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Display Responses of Galápagos Lava Lizards (*Microlophus bivittatus*) to Manipulation of Male Shoulder Epaulets on Conspecific-Mimicking Robots

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Abstract: Many animal taxa perform stereotyped displays during ritualized contests over territory and mates. Such displays facilitate assessment of an opponent's prowess and reduce the probability of physical injury. Color patterns likewise can serve as indicators of an individual's body condition. Male San Cristóbal Lava Lizards (*Microlophus bivittatus*) of the Galápagos Islands possess a black epaulet on each shoulder that contrasts with their surrounding body coloration. We created robots with the appearance of conspecific males to explore the potential function(s) of the epaulets in a series of four experiments. Our experiments focused on epaulet presence/absence, body location, and location relative to the axis of body motion (pectoral versus pelvic girdle) during pushups. Paired trials were conducted with adult males and females using a robot that performed *M. bivittatus* signature displays and that differed on its two sides in epaulet attributes. We quantified two kinds of bobbing displays in subjects: signature displays and two-bob displays. We also computed a composite response (CR) score, in which point values were assigned to types of nonbobbing displays and display combinations according to the apparent level of subject aggression. Results of Experiment 1 showed that males (but not females) performed more signature displays to the side of the robot with the epaulet present than to the side with the epaulet absent, suggesting that epaulets serve a signaling function. Composite response scores did not differ between treatments for either sex. In Experiment 2 neither males nor females performed more bobbing displays to an enlarged epaulet than to an epaulet reduced in size. However, males exhibited greater CR scores to the enlarged epaulet, suggesting that epaulet size or conspicuousness is important to its function. In Experiment 3 neither sex produced more bobbing displays to an epaulet on the robot's shoulder than to one on its hip. Yet, males accumulated significantly larger CR scores in response to the shoulder epaulet than to the hip epaulet, indicating that males were aware of normal epaulet location. Finally, in Experiment 4, where our robot performed hindlimb rather than forelimb pushups, subjects failed to exhibit more bobbing displays in response to a shoulder epaulet than to a hip epaulet. CR scores also did not differ between treatments for either sex, perhaps due to the striking abnormality of hindlimb-driven bobbing displays. Although the function of *M. bivittatus* epaulets remains elusive, these markings clearly are salient to male conspecifics.

Key words: Bobbing displays; Communication; Pushups; Signal function; Signature display; Two-bob display; Visual signals

Some of the most fascinating behaviors that have evolved in animals are visual displays used to defend resources, court members of the opposite sex, and dissuade predators from attack (Bradbury and Vehrencamp 2011; Eliason 2018). In reptiles, visual displays are particularly diverse among diurnal lizards (Carpenter and Ferguson 1977). In the Iguania clade of lizards, adult males hold territories that encompass or partially overlap smaller territories of several females (e.g., see Kamath and Losos 2017 for a review). As males compete for territories and the females that reside within them, engagement in ritualized combat involves escalating aggressive postures and movements that facilitate a sequential assessment of fighting ability (Jenssen 1977, 1978; Olsson 1992; Molina-Borja et al. 1998; López and Martin 2001; Jenssen et al. 2005; Sacchi et al. 2009; Clark et al. 2019). The most widely described displays that occur in lizard contests are actions in which the torso is displaced vertically in a series of stereotyped movements, namely, "headbobs" or "pushups." Whereas headbobs utilize only the neck muscles, pushups involve girdle and limb muscles as well. We refer to these motion signals collectively as "bobbing displays." In most lizard taxa pushups are produced either with the forelimbs only or simultaneously with the forelimbs and hindlimbs. Some exceptions include agamid lizards in the *Ctenophorus decresii* complex (and *C. pictus*) that perform pushups largely with the hindlimbs (Gibbons 1979; Ramos and Peters 2016). Several species of anoles also perform tail lift displays in which the hindlimbs produce pushups, such as members of the *Anolis roquet* species group (e.g., *A. extremus* and *A. roquet*; Gorman 1968). In all lizard taxa, bobbing displays are produced by both sexes and may communicate attributes of the signaler as varied as species identity, possession of a territory, interest in courtship, or body condition (Carpenter and Ferguson 1977; Losos 2009). By convention (Carpenter and Grubitz 1961) bobbing displays are visualized graphically as a display-action-pattern (DAP), and DAP graphs have been published for legions of lizard taxa (e.g., Carpenter and Ferguson 1977; Jenssen 1977, 1978; Gibbons 1979; Carpenter 1986; Martins 1993; Martins et al. 2004; Ord and Martins 2006; Peters et al. 2021).

One means for investigators to elicit lizard displays for analysis while maintaining stimulus control is to present subjects with artificial stimuli. Numerous studies have used film (Jenssen 1970) or video playbacks to evoke displays from lizards (Macedonia and Stamps 1994; Macedonia et al. 1994; Clark et al. 1997; Yang et al. 2001; Ord and Evans 2002; Ord et al. 2002; Van Dyk et al. 2007; Van Dyk and Evans 2008). Although the use of color monitors in video playback experiments have been successful in many studies (including those using computer-generated stimuli), video monitors are designed specifically for the human visual system. Playback of video sequences to nonhuman animals therefore poses a range of problems, including (1) the likely mismatch between the study species' spectral sensitivity and monitor

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phosphor radiance, (2) interspecific differences in perceived chromatic and luminance contrast, (3) potential discrepancies in flicker-fusion frequency of the study species versus the refresh rates of monitors, and (4) interspecific differences in spatial resolution (for reviews see D'Eath 1998; Fleishman and Endler 2000; Frohnwieser et al. 2016).

The use of robots can avoid potential problems with color video playbacks and has become increasingly common in the study of animal behavior (see Krause et al. 2011; Frohnwieser et al. 2016; Abdai et al. 2018; Romano et al. 2018 for reviews). Indeed, the use of robotic stimuli is now a well-established method in research on lizard displays. For example, lizard robots have been used to test for conspecific display recognition in numerous genera, including *Anolis* (Ord and Stamps 2008, 2009; Partan et al. 2011; Macedonia et al. 2013, 2015; Gunderson et al. 2018), *Draco* (Klomp et al. 2017), *Microlophus* (Clark et al. 2015, 2016, 2017, 2019), *Psammophilus* (Batabyal and Thaker 2018), *Sarada* (Zambre and Thaker 2017), and *Sceloporus* (Martins et al. 2005; Smith and Martins 2006; Kelso and Martins 2008; Thompson et al. 2008; Nava et al. 2012). In addition, robots have been used to investigate the significance of lizard coloration and its contrast with the visual background (e.g., Macedonia et al. 2013; Klomp et al. 2017; Zambre and Thaker 2017; Batabyal and Thaker 2018; Gunderson et al. 2018; Ord et al. 2021).

