



# Galápagos lava lizards (*Microlophus bivittatus*) respond dynamically to displays from interactive conspecific robots

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## Abstract

In many species, outcomes of male duels determine access to females and, ultimately, male reproductive success. Ritualization of behavior in male contests can reduce the probability of injury, which benefits both contestants. Components of ritualized combat often include postures and displays that showcase a male's quality in a sequential assessment of fighting ability. Among the most common contest acts in iguanine lizards are bobbing displays. Investigations of bobbing display dynamics often include experimental "playbacks," in which video or robotic representations of conspecifics are presented to subjects. In most "playback" research, pre-programmed stimuli exhibit behavior that is independent of subjects' responses, despite the fact that actual animal contests are highly interactive. In the present study, we utilized a robotic Galápagos lava lizard (*Microlophus bivittatus*) to investigate the importance of interaction in simulated contests under field conditions. Using a matched pairs design where each subject experienced two behavioral variants of the robotic stimulus, we tested the effect of a robot that displayed immediately following a subject's display versus when the same robot display was postponed 30 s. Results showed that immediate response from the robot stimulated subjects to display significantly more often than when the stimulus was delayed. We speculate that subjects perceived a rapid response from their robotic contestant as being more aggressive than a delayed response. We discuss our results in light of relevant previous work, and we suggest possibilities for future research using interactive lizard robots.

## Significance statement

Some of the most impressive examples of ritualized animal behavior can be observed in male contests for access to reproductive females. The use of stereotyped displays in such duels allows males to assess one another's quality while avoiding dangerous fighting that can lead to injury. For example, males in many lizard species perform bobbing displays where contestants respond to each other in reciprocal fashion. In this study, we used a realistic lizard robot as a stand-in for a contestant in simulated contests. We found that an immediate display response by the robot to a subject's bobbing display stimulated subjects to display significantly more often than when the robot's response was delayed by 30 s. To our knowledge, this is the first interactive robot "playback" experiment with lizards. Future research will further explore the "rules" underlying display behavior in lizard contests.

**Keywords** Animal contests · Assessment of fighting ability · Bobbing displays · Communication · Lava lizard

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## Introduction

In many animal species, a male's reproductive success is determined by his ability to maintain exclusive access to one or more females (Darwin 1871; Andersson 1994). Defending access to females can be costly, however, and frequently involves combat with the risk of injury (Lappin and Husak 2005; Rico-Guevara and Hurme 2019). Male combat also distracts combatants from being vigilant for predators (Jakobsson et al. 1995; Kelly and Godin 2001). Risks associated with territory defense may be reduced by the conflict

resolution facilitated through ritualized contests (Huntingford and Turner 1987; Amott and Elwood 2009).

In some species, male contests take the form of a “war of attrition,” where a contestant’s endurance is tested through repeated, energy-consuming displays (Marden and Waage 1990; Kemp and Alcock 2003). In other species, contests proceed as a sequential assessment of fighting ability (Enquist and Leimar 1983; Leimar et al. 1991), where outcomes can be influenced by body size (Pratt et al. 2003; Green and Patek 2018; Lobregat et al. 2019), residency status and habitat resources (Jenssen et al. 2005; Fuxjager et al. 2010; McLain et al. 2019), contest experience (Kar et al. 2016), familiarity with an opponent (Johnsson and Åckerman 1998; López and Martín 2001), bite force and its anatomical correlates (Husak et al. 2006, 2009; Lappin et al. 2006), or some combination of these factors (Kemp et al. 2006). In a sequential assessment contest, opponents usually have a choice to escalate the duel with increasingly aggressive behavior, de-escalate through the use of submissive or appeasement gestures (Crews 1975; Martins and Lacy 2004; Van Dyk and Evans 2008), or terminate the conflict by retreating (Green and Patek 2018).

One conspicuous aspect of ritualized aggression in contests is the use of stereotyped signals. In diurnal lizards, male contests often include postures, color changes, and motions (display modifiers; Jenssen 1977) that highlight or exaggerate features associated with fighting prowess, like body size, skull dimensions, intensity of aggression, or intent to bite (Greenberg 1977; Jenssen 1979; Macedonia and Stamps 1994; Lappin et al. 2006). Perhaps the most striking feature of lizard contests is the bobbing display: a stereotyped sequence of movements in which the head and limbs are abruptly displaced in the vertical plane (Carpenter and Ferguson 1977). Lizard bobbing displays typically exhibit species-specific structure and occur not only in contests but also during undirected territorial signaling, courtship (Carpenter and Ferguson 1977; Jenssen 1977; Martins and Lamont 1998; Martins et al. 2004; Ord and Martins 2006), and anti-predator behavior (Leal and Rodríguez-Robles 1997; Leal 1999).

