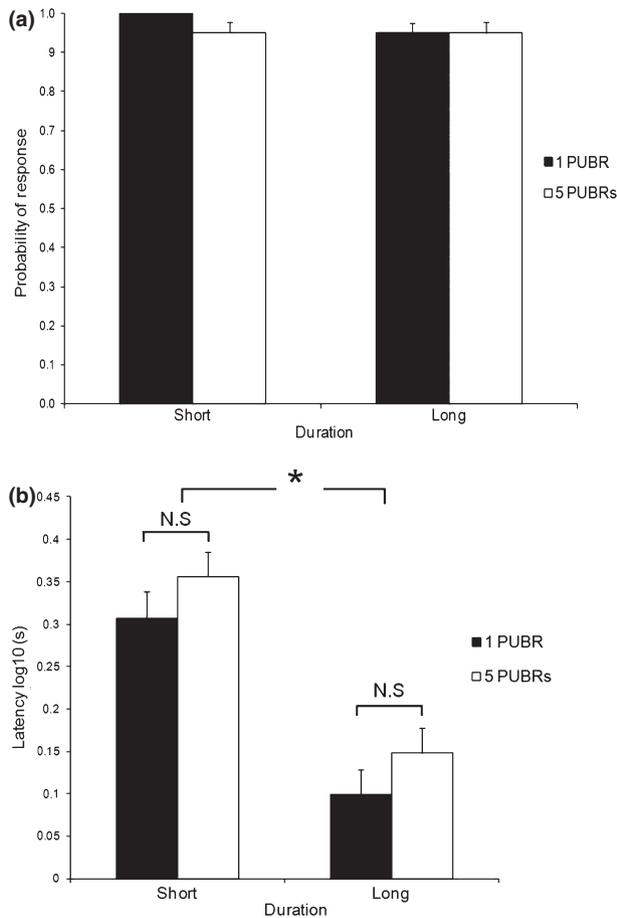
### Experiment 2

We found neither a significant main effect of signal duration ( $F_{1,195} = 0.94$ ,  $p = 0.33$ ), PUBRs frequency ( $F_{1,195} = 0.77$ ,  $p = 0.38$ ), nor a significant interaction between these two factors ( $F_{1,159} = 0.86$ ,  $p = 0.36$ ; Fig. 5a) for probability of an orienting response to the different display combinations. Our Tukey's *post hoc* analysis did not reveal any significant difference between the two levels of duration (short vs.

**Table 2:** Focal Jacky dragons' latency to respond to the different presented stimuli (untransformed data) in the two experiments

Stimulus	Latency (mean values in seconds)	Standard
<i>Experiment 1</i>		
Control	Absence of response	–
PUBR1	2.57	0.268
PUBR2	2.85	0.268
PUBR3	2.93	0.242
PUBR4	2.06	0.240
PUBR5	2.44	0.246
Tail-flick	2.67	0.254
<i>Experiment 2</i>		
Duration – frequency		
Short-1	2.17	1.09
Short-5	2.28	0.83
Long-1	1.38	0.56
Long-5	1.41	0.56

All results are expressed as a mean and its standard error.



**Fig. 5:** Experiment 2: (a) response probability (mean  $\pm$  SEM), illustrating lack of significant variation and (b) subjects had shorter response latencies (mean  $\pm$  SEM) to stimuli with greater duration. \* $p < 0.05$ .

long:  $p = 0.60$ ) or between the two levels of PUBRs frequency (1 PUBR vs. five consecutive PUBRs:  $p = 0.64$ ) even though both significantly differed from the control treatment (sequence of a lizard sitting motionless on a perch) that failed to elicit any behavioural response from the focal subjects.