Previously we have used robots in field experiments with the San Cristóbal Lava Lizard (*Microlophus bivittatus*) of the Galápagos Islands to address (1) why some but not all species of Lava Lizards exhibit conspecific display recognition (Clark et al. 2016), (2) how males and females respond to the presence and extent of female nuptial coloration (Clark et al. 2017), and (3) how the timing of male bobbing displays affects interactions in male–male contests (Clark et al. 2019). Here we explore a different issue associated with *M. bivittatus* displays. Adult males in this species exhibit conspicuous black shoulder patches, or epaulets. In many postures the epaulets are partially concealed by a small skin fold, but they are fully exposed when the torso is elevated.

In a series of four experiments with adult male and female subjects we attempted to discover the function(s) of the epaulets by manipulating epaulet presence–absence, size, and body location on robots designed to mimic *M. bivittatus* conspecific males. Given that females use most of the same displays that are used by males in contests, we anticipated both sexes to respond similarly to our robotic stimuli. We made the following predictions for the outcomes of the experiments. In our first experiment we predicted that the presence of an average-sized shoulder epaulet on one side of a robot would stimulate more displays in conspecific viewers than would the absence of an epaulet on the robot's opposite side. The prediction follows from the hypothesis that epaulets serve a signaling function. In our second experiment we predicted that a robot with an enlarged epaulet would elicit more displays from subjects than would an epaulet reduced in size. Our prediction here is based on the hypothesis that epaulet size conveys one or more attributes of bearer condition, or quality, to viewers. In our third experiment we predicted that an average-sized epaulet in the anatomically correct location, the shoulder, would result in more displays from subjects than an epaulet on the hip. We reasoned that epaulets occur on the shoulders of actual *M. bivitttatus* males because this location is the primary axis of motion during pushups, which maximizes signal visibility. In our final experiment we replicated our third experiment with the difference that the robot performed hindlimb-driven rather than forelimb-driven pushups. We reasoned that stronger display to a hip epaulet than to a shoulder epaulet would suggest a required association of the epaulets with the body axis of greatest motion during pushups. Manipulations of conspecific-mimicking robots in this study allow us to explore the functional significance of male *M. bivittatus* epaulets in a highly controlled fashion under natural field conditions.

Materials and Methods

Study Species

The nine allopatric species of Galápagos Lava Lizards (*Microlophus* spp., Tropiduridae) comprise two independent evolutionary radiations: a larger seven-species western radiation and a smaller, two-species eastern radiation (Kizirian et al. 2004; Benavides et al. 2009). Our study species, *M. bivittatus*, is part of the smaller eastern radiation and is located only on the island of San Cristóbal and its adjacent islets.

Robot Construction

Lava Lizard models were constructed using 3D modeling software (Meshmixer v3.5, Autodesk, Inc., San Francisco, CA, USA) by shaping and sculpting the scanned image of a juvenile bearded dragon. Models were scaled to the average-sized male Lava Lizard (74 mm SVL for the Puerto Baquerizo population on San Cristóbal; D. Clark and J. Rowe, personal observations) and then 3D printed using a Prusa i3 MK3 3D printer. To obtain the necessary flexibility for the movements of the Lava Lizard pushup display, we used a TPU print filament (NinjaTek Inc., NinjaFlex® 1.75-mm filament). Using digital images of male lizards from our study populations for reference, we painted the models to resemble living male *M. bivittatus* (Fig. 1). We did not consider body coloration of our model *M. bivittatus* to be of critical importance, however, as our experiments were focused on the epaulets. Nevertheless, we reasoned that models with a realistic appearance (at least to the human eye) could raise the baseline of responses in subjects compared to a more abstract (e.g., solid color) model.

With small metal screws we fastened each lizard model to the top of an opaque plastic box (25 cm long × 15 cm wide × 10 cm high; see Supplemental Image S1, available online). To produce the robot pushup displays, we secured a HiTec HS-225BB Mighty Mini servomotor (HITEC RCD USA, Inc.) inside the box and attached the servomotor to the lizard model using a short metal push rod. To control the servomotor, we fitted an Arduino® Uno R3 programmable computer board inside the box adjacent to the servomotor. A 9-V–2ADC Li-ion battery (SHANQIU Mini UPS, Model FX 5-12, Shenzhen Feixing Technology Co., Ltd.) was used to power the robot and control system. In the field, the robot was activated remotely with an on/off switch attached to a 3-m-long extension wire.

Epaulet Reflectance Spectra

To compare the epaulet color treatments on our robots with the epaulets of actual males, we gathered reflectance