Several techniques have been employed in experimental studies of lizard contests and bobbing displays. Visual “playbacks” (film and video) have been used to test conspecific display recognition in the contexts of male competition and female mate preference (Jenssen 1970; Macedonia and Stamps 1994; Macedonia et al. 1994; Van Dyk and Evans 2007; Van Dyk et al. 2007; Woo and Rieucau 2012). Likewise, lizard robots (Frohnwieser 2016) have been used in similar investigations, and the growing list of lizard genera now includes *Sceloporus* (Martins et al. 2005; Smith and Martins 2006; Kelso and Martins 2008; Thompson et al. 2008; Nava et al. 2012), *Anolis* (Ord and Stamps 2008, 2009; Partan et al. 2011; Macedonia et al. 2013, 2015;

Gunderson et al. 2018), *Microlophus* (Clark et al. 2015, 2016, 2017), *Draco* (Klomp et al. 2017), *Sarada* (Zambre and Thaker 2017), and *Psammophilus* (Batabyal and Thaker 2018). In most of these experiments, stimuli have been presented in a predetermined fashion that was unaffected by subjects’ responses. However, as animal communication frequently takes the form of ongoing signaling interaction, controlling one side of this exchange is a primary goal of interactive playbacks (Evans 1991; Krause et al. 2011; King 2015). In a simulated contest, evaluating how the interplay between contestants affects contest dynamics requires a stimulus that reacts to the conditional responses of a challenger. To date, only a few video playback experiments with lizards have been interactive (Ord and Evans 2002; Van Dyk and Evans 2008), and to our knowledge, no interactive playback experiment has utilized a realistic lizard robot.

In this study, we describe the first experiment that features an interactive lizard robot as a contestant in simulated dyadic aggressive contests. In this experiment, the timing of subjects’ bobbing displays determined the timing of the robot’s bobbing display “responses.” We used a within-subject matched pairs design, where each subject experienced two robot display sequences that differed only in how quickly they followed a subject’s display. In one treatment, the robot began displaying immediately after the end of the subject’s display, and in the other treatment, the same robot display sequence was delayed 30 s following the subject’s display. Given that prior research into lizard contests has shown that the more aggressive member of a combating pair tends to display more often than the less aggressive contestant (Carpenter and Ferguson 1977; Stamps and Krishnan 1997; Husak 2004), we reasoned that an immediate response from the robot might be perceived as more aggressive and elicit more display from subjects than would a delayed response from the robot. Specifically, we hypothesized that the immediate robot response would elicit greater sums of display duration and shorter display latencies from subjects than those evoked by the delayed robot response.

## Materials and methods

### Subjects and study area

Galápagos lava lizards (*Microlophus* spp., Tropiduridae) comprise nine allopatric species from two radiations (Eastern and Western) in which evolutionary relationships are well established and island colonization sequences have been deduced (Kizirian et al. 2004; Benavides et al. 2009). As typical iguanians, all lava lizards exhibit female-defense polygyny with male-male competition for territories and male-biased sexual size dimorphism in snout-vent length (Clark et al. 2015; Rowe et al. 2019). Our study species, *Microlophus*

*bivittatus* (Fig. 1a), is one of only two species in the Eastern radiation and is endemic to the Galápagos Island of San Cristóbal.

### Robot construction and display programming

Our methods for constructing lava lizard robots and programming their displays have been detailed elsewhere (Clark et al. 2015, 2016, 2017). Briefly, adult male-sized robot bodies (~75 mm SVL) were hand-carved from wood and secured with eyelets to a pushrod and servomotor that controlled the robot displays. Each half (left and right) of the robot body was covered with a sticky-backed, high-resolution photo, scaled to life-sized proportions of an adult male *M. bivittatus* standing in profile. The image was mirrored in Adobe Photoshop® and printed at a local commercial photo center. The robot's latex hind limbs and tail were cast from a plaster of Paris mold of a preserved *Microlophus* specimen. These hindquarters were glued to the robot's wooden body and to the top of the case that housed the mechanism responsible for robot movement (Fig. 1b). The robot's forelimbs (also glued to the wooden body and housing case) were made of thick yarn that flexed and extended easily when the front half of the robot body was moved upward and downward during displays (video clips and an image of subjects interacting with the robot are available as [Online Resources](#)).