Our focal lizards responded faster to longer duration displays (Fig. 5b). There was a significant main effect on response latency for duration ( $F_{1,195} = 9.79$ ,  $p = 0.002$ ), but not PUBRs frequency ( $F_{1,195} = 0.09$ ,  $p = 0.76$ ) or for the interaction between these two factors ( $F_{1,195} = 0.65$ ,  $p = 0.42$ ). Our Tukey's *post hoc* tests showed that lizards had a shorter latency to respond to the long duration sequences than to the shorter duration sequences (short vs. long:  $p = 0.006$ ) (Table 2). Combined with the absence of a significant difference of response latency to changes in PUBRs frequency (Tukey's *post hoc* test: 1 PUBR vs. five consecutive PUBRs,  $p = 0.95$ ), our results showed that duration is the critical feature of

the aggressive signal efficiency in the Jacky dragon (see predictions in Fig. 3).

## Discussion

Our results revealed that duration is critically important for signal efficiency in the aggressive push-up body rock display, as it has been previously demonstrated for the TF (Peters & Evans 2003b). We found that, as in the TF, signal efficiency of the push-up body rock display is not dependent on speed, suggesting that duration may be the common determinant of efficiency in Jacky dragon display motor patterns. In addition, our results suggested that the number of consecutive PUBRs displayed also affects the efficiency of the aggressive signal to elicit a behavioural response from an observer.

The results of Experiment 1 suggested that an increase in the overall display duration to four consecutive push-up body rocks exhibited by our digitally animated lizard induced the maximal response from observers, which was represented by a 15% increase in overall probability of an orienting response. Shorter displays made of one to three push-up body rocks are less effective in eliciting an orienting response from focal lizards than lengthier displays made of four consecutive push-up body rocks. However, when the diffused sequence was made of five consecutive push-ups body rocks, no significant difference of orienting responses of focal lizards was observed between four and five push-up body rocks or when compared with the matched duration of a population typical TF.

In Experiment 2, we found that speed is not a critical feature for signal efficiency in the aggressive push-up body rock display. Like the TF (Peters & Evans 2003b), there was neither a reduction in efficiency to induce responses from observers when the motor pattern is slow (Long-1) nor an increase in efficiency when speed was experimentally increased (Short-5). Similarly, we did not find any difference in conspicuousness when compared with a single PUBR (Short-1) matched to normal duration. Lizards produced similar orienting responses to all motor pattern combinations, but seemed to respond faster to displays that were longer (Long-1 and Long-5). Thus, aggressive display length seems to be an important characteristic in signal design and efficiency. At first glance, these results can be intriguing because display speed has been reported to be the most important feature of visual displays in other species (e.g. *Anolis*), where animals displayed faster motion signals under noisy environments

(Fleishman 1988; Ord et al. 2007). However, our results support Peters et al. (2007)'s findings reporting that *Amphibolurus muricatus* increased signal length rather than speed when signalling against fast moving vegetation background, suggesting that *A. muricatus* adopted an alternative strategy to cope with an increase in environmental visual noise. According to Peters et al. (2007; 2008), such divergence in visual signal design is under the influence of the environmental signalling conditions. Jacky dragons are generally found in visually complex semiopened habitats ranging from coastal heathlands and shrublands to sclerophyll forests mostly composed of *Banksia* spp. Under windy conditions, displaying visual signal at speeds faster than the speed of the wind-blown vegetation motion may be difficult and energetically costly and producing lengthier displays seems to improve signal efficiency. Therefore, environmental conditions may have provided similar selection pressures that have shaped visual displays in *Anolis* lizards (Fleishman 1988, 1992; Fleishman & Persons 2001).

An interesting result is certainly that the number of consecutive push-up body rocks that can be displayed seems not open-ended. After three push-up body rocks, response probability was similar across treatments, and this seems to reflect the results by Peters & Evans (2003a,b) where lengthy TFs elicit a comparable response pattern. This prediction could be further tested empirically by using supernormal stimuli. In a previous study, female sticklebacks (*Gasterosteus aculeatus*) were found to reliably choose dummy males that were artificially enlarged to 25% of the length of the largest male (Rowland 1989). To test this, the computer animation technique can provide an effective means allowing us to design supernormal display durations that could surpass five push-up body rocks. If the results maintain an asymptotic trend, then there may be no benefit for displaying more aggressive push-up body rocks. However, if the response pattern decreases dramatically, this limitation may be indicative of an honest signal for condition.