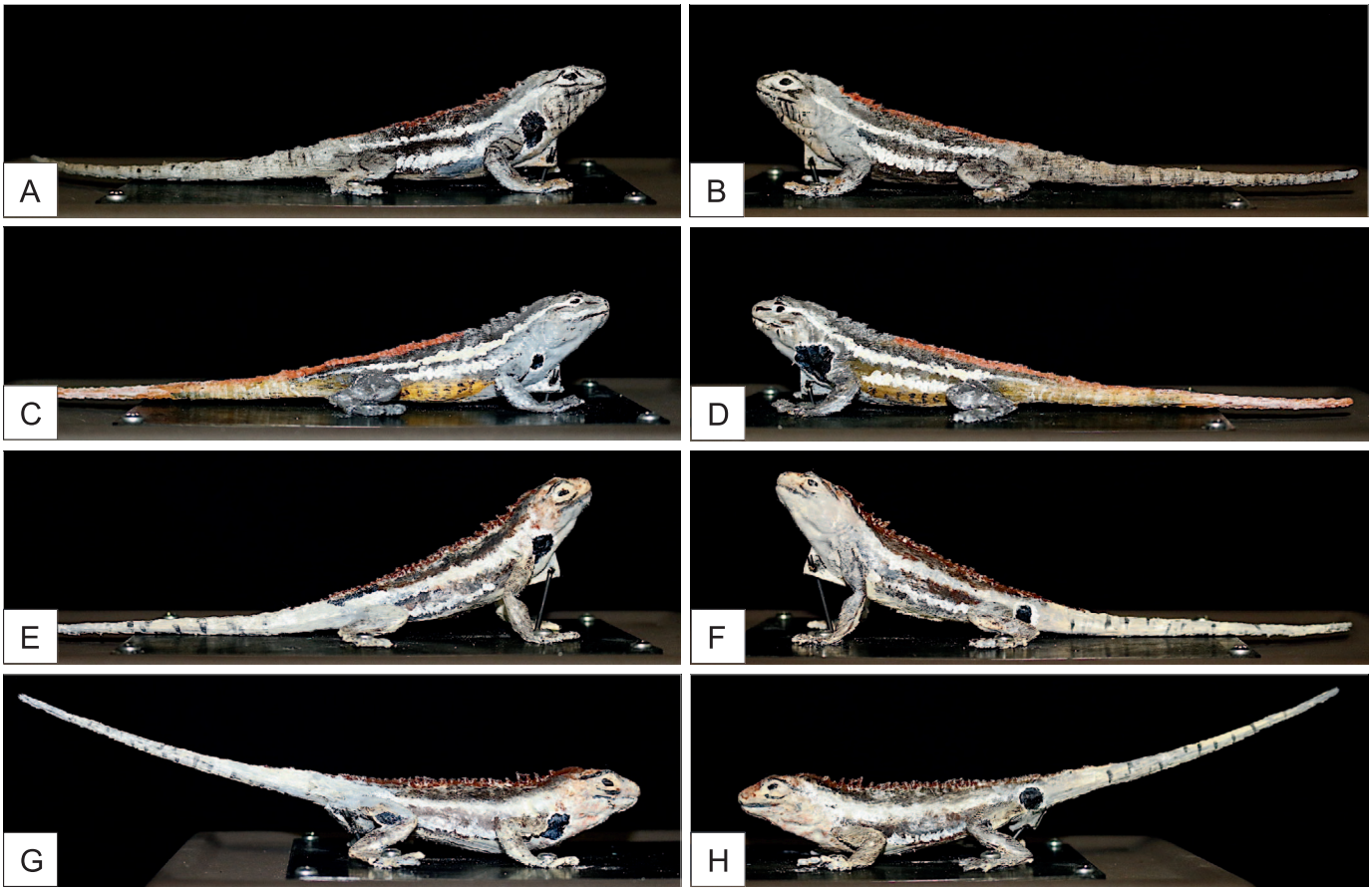

Fig. 1.—Robot models presented to *M. bivittatus* adult male and female subjects in the series of four experiments. Experiment 1: (A) Side of a robot with average-sized shoulder epaulet; (B) opposite side of the same robot as in (A), which lacks the epaulet. Experiment 2: (C) Side of a robot with a reduced shoulder epaulet; (D) opposite side of same robot as in (C) with an enlarged shoulder epaulet. Experiment 3: (E) Same stimulus type as in (A) above in forelimb pushup pose; (F) opposite side of the same robot as in (E), on which the black epaulet is positioned above and just posterior to hip rather than above the shoulder. Experiment 4: (G) Same stimulus type as in (A) and (E), except the robot performs signature displays with the hindlimbs rather than the forelimbs; (H) same stimulus type as in (F), except that the robot displays with the hindlimbs rather than the forelimbs.

spectra over 320–700 nm from the black epaulet and white ring surrounding it on live males ($n = 24$) and robotic males ($n = 5$). To obtain reflectance spectra we used an Ocean Optics USB-4000 spectrometer (Ocean Insight, Inc.) that was calibrated with an Ocean Optics LS-1-CAL calibration lamp, an AIS Mini-DT deuterium-halogen lamp as a light source, and a reflectance probe (Ocean Optics R400-7) with a custom-made black matte plastic probe holder. The sampling end of the plastic holder was cut at a 45-degree angle so that the probe could be held against the live male or robot without the risk of specular reflectance from the target surface. Reflectance measurements were taken relative to a diffuse white standard (Spectralon WS-1-SL, Labsphere, Inc.). The reflectance acquisition setup was run on a notebook or laptop computer using Ocean Optics Spectra Suite (v4.1, Ocean Insight, Inc., Dunedin, FL) software. The spectral data revealed that black epaulet reflectance is minimally larger (approximately 1.0–2.5%) in live males compared to the black painted epaulets on our robots (Supplemental Fig. S1, available online). In contrast, the white ring surrounding the epaulets in live males reflects more UV and less in the visible wavelengths than in our models (Supplemental Fig. S1). Although subjects undoubtedly could perceive the difference between live and robotic males in the white coloration surrounding the epaulets, our experimental manipulations were focused on the presence, size, and position of the epaulets on the body, not on precisely matching their coloration. Moreover, the coloration of the black epaulets and their white surrounding ring was the same for all our models and therefore was a constant across our experimental treatments.

Robot Display Programming

Our robot display sequence comprised a volley (i.e., series) of three species-specific signature displays (Stamps and Barlow 1973; Jenssen 1977), each lasting 1.5 s and separated by a pause of 4.5 s. A period of nondisplay followed the volley of three displays that lasted 30.0 s. The entire cycle lasted 43.5 s from the first robot display to the end of the nondisplay interval. Once initiated, this cycle continued for the duration of the half-trial, that is, exposure to one of the two sides of the robot (see the following). A video of each robot stimulus performing two signature displays is provided in the online supplemental materials.

Robot Presentation Protocol

We conducted our experiments with adult male and female *M. bivittatus* in and around Puerto Baquerizo Moreno on San Cristóbal (longitude –89.614342, latitude –0.909200; elevation 6.0 m; datum = WGS84). Lava Lizards inhabit the arid coastal beach and lava rock zones, which range in topography from flat, sandy soils to gently sloping terrain strewn with lava stones and boulders. The predominant vegetation includes Palo Santo trees (*Bursera graveolens*), evergreen shrubs, and small trees such as Galápagos Croton (*Croton scouleri*), and Jerusalem Thorn (*Parkinsonia aculeata*), as well as herbaceous plants, chiefly Stickleaf (*Mentzelia aspera*) and Bastardia (*Bastardia viscosa*). The cacti *Opuntia galapageia* and *Jasminocereus thouarsii* are common in both lowland and upland rocky areas.