To construct the MIDI controller files that animated the robot (Logic Pro v. 9.1 for Macintosh OS), we modeled our *M. bivittatus* bobbing sequences after Carpenter's (1966) representative display action pattern (DAP) graph—a time X amplitude plot for this species. Two variants of the stimulus were constructed that comprised a volley (i.e., series) of three “signature” displays (Jenssen 1977) lasting a combined total of

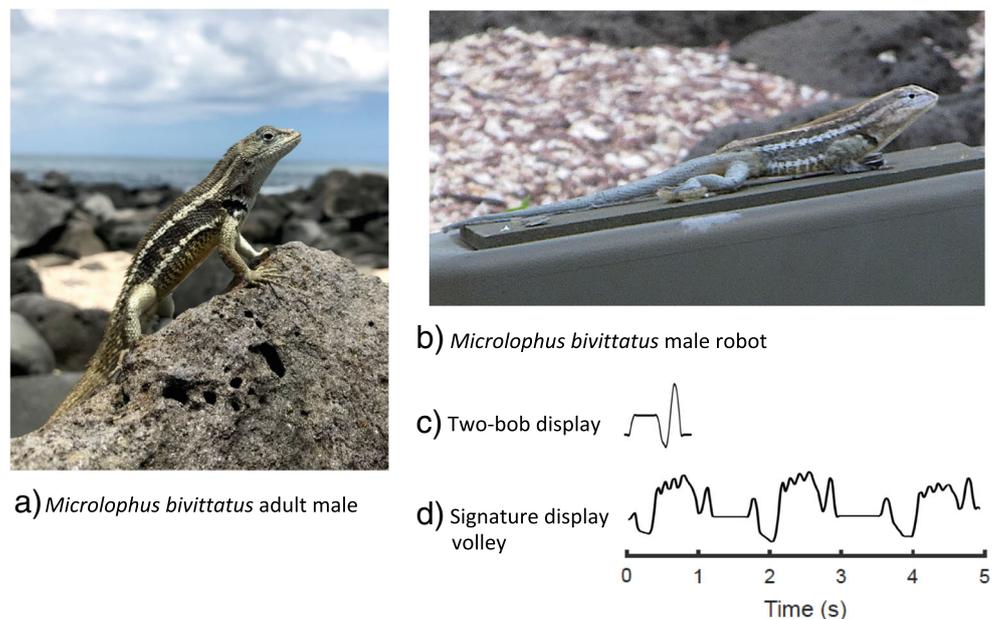
5 s, plus a 30 s pause. We use Jenssen's (1977) term “signature display” to distinguish this advertisement display from a second type of bobbing display that is associated exclusively with movement or locomotion—the two-bob display (see Subject Responses Scored below, Fig. 1, and [Online Resources](#)). Among the *Microlophus* species that we have studied to date (Clark et al. 2015, 2016, 2017), *M. bivittatus* is the only species to produce a bobbing display type other than its signature display (Macedonia et al. 2019). Our immediate response sequence triggered the robot to begin displaying at the moment a subject's display was completed, whereas our delayed response stimulus initiated a 30-s lag between the end of a subject's display and the start of the robot's display. In both sequences, the robot displayed automatically every 30 s unless the clock was reset by a subject's display (Fig. 2).