The production of lengthy signals may entail two important costs: (1) a greater energetic demand (Ryan 1998; Vehrencamp et al. 1989) and (2) a higher probability of predation owing to conspicuousness (Yasukawa 1989). Animals may hence trade-off efficiency against the possibility of exhaustion, particularly when strength and endurance are required for future social interactions (Magnhagen 1991; Endler 1992; Brandt 2003). It is thus likely that an individual's capacity to withstand the

demands of energetic costs that may cause one to repeatedly win contests (cichlid, *Tilapia zillii*: Neat et al. 1998) or successfully invade an occupied territory (fiddler crab, *Uca lactea perplexa*: Matsumasa & Murai 2005). In a study where side-blotched lizards (*Uta stansburiana*) have been experimentally fatigued, therefore reducing their endurance to perform continuous signalling, experimental subjects were found to be handicapped when it came to generating aggressive push-up threat displays during staged encounters (Brandt 2003; Brandt & Allen 2004). In addition, Kotiaho et al. (1998) reported that an increase in the drumming display performed by courting male wolf spiders (*Hygrolycosa rubrofasciata*) enhances conspicuousness; however, this sexual signalling is highly energetically demanding (four times higher than locomotion), thus constraining the duration of the drumming display. Moreover, male wolf spiders that were induced to exhibit more intense and vigorous drumming displays were found to suffer higher mortality, an effect that was nevertheless mediated by male body condition (Kotiaho 2000). This indicates, thus, that producing and sustaining lengthy signals may entail some important metabolic costs that can ultimately impact animals' fitness.

Conspicuous signals designed to stimulate conspecific sensory systems may also inadvertently attract the attention of predators (Smith 1992). Lengthy displays can increase the potential risk of predation (Ribeiro et al. 2003; Brown et al. 2004). For example, female greater wax moths (*Galleria mellonella*) decrease the duration of their wing fanning display in response to male ultrasonic calls during courtship to further reduce the conspicuousness of this signal to echolocating predator bats (Jones et al. 2002).

Our results indicate that the number of consecutive push-up body rocks that an individual can display is constrained, which suggests an eventual trade-off between peak sensitivity and costs. Stronger individuals may produce more displays over time, but here, it seems that Jacky lizards are restricted to five consecutive push-up body rocks. It may also seem likely that stronger individuals may perform more consecutive push-up body rocks, but are possibly limited by the risk of predation and cost of energetic constraints. Although we did not specifically test for a trade-off between signalling and energetic constraints, our results hint that this is a likely consideration, and we propose that we should examine the cost of energetic demands on Jacky signals in future studies. In particular it will be of great interest to test whether the production of lengthy and repetitive displays in Jacky dragons plays a critical

role during assessment of fighting ability of opponents and whether the opponent that invests the greatest amount of energy into the production of lengthy signals would increase its chances of victory; a prediction akin to those of the energetic war of attrition model (Payne & Pagel 1996; Payne & Pagel 1997a,b).

One possible limitation of the present study could be the control sequence employed during the experimental tests. In both experiments, we used a video sequence of a computer-generated lizard sitting motionless on a perch as an experimental control. This sequence did not trigger any behavioural response from the experimental lizards through all the control trials. A better control would have been the use of a 'null control' sequence that would only include the moving background without the motionless computer-generated lizard. However, given the absence of orienting responses in the control treatment, we are confident that our focal lizards did not simply orient their gaze towards the screen in response to the natural moving background of wind-blown vegetation.

Among lizards, the *Anolis* genus has become one of the most important model systems for the study of motion-based signalling. Numerous studies have been conducted to explore the physical characteristic of lizard visual stimuli and the influence of environmental signalling conditions (Fleishman 1992; Peters et al. 2002, Ord et al. 2007; Peters et al. 2008; Ord & Stamps 2008) as well as investigating display design differences at the population (Martins et al. 1998; Leal & Fleishman 2004; Bloch & Irschick 2006) and species level (Ord & Martins 2006; Ord et al. 2007). However, if we are to understand the design characteristics of signals used in lizard communication, then it appears important to also consider the trade-off between signal efficiency and costs.

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