Trials were run daily from 20 February to 2 March 2022, between 0900 and 1700 h, in a temperature range of approximately 24–30°C. We searched for adult *M. bivittatus* by walking dirt roads and paths in undeveloped areas, as well as in neighborhoods adjacent to those areas. Individuals frequently were found on top of lava rocks at roughly 0.5–1.0 m above the ground. Lizards tended to perch in boulder clusters that rose above surrounding low vegetation, potentially facilitating view by conspecifics during display. However, subjects responded to our robots from wherever they happened to be at the time, including on the ground.

When finding a potential subject, we carefully placed the robot on the substrate (usually a lava rock) at a distance of approximately 2 m (range approximately 1–3 m) from the subject in broadside view. The precise distance between the subject and robot at the start of a trial was not crucial because the lizards readily moved closer to, or farther from, the robot upon detecting it. We then positioned a tripod-mounted video camera (Panasonic HC-WX970 WiFi camcorder), with which we recorded trials, approximately 3 m from the test subject. A second tripod-mounted video camera, also positioned about 3 m from the test subject but some distance away from the first camera, was focused on the robot. The second camera broadcast its video signal to the first camera in real time via WiFi. The communication between the two cameras allowed us to record subjects' responses together with a picture-in-picture video of the displaying robot in the lower left corner of the trial footage. As in our prior studies of *M. bivittatus* using robotic stimuli, we avoided retesting subjects by running our trials in disparately spaced areas (>100 m) in each field session. Radiotelemetry data indicate that home range diameters in our study species are far smaller (≤30 m) than the distances between locations in which we conducted our experiments (Rowe et al. 2019).

During each experiment, we alternated the side of the robot that subjects saw first to avoid introducing bias that might arise from sensitization or habituation within a trial. Based on our previous work (Clark et al. 2017, 2019), we aimed for a maximum half-trial duration of 6 min, after which the robot would be turned to expose its opposite side to the subject for 6 min. Because subjects sometimes fled the testing location before the second half-trial could run a full 6 min, across our four experiments (two sexes × eight stimuli; $n = 16$) the average half-trial duration lasted 5 min 14 s (± 5.6 s SE). In addition, although we sought to test 12 subjects of each sex in every experiment, failure of some subjects to complete a trial frequently resulted in samples sizes of less than 12.

Bobbing Display Types Quantified and Data Acquisition

San Cristóbal Lava Lizards (*Microlophus bivittatus*; Fig. 2A, B) produce two distinct types of bobbing displays: a species-specific signature display and a simpler, quick two-bob display (Clark et al. 2017, 2019). Signature displays serve multiple functions, such as broadcast of territory ownership and attraction of mates (Jenssen 1977, 1978). In our study species signature displays commonly occur in groups ("volleys"; Jenssen and Hover 1976) of three (Fig. 2C), but can be performed singly or in volleys containing up to five or six displays. The brief (approximately 0.3 s) two-bob display (Fig. 2D) is most often produced immediately before locomotion, even when moving a very short distance, and appears to broadcast to potential viewers that locomotion is imminent (Clark et al. 2017; Macedonia et al. 2019).

When scoring subjects' responses, we considered a half-trial to begin at the initiation of the robot's first display, as seen in the picture-in-picture video window. In a few cases, where a subject began to display before the picture-in-picture video camera was trained on the robot, scoring began at the start of the subject's first display. From our video trial recordings, we counted the number of times a subject produced a signature display or two-bob display during each half-trial. In accordance with prior experiments (Clark et al. 2015, 2016, 2017) we converted the quantity of bobbing displays performed by a subject in response to one stimulus, to a proportion of the displays performed to both stimuli. For example, if a subject responded with 12 signature displays to one side of a robot, and 8 signature displays to the other side of the robot, the proportions of displays would be 0.6 and 0.4, respectively (or, if multiplied by 100, 60% and 40%). Transforming display quantities to proportions adjusts for the fact that half-trials were not always identical in duration, as subjects sometimes moved out of view (e.g., behind a rock) for brief periods or left the staging area before the second half-trial was complete. Trials in which subjects fled long before the end of the second half-trial were discarded. Prior to analyzing each subject's display proportions, values were transformed using the Logit transform to ensure their linearity (Warton and Hui 2011).

Composite Response Score

Subjects exhibited a variety of nonbobbing displays when presented with our robotic stimuli. To accommodate these responses, we created a scale of aggressive escalation (Table 1) in which different display types were assigned point values. With the constraint that a given display type could be counted only once in a half-trial, points were summed over the half-trial to produce a composite response (CR) score. The rationale for this index is that different kinds of displays emerge as contests progress, with display types of lower assigned values virtually always appearing before display types of higher assigned values. Aside from tongue-touching to the substrate (tongue touch; Table 1), a subject's use of nonbobbing display types in a contest resembles a rachet, where only the same display type or those assigned larger values are performed.