### Robot presentation protocol

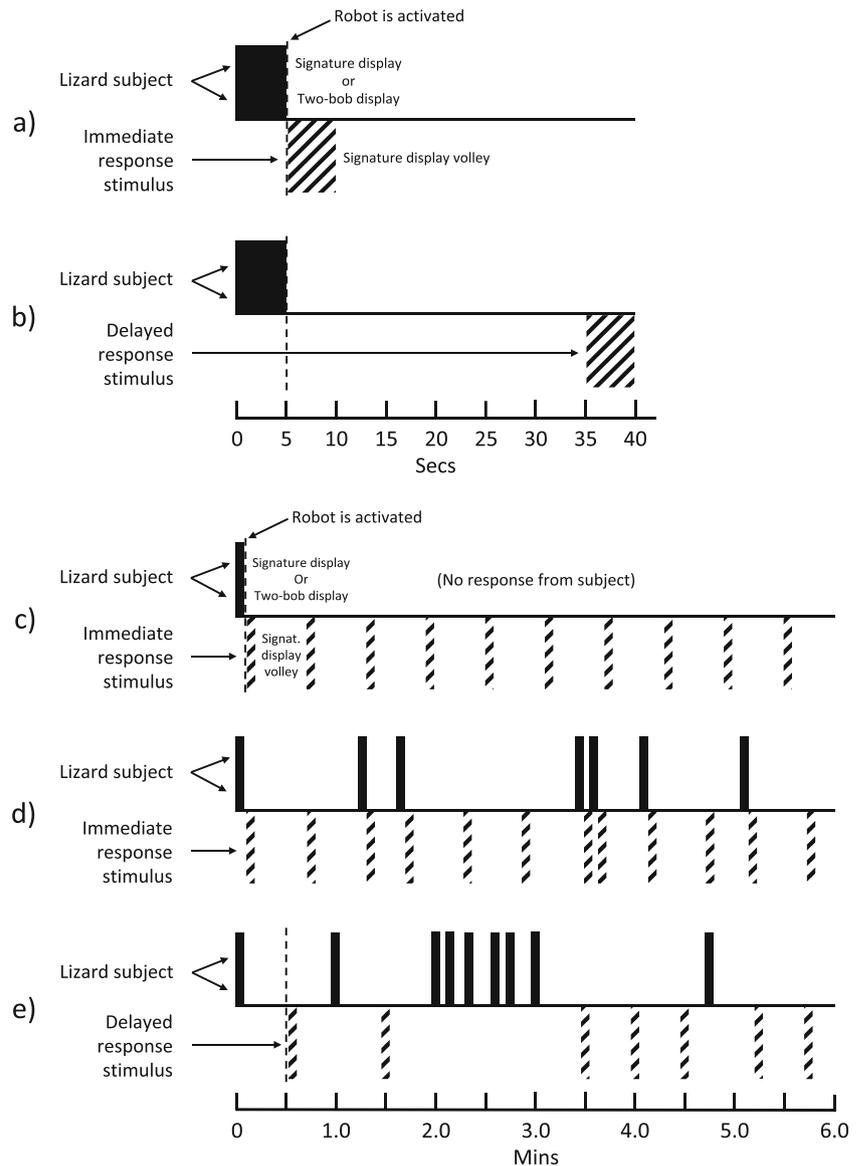
We conducted interactive robot playbacks with adult male *M. bivittatus* in, and around, Puerto Baquerizo Moreno (0° 53' 45.13" S 89° 36' 24.70" W) on San Cristóbal (datum = WGS84). Robot stimuli were presented to subjects from February 23 to March 1, 2018, between 0900 and 1700 h daily, except during periodic rains. Daytime temperatures ranged from ~25–30 °C. We traversed dirt roads and paths while visually searching rock walls and outcrops to locate potential adult male subjects (visual estimate of  $\geq 65$  mm SVL). Upon choosing a subject, we positioned our robot at a distance of approximately 1–3 m from it and at a similar height above the ground as the subject (Fig. S1; see also online supplemental figures in Clark et al. 2017).

To remotely control the robot in field trials, we exported a Logic Pro MIDI controller file to an iPod touch using a Line 6

**Fig. 1** Representative *Microlophus bivittatus* **a** adult male, **b** robot of adult male, **c** two-bob display action pattern (DAP) graph, and **d** signature display volley DAP graph illustrating three consecutive head-bob displays



**Fig. 2** Schematic illustration of **a**, **b** the two robot display sequences used and **c–e** simulated subject-robot interactions: **a** robot immediate response stimulus, **b** robot delayed response stimulus, **c** absence of subject display to the robot immediate response stimulus, **d** subject responding to the robot immediate response stimulus, and **e** subject responding to the robot delayed response stimulus



MIDI Mobilizer. If our intended subject did not display or flee while we were readying the robot for a trial (~2–3 min), a stimulus sequence was initiated. Each subject received a trial that was divided into two equal parts or “half-trials.” Presentation order of the two stimuli was alternated (counterbalanced) with each subject. Although we sought to conduct a 6-min half-trial presentation for each subject, for several reasons, attaining this goal proved difficult under field conditions. First, subjects frequently changed locations when responding to the robot and sometimes became obscured by rocks or vegetation. We attempted to correct for such events in real time by providing additional cycles of robot display, and this tactic sometimes resulted in half-trials longer than 6 min. Second, if a subject fled during its second half-trial presentation before 6 min had transpired, that half-trial was shorter than 6 min. Finally, if a subject continued to display toward

the robot following the final robot display in a half-trial, we continued to record (and we subsequently scored) that subject’s responses until ceased to respond for 15 s. Importantly, given that we analyzed subjects’ responses as proportions of their half-trial durations, departures from our goal of achieving 6-min half-trials did not introduce systematic bias (see [Statistical Analysis](#) section below).

During playbacks, one investigator controlled the robot’s interaction with the subject while the other investigator video-recorded the trial. As we were not permitted to capture and mark subjects, we avoided retesting subjects by moving linearly along a path at a given location and by not returning to that specific area to conduct additional trials (see Clark et al. 2017 for additional details). Subjects’ responses were recorded on a tripod-mounted video camera (Panasonic Full HD HC-V770 WiFi) that was positioned ~2 m from the robot.

Video of subjects' trials was combined in real time with a separate video signal coming from a camera (same model camcorder) that was trained on the robot. The two video signals were combined to produce a composite image (i.e., "picture-in-picture"), in which a smaller image of the displaying robot appeared in the lower left-hand corner of the screen that contained the image of the test subject. This technique facilitated scoring responses of test subjects with direct reference to the timing of the robot's displays.

### Subject responses scored

We used several measurement variables (durations) and a frequency variable (counts) to quantify subjects' responses to our robot stimuli (Table 1). Subjects regularly performed two distinct types of bobbing displays: a species-specific ("signature") display and a quick "up-down-up-down" two-bob display (Table 1; Fig. 1c, d). The very brief (~0.3–0.5 s) two-bob display occurred frequently and always was followed immediately either by locomotion or a change in subject body orientation with respect to the robot (for video clips of these display types, see [Online Resources](#)).

We used event-recording software (Scribe v. 4.2, Duke and Stammen 2011) to mark the video locations of subjects' responses to our robotic stimuli. The individual who gathered the data from the trial videos was blind to the hypotheses and goals of the experiment. The total amount of time (in seconds)

that subjects spent performing signature displays was calculated from trial videos by measuring the durations of signature displays each time they occurred and then summing these durations for each half-trial. In addition, the latencies of subjects to respond to robot displays with a signature display were computed as the time lag (in seconds) following the last robot display volley that had occurred prior to the response of the subject.

In addition to our measurement variables, we calculated frequencies of subjects' two-bob displays and attempted to quantify two display modifiers (see the [Introduction](#) section) that sometimes accompanied subjects' signature displays. These modifiers included "gular expansion" (enlargement of the ventral area of the throat) and "lateral presentation" (re-orientation of the body to an angle roughly perpendicular to the robot while simultaneously compressing the sides inward, i.e., "lateral compression," Jenssen 1977, 1979, or "sagittal compression," Jenssen et al. 2005). Ultimately, we deemed that neither variable could be scored from the field trial videos with sufficient accuracy to be included in our analyses.

### Statistical analysis

Twenty-four adult male *M. bivittatus* subjects received full playback trials (i.e., two half-trials in tandem). To be included in our analyses, we required subjects to respond with a bobbing display at least once to the robot stimulus during a half-

**Table 1** Terms and response variables as defined in this study

Term	Definition
a. Display action pattern (DAP)	a. Line graph of a bobbing display that depicts changes in head amplitude (y-axis) over time (x-axis).
b. Signature display	b. Species-specific bobbing display performed in agonistic, courtship, and male-alone contexts
c. Two-bob display	c. Quick "up-down-up-down" bobbing display, followed immediately by short-distance movement or locomotion.
d. Display volley	d. Series of two or more bobbing displays performed within 3 s of each other.
e. Immediate robot response stimulus	e. Volley of 3 signature displays that, when triggered, begins immediately following end of a subject's display
f. Delayed robot response stimulus	f. Volley of 3 Signature Displays that, when triggered, begins 30s following end of a subject's display
Measurement variables (durations)	Definition
g. Half-trial duration	g. Presentation period for a given robot display sequence during the 1st or 2nd half of a subject's trial
h. Robot display duration sum	h. Amount of time the robot spent performing displays during a half-trial
i. Signature display duration sum	i. Amount of time a subject spent responding to a robot display sequence with signature displays in a half-trial
j. Signature display latency	j. Median time elapsed from initiation of a robot display volley to a subsequent signature display by the subject
Frequency variable (counts)	Definition
k. Two-bob display frequency	k. Total number of two-bob displays performed by a subject during a half-trial