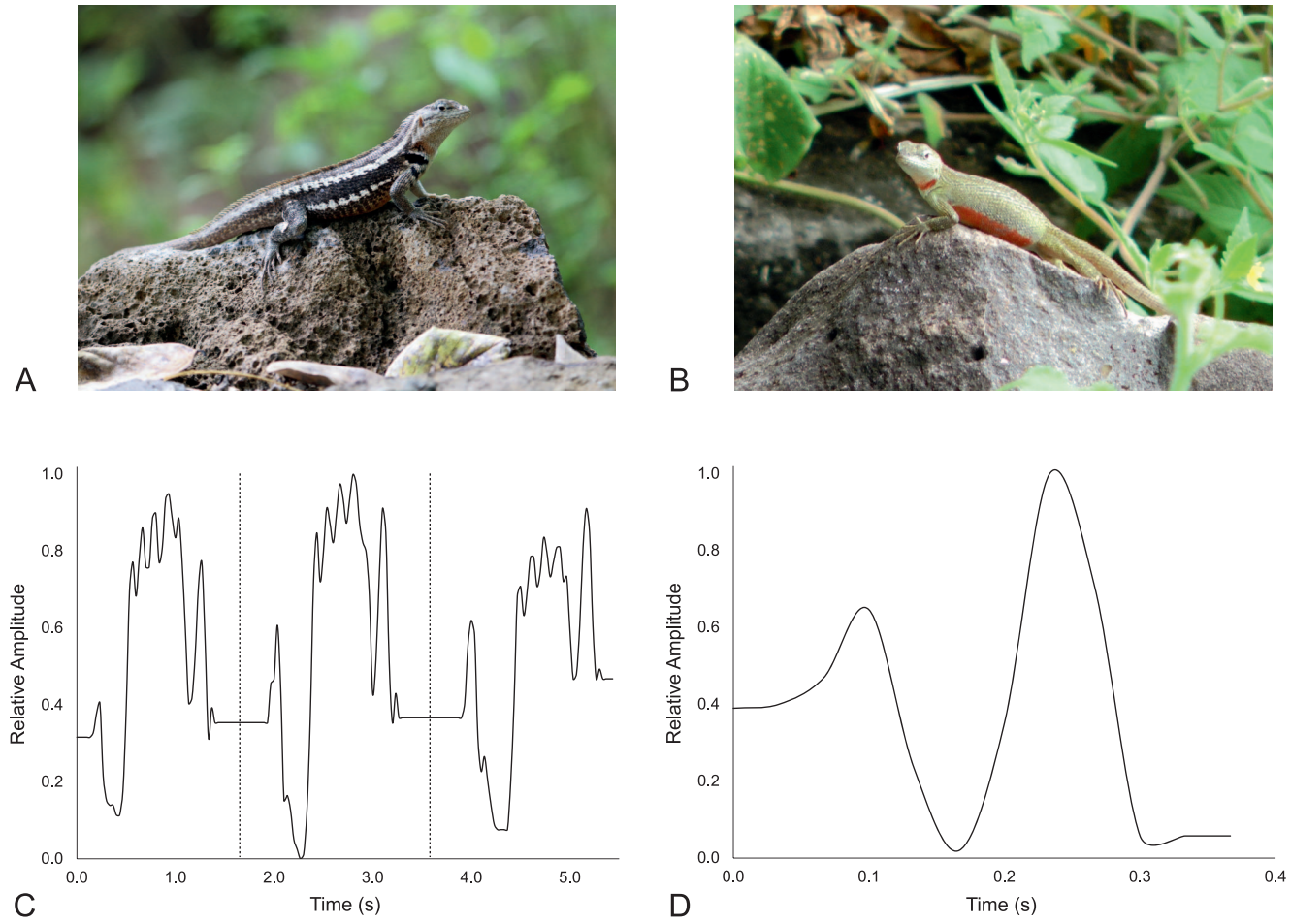

Fig. 2.—Adult *M. bivittatus* and display action patterns of their bobbing displays. (A) adult male, (B) adult female, (C) volley of three signature displays, and (D) a two-bob display. Adult sizes not to scale. Vertical dotted lines within the signature display volley separate individual displays.

Table 1.—Terms and response variables quantified in this study, including point values assigned to behaviors used to compute composite response (CR) scores.

Term	Points	Definition
Display volley	—	A cluster of bobbing displays, each separated in time by a brief pause (Fig. 2C).
Signature display	—	Species-specific bobbing display (Fig. 2C, each display; Supplemental Videos S2, S3, S7, available online) that occurs in a diversity of lizard taxa.[1]
Two-bob display	—	Rapid up-down-up-down bobbing display performed immediately before locomotion in *M. bivittatus* (Fig 2D; Supplemental Videos S2, S3).
Tongue touch	1 point	Subject briefly extends tongue and touches substrate, potentially for vomeronasal analysis (Supplemental Videos S2, S3).
Tail lashing	2 points	Slow wriggling to rapid whipping of tail back and forth (Supplemental Videos S4, S5, available online).
Rapid reorientation	3 points	Swivel of body on the substrate in one or more rapid shifts of roughly 30–180 degrees (Supplemental Video S6, available online).
Gular expansion	3 points	Outward expansion of gular sac via hyoid apparatus; common across lizard taxa[2] (Supplemental Video S7, available online).
Displacement jump	4 points	Displacement of body from substrate in an abrupt, exaggerated manner, with one or more feet briefly leaving the ground (Supplemental Video S7).
Lateral presentation	4 points	Reorientation of the body specifically to maximize lateral view by opponent. Compression of the sides and elevation of stance likely make subject appear larger and more formidable (Supplemental Video S8, available online).
Challenge display	5 points	Simultaneous lateral compression and gular expansion while performing a signature display with a strongly arched back[3] (Supplemental Video S7).

[1] Jenssen (1977).

[2] Ord et al. (2015).

[3] Carpenter (1966).

In the study of Clark et al. (2015), a subject's CR score simply was the numerical value of the display type observed that had been assigned the largest number of points. In the present study we expanded the diversity of display types assigned point values and incorporated the additive (i.e., summed) component. As a hypothetical example, in a half-trial a subject might exhibit gular expansion (3 points) twice, lateral presentation (4 points) three times, and a challenge display (5 points) once. Given that the number of times a subject exhibits a particular display type is excluded from CR score computation, the CR score in this example equals 3 points + 4 points + 5 points for a total of 12 points. We feel that our modifications to CR score calculation render it a more sensitive assay of subjects' responses to our robots than did its earlier formulation.

Statistical Analysis

As our Logit-transformed display data originated as frequencies, that is, counts, they are noncontinuous. We therefore used the Wilcoxon matched-pairs signed-rank test to compare frequencies as proportions of bobbing displays and CR scores exhibited in response to our paired robotic stimuli. All statistical tests are two-tailed. Between-sex differences in our reported sample sizes for paired stimulus comparisons are due largely to ties in the Wilcoxon test. Likewise, as each tie in a Wilcoxon test effectively removes that subject from the analysis, sample sizes for test results reported below often are lower than the number of subjects for which data are illustrated in the figures.