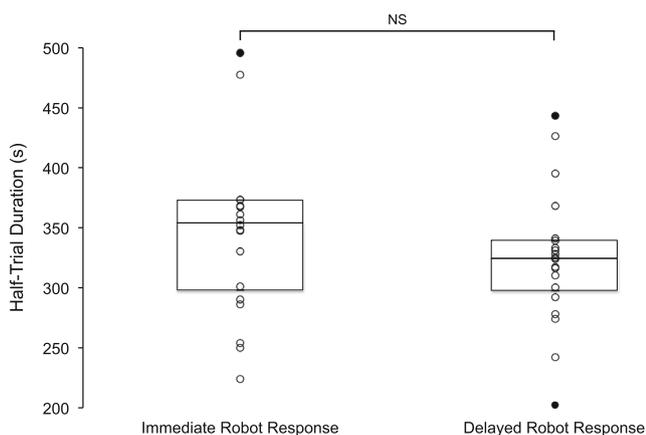
trial. Three subjects failed to respond in one of their half-trials, and one subject's trial was accidentally not recorded, leaving 20 subjects for data analysis. Prior to analysis, time spent off-camera by a subject was deducted from its half-trial durations.

As in our previous experiments using robotic lava lizards (Clark et al. 2015, 2016, 2017), our response variables were converted to proportions of trial durations (in the present study: half-trial durations) prior to statistical analysis. Subjects that did not respond in a half-trial with a signature display were excluded from latency-to-respond calculations, rather than assigning such individuals an arbitrary maximum latency duration. Given that half of our subjects witnessed the immediate response stimulus first, whereas the remaining subjects saw the delayed response stimulus first, we tested the magnitude of subjects' responses by stimulus order (regardless of stimulus type), as well as by stimulus type (regardless of stimulus order).

Exploratory data analysis in SPSS (v 21.0, IBM Inc., Armonk, NY) revealed that many of our response variables were non-normally distributed. As several variables still remained non-normal following attempts to transform them, we used the Wilcoxon matched-pairs signed-rank test to test for differences in subjects' responses to the two robotic stimuli. In the Wilcoxon tests, all  $P$  values reported are two-tailed and were performed in Vassarstats (Lowry 2014).

## Results

Half-trial durations did not differ significantly between the immediate robot response treatment and delayed robot response treatment (Wilcoxon  $Z = -1.75$ ,  $P = 0.08$ ,  $N = 20$ ; Fig. 3). Although the order in which subjects witnessed the two robot stimuli had no detectable effect on robot display

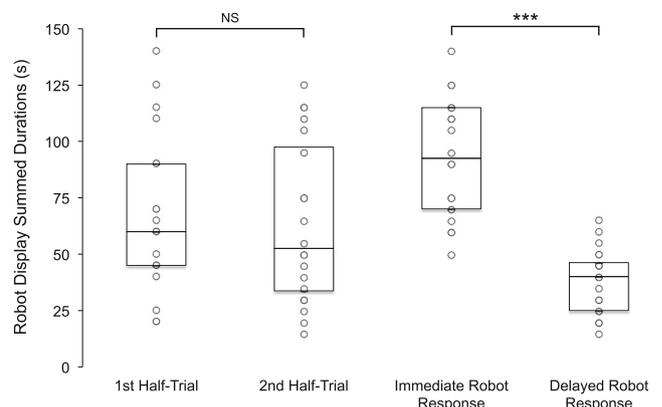


**Fig. 3** Half-trial durations of the immediate and delayed robot response treatments. The central 50% of the data (i.e., the interquartile range (IQR)) is contained within each box. The horizontal line in the box represents the median. Open circles indicate each subject's half-trial duration for the two experimental treatments. Filled circles depict the maximum and minimum outliers

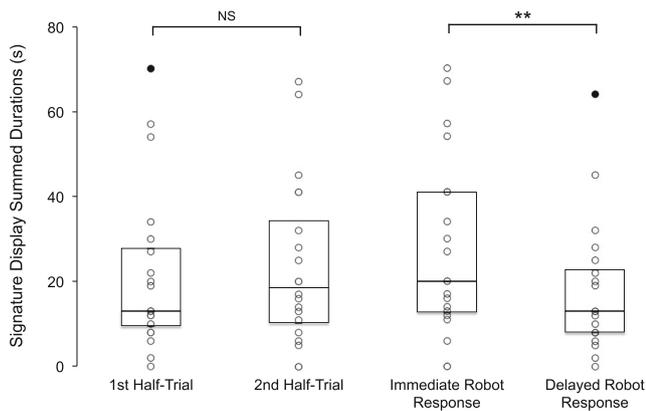
durations (Wilcoxon  $Z = 0.51$ ,  $P = 0.610$ ,  $N = 20$ ), significantly more robot display occurred in the immediate response treatment than in the delayed response treatment (Wilcoxon  $Z = -3.91$ ,  $P < 0.0001$ ,  $N = 20$ ; Fig. 4). In addition, whereas the summed durations of each subject's signature displays in half-trials did not differ by stimulus order (Wilcoxon  $Z = 0$ ,  $P = 1.0$ ,  $N = 20$ ), subjects spent significantly more time engaging in signature displays in the immediate robot response treatment than in the delayed robot response treatment (Wilcoxon  $Z = -2.45$ ,  $P = 0.002$ ,  $N = 20$ ; Fig. 5). Furthermore, latencies of subjects to perform signature displays did not differ by stimulus order (Wilcoxon  $Z = 0.49$ ,  $P = 0.624$ ,  $N = 17$ ), but subjects exhibited significantly shorter latencies to perform signature displays in the immediate robot response treatment than to the delayed robot response treatment (Wilcoxon  $Z = 2.38$ ,  $P = 0.017$ ,  $N = 17$ ; Fig. 6). Finally, we found no evidence of a difference in the frequencies of two-bob displays performed by subjects to the two robotic stimuli, either by stimulus order (Wilcoxon  $Z = -0.79$ ,  $P = 0.430$ ,  $N = 20$ ) or by stimulus type (Wilcoxon  $Z = -0.05$ ,  $P = 0.960$ ,  $N = 20$ ).

## Discussion

Results of our interactive lizard robot playback experiment have shown that adult male lava lizards are sensitive to the timing of opponents' displays in simulated display contests. Although subjects' responses were not affected by the order in which the two robot display sequences were presented in this experiment (or a previous one, Clark et al. 2015), the immediate robot response treatment elicited more display from subjects with shorter display latencies than did the delayed robot response treatment. As our two stimulus sequences were identical except for the lag in robot response, differences in subjects' responses to the two stimuli can be explained by the timing of robot responsiveness to subjects' displays. In a



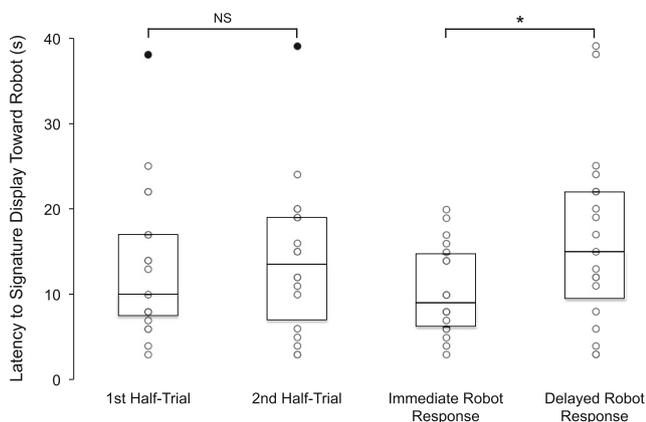
**Fig. 4** Durations of robot displays compared by stimulus order and stimulus type. Open circles indicate each subject's response as grouped by half-trial and by treatment. NS, not significant, \*\*\* =  $P \leq 0.0001$ . Legend as in Fig. 3



**Fig. 5** Durations of subjects' signature displays compared by half-trial and by treatment. \*\* =  $P \leq 0.01$ . Legend as in Figs. 3 and 4

few prior studies of lizard dyadic contests, researchers have found that prior experience with a real or simulated (video) opponent can sometimes have a detectable effect on contest outcome and aggression (Stuart-Fox and Johnston 2005; Van Dyk and Evans 2007). In contrast to our study, such order effects have been observed in subjects whose inter-trial periods ranged from 1 day (Van Dyk and Evans 2007) to several weeks (Stuart-Fox and Johnston 2005). As the inter (half)-trial period for subjects in our study lasted only a few seconds (i.e., the amount of time it took to trigger the alternative stimulus on the iPod touch), we do not know if our inability to detect an order effect would have been different had subjects been given days or weeks between stimulus presentations.