Results

Experiment 1: Forelimb Pushups with Shoulder Epaulet Present or Absent

Male subjects produced significantly more signature displays in response to the side of the robot with an average-sized shoulder epaulet than to the side of the robot lacking the epaulet ($n = 10$, W = 1.5, $P = 0.0164$; Fig. 3). In contrast, females did not perform significantly more signature displays to one side of the robot versus the other ($n = 9$, W = 19, $P > 0.05$; Fig. 3). No effect of stimulus order (i.e., which stimulus was presented first) was detected in the number of signature displays produced (males, $n = 10$, W = 27.5, $P > 0.05$; females, $n = 9$, W = 8, $P > 0.05$). Subjects also did not perform more two-bob displays to one side of the robot versus the other (males, $n = 9$, W = 20.5, $P > 0.05$; females, $n = 11$, W = 25.5, $P > 0.05$). No significant effects of stimulus order were detected for two-bob displays (males, $n = 10$, W = 23.5, $P > 0.05$; females, $n = 11$, W = 28.5, $P > 0.05$).

CR scores did not differ significantly between epaulet presence or absence (males, $n = 8$, W = 10.5, $P > 0.05$; females, $n = 3$, sample size too small to test; Fig. 4). No order effects were detected for either sex (males, $n = 8$, W = 15, $P > 0.05$; females, $n = 3$, sample size too small to test).

Experiment 2: Forelimb Pushups with an Enlarged or Reduced Shoulder Epaulet

Subjects did not produce significantly more signature displays to the side of the robot with an enlarged epaulet than to the side of the robot with a reduced epaulet (males, $n = 12$, W = 27, $P > 0.05$; females, $n = 7$, W = 11, $P > 0.05$; Fig. 5). No stimulus presentation order effects were detected (males, $n = 12$ W = 36.5, $P > 0.05$; females, $n = 7$, W = 11, $P > 0.05$). Similarly, subjects did not perform more two-bob displays to the larger epaulet stimulus than to the smaller epaulet stimulus (males, $n = 11$, W = 32.5, $P > 0.05$; females, $n = 6$, W = 9, $P > 0.05$). Again, no presentation order effects were found (males, $n = 11$, W = 15, $P > 0.05$; females, $n = 6$, W = 10, $P > 0.05$).

In contrast to Experiment 1, males exhibited higher CR scores when shown the side of the robot with the larger epaulet compared to the side of the robot with the smaller epaulet ($n = 11$, W = 0, $P = 0.0034$; Fig. 6). For females, no difference was found in CR scores to the larger epaulet versus the smaller epaulet ($n = 7$, W = 12.5, $P > 0.05$; Fig.

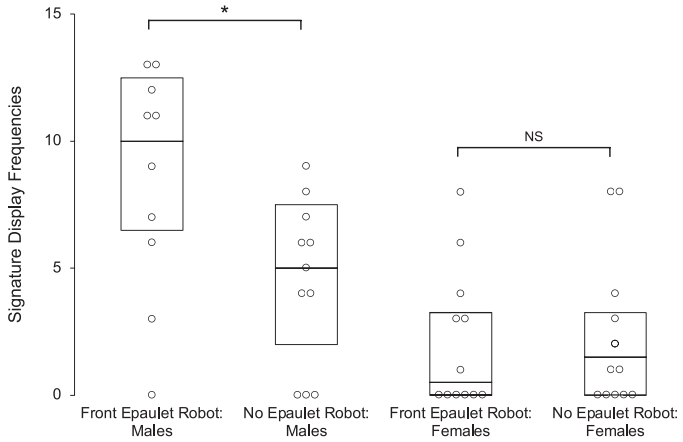

Fig. 3.—Box plots showing signature display frequencies of *M. bivittatus* subjects in response to a robot that performed signature displays and that had a shoulder epaulet either present or absent. Each circle represents a different subject's response. Multiple circles with the same value indicate that more than one subject exhibited the same level of response. In this figure, an outlier value of 30 for "Front Epaulet Robot: Males" is not shown. In each box plot, the central 50% of the data distribution (i.e., the interquartile range: IQR) is contained within the box, with the horizontal line in each box representing the median. The lower edge of each box indicates the first quartile (25th percentile), and the upper edge indicates the third quartile (75th percentile). *$P < 0.05$. NS = not significant ($P > 0.05$).

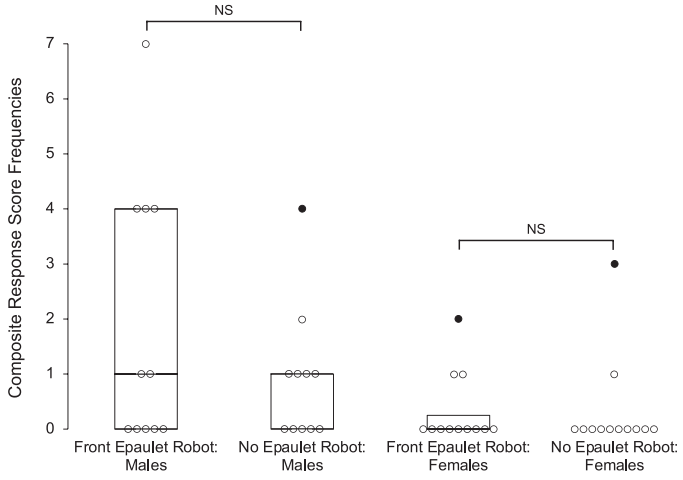

Fig. 4.—Box plots showing composite response score frequencies in response to a robot with a shoulder epaulet present or absent. Filled circles indicate maximum outliers. Legend as in Fig. 3.

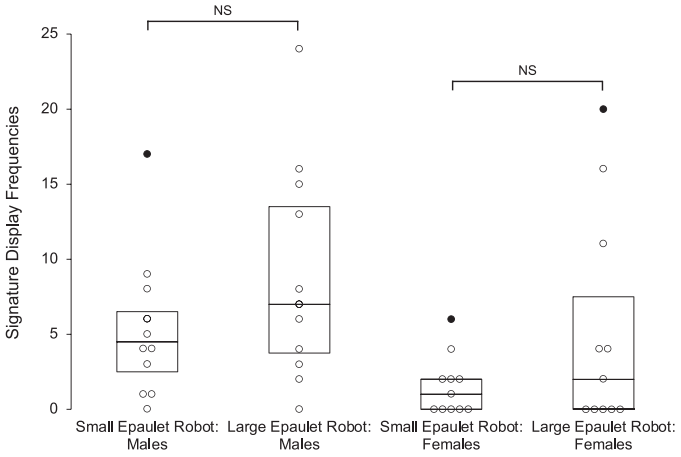

FIG. 5.—Box plots showing signature display frequencies of *M. bivittatus* subjects in response to a robot with a small or large shoulder epaulet. Filled circles indicate maximum outliers. Legend as in Fig. 3.

6), and no order effects were detected for either sex (males, $n = 11$, W = 24, $P > 0.05$; females, $n = 7$, W = 10.5, $P > 0.05$).

Experiment 3: Forelimb Pushups with Shoulder Epaulet or Hip Epaulet

Subjects did not perform significantly more signature displays to the side of the robot with an epaulet on the shoulder than to the side with an epaulet on the hip (males, $n = 7$, W = 9, $P > 0.05$; females, $n = 7$, W = 13, $P > 0.05$; Fig. 7). No stimulus presentation order effects were detected (males, $n = 7$, W = 12.5, $P > 0.05$; females, $n = 11$, W = 22.5, $P > 0.05$). Likewise, subjects did not perform more two-bob displays to one side of the robot versus the other (males, $n = 5$, W = 7, $P > 0.05$; females, $n = 7$, W = 13, $P > 0.05$). Again, no effects of stimulus order were found (males, $n = 5$, W = 3, $P > 0.05$; females, $n = 7$, W = 10, $P > 0.05$).

Interestingly, males exhibited larger CR scores when shown the side of the robot with the shoulder epaulet than when shown the side with the hip epaulet ($n = 7$, W = 0, $P < 0.05$; Fig. 8). Females did not exhibit larger CR scores,

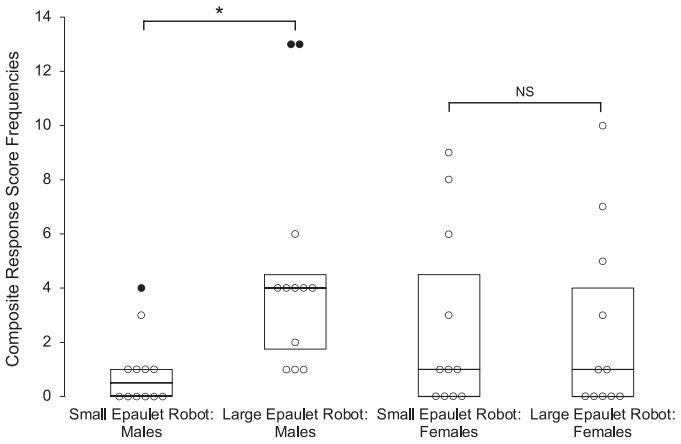

FIG. 6.—Box plots showing composite response score frequencies in response to a robot with a small or large shoulder epaulet. Filled circles indicate maximum outliers. Filled circles indicate maximum outliers. Legend as in Fig. 3.

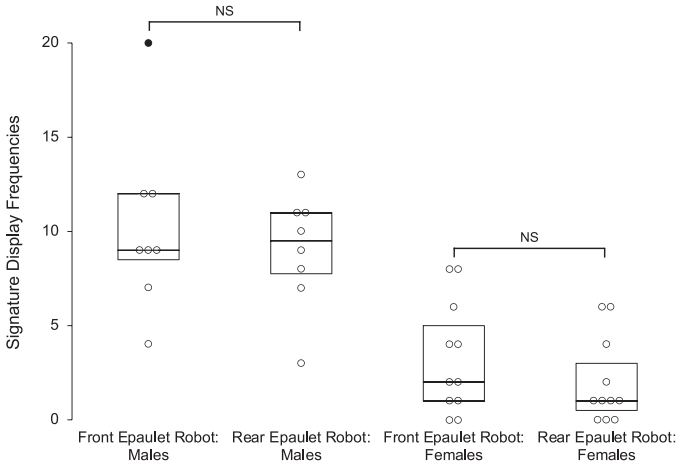

FIG. 7.—Box plots showing signature display frequencies of male and female *M. bivittatus* subjects in response to a robot with an epaulet above the shoulder or above the hip. Filled circle indicates maximum outlier. Legend as in Fig. 3.

however, when viewing the shoulder epaulet versus the hip epaulet ($n = 7$, W = 14, $P > 0.05$; Fig. 8), and no order effects were detected for either sex (males, $n = 7$, W = 13, $P > 0.05$; females, $n = 7$, W = 11, $P > 0.05$).

Experiment 4: Hindlimb Pushups with Shoulder Epaulet or Hip Epaulet

When the robot performed pushups with the hindlimbs rather than with the forelimbs—a manipulation that made the pelvic girdle rather than the pectoral girdle the primary axis of vertical motion—subjects did not produce more signature displays to the side of the robot with the hip epaulet than to the side of the robot with the shoulder epaulet (males, $n = 9$, W = 15, $P > 0.05$; females, $n = 11$, W = 29, $P > 0.05$; Fig. 9). No stimulus presentation order effects were found (males, $n = 9$, W = 22, $P > 0.05$; females, $n = 11$, W = 28.5, $P > 0.05$). Similarly, subjects did not produce more two-bob displays in response to the shoulder epaulet than the hip epaulet (males, $n = 4$, sample size too

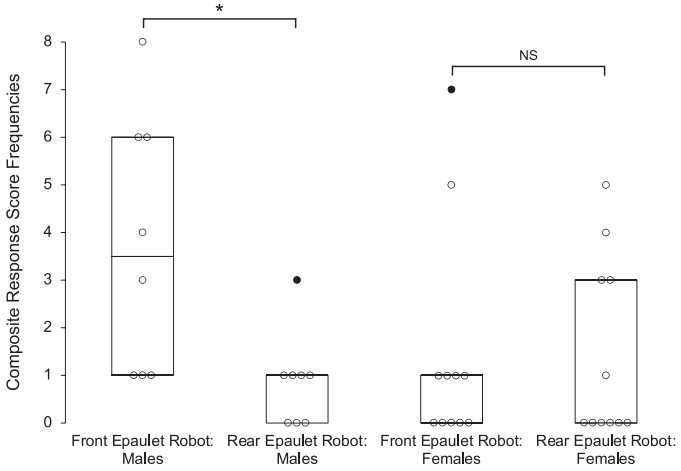

FIG. 8.—Box plots showing composite response score frequencies of male and female *M. bivittatus* subjects in response to a robot with an epaulet above the shoulder or above the hip. Filled circles indicate maximum outliers. Legend as in Fig. 3.