Our results are consistent with our hypothesis that subjects would respond more strongly and quickly in the immediate robot response treatment than in the delayed robot response treatment. Our results also seem consistent with those of Ord and Evans (2002) who showed in a video playback experiment that male jacky dragon (*Amphibolurus muricatus*) display behavior varied with whether or not the stimulus lizard appeared to interact with subjects. In the Ord and Evans (2002) experiment, subjects that were provided with the



**Fig. 6** Latency of subjects to display compared by half-trial and by treatment. \* =  $P \leq 0.05$ . Legend as in Figs. 3 and 4

illusion of interaction responded to the male stimulus lizard largely with aggressive displays, whereas “yoked control” subjects (i.e., subjects that witnessed the same stimulus in real time but whose behavior had no influence on stimulus behavior) responded to the simulated male conspecific with a mixture of aggressive and appeasement displays. Although our experiment did not explicitly include a non-interactive stimulus, and whereas lava lizards do not appear to exhibit appeasement displays, our delayed robot response treatment bore a much stronger resemblance to a non-interactive stimulus than to an interactive one. Consequently, like the Ord and Evans (2002) non-interactive video stimulus, our delayed robot response treatment elicited less display from subjects with longer latencies than did our immediate robot response treatment.

Non-lizard taxa also have taken part in interactive playback experiments, where subjects' responses depended on whether their simulated opponent interacted in anticipated or unanticipated ways. For example, in one such experiment with songbirds, Dabelsteen et al. (1997) showed that male robins exhibited significantly higher levels of aggression when the simulated contestant's song overlapped the subject's song, as compared to songs played back on a predetermined time loop or that were alternated with subjects' songs. Likewise, interactive call playbacks to common marmosets (*Callithrix jacchus*) revealed that subjects engaged in antiphonal calling progressively more quickly to playbacks with a short delay following a subject's vocalization than to playbacks with longer delay times (Miller et al. 2009). Thus, whether an interaction is actual or simulated, the timing of a conspecific's responses appears to have strong effects on how communication signals are interpreted.

Regardless of sensory modality, interactive playback experiments promise to continue facilitating exploration of the decision rules underlying animal communication, particularly when those rules are violated. To date, we have used lava lizard robots to examine questions about (1) whether the order in which conspecific and heterospecific bobbing displays are presented affects the magnitude of subjects' responses (Clark et al. 2015), (2) what effects large manipulations of bobbing display structure (e.g., typical structure vs. reversed-inverted structure) have on conspecific display recognition (Clark et al. 2016), and (3) what impact manipulations of female nuptial color have on males courtship responses (Clark et al. 2017). One potential avenue for future research would be to further explore the limits of bobbing display recognition in lava lizards by systematically altering the features of display structure, such as display speed, component timing, and bobbing amplitudes, both within and beyond the natural range of variation. Another possible direction to take would be to provide our robot with the ability to approach or retreat from subjects. Gillingham et al. (1995) utilized this idea in studying the social behavior of the tuatara (*Sphenodon punctatus*) by securing a robotic tuatara to a camouflaged platform that was

mounted atop a small radio-controlled all-terrain vehicle. Such a technique would allow us to examine experimentally how approach and retreat from subjects affect escalation and de-escalation in contests.

The dynamic use of bobbing displays by male Galápagos lava lizards in contests exemplifies how ritualized aggression may reduce the likelihood of dangerous injury. In this study, we have shown that altering the timing of responses can effectively convey dynamic changes in a motivational state—even within a limited communication system of highly stereotyped behavior. In the end, settling disputes with signals rather than with combat benefits both contestants and leaves more time for life-sustaining activities such as finding food, courtship, and vigilance for predators.

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**Data availability** The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This was a strict observational study and no animals were directly handled or harmed during data collection, so ethical approval from an ethics committee was not required.

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