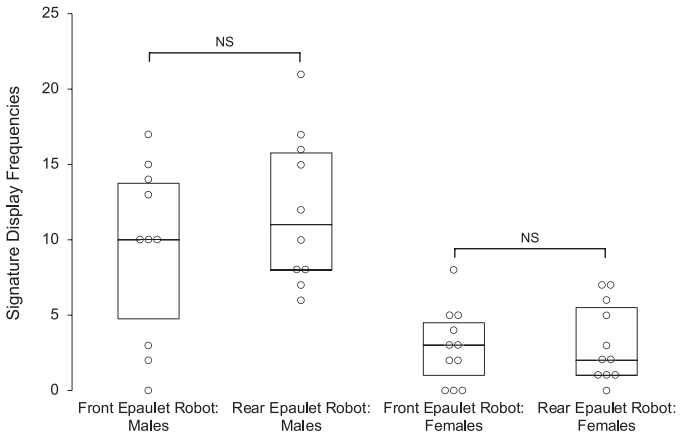

FIG. 9.—Box plots showing signature display frequencies of male and female *M. bivittatus* subjects in response to a robot that performed hindlimb-driven signature displays and that either had an epaulet above the shoulder or above the hip. Legend as in Fig. 3.

small to test; females, $n = 6$, W = 5, $P > 0.05$), and no order effects were detected for two-bob displays (males, $n = 4$, sample size too small to test; females, $n = 6$, W = 9, $P > 0.05$).

In contrast to the results of Experiment 3, males did not exhibit larger CR scores in response to the shoulder epaulet than to the hip epaulet ($n = 8$, W = 16, $P > 0.05$; Fig. 10). Likewise, we found no difference in female CR scores when they were shown the shoulder epaulet versus when they were shown the hip epaulet ($n = 8$, W = 11, $P > 0.05$; Fig. 10), and no order effects were found for either sex (males, $n = 8$, W = 13, $P > 0.05$; females, $n = 8$, W = 16.5, $P > 0.05$).

DISCUSSION

In this study we have shown that the black shoulder epaulets of male San Cristóbal Lava Lizards are salient to conspecific males. By varying epaulet attributes on robots having the appearance and bobbing display behavior of conspecifics, we determined in paired half-trials how differences in the naturally varying feature of epaulet size affected subjects' responses. Our use of conspecific-mimicking robots also facilitated manipulating invariant features, such as the presence versus absence of male epaulets, as well as their location relative to the primary girdle axis of vertical motion during pushups.

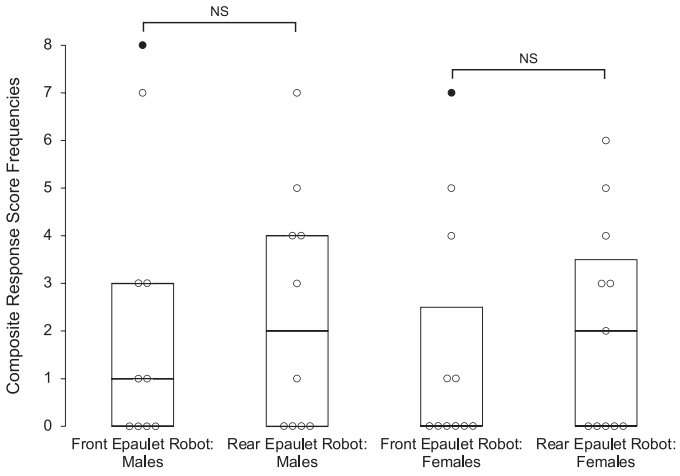

FIG. 10.—Box plots showing composite response score frequencies of male and female *M. bivittatus* subjects in response to a robot that performed hindlimb-driven signature displays and that had an epaulet either above the shoulder or above the hip. Filled circles indicate maximum outliers. Legend as in Fig. 3.

In Experiment 1, males, but not females, responded with significantly more signature displays to an average-sized epaulet than to the absence of the epaulet. Therefore, male subjects apparently viewed the lack of epaulets as nonequivalent to an adult conspecific male. The fact that females did not respond with bobbing displays differently to the presence or absence of epaulets may indicate that epaulets are unimportant in female mate choice. Such an explanation would account for the absence of response differences in females to epaulet manipulations across experiments. Alternatively, it is possible that females exhibited discrimination between our paired experimental stimuli in a manner that we did not quantify. When using CR scores to account for behaviors other than bobbing displays, results from Experiment 2 revealed that male subjects exhibited higher CR scores to the enlarged shoulder epaulet than to the epaulet that was reduced in size. Male subjects, therefore, are sensitive to strong deviations from typical epaulet size, given that large, conspicuous epaulets were more effective in stimulating responses than were small, less conspicuous epaulets. In Experiment 3 males exhibited larger CR scores when shown a robot with a shoulder epaulet as compared to a hip epaulet. This outcome suggests that individuals either were sensitive to epaulet body location, or their responses were linked to the epaulet being located near the axis of largest vertical displacement during pushups. By having the robot perform hindlimb-driven signature displays in Experiment 4, greater responses to the hip epaulet than to the shoulder epaulet would suggest that coupling of the epaulets with the axis of greatest vertical motion is crucial for the signal to be effective, in light of the natural coupling between the shoulder epaulets and pectoral girdle. By contrast, stronger responses to a shoulder epaulet than to a hip epaulet would suggest that the shoulder location of the epaulets outweighs the coupling of the signal with the body axis of vertical displacement during pushups. However, we did not detect a difference in subjects' responses in this experiment to an epaulet on the robot's shoulder versus the hip. In lieu of additional testing with a larger sample size of subjects, we must conclude that a robot performing hindlimb pushups may have been too unlike an adult male conspecific for subjects to produce responses that were consistently stronger to one stimulus versus the other.

Potential Epaulet Functions and Future Directions

Several non–mutually exclusive hypotheses are possible for the function of shoulder epaulets in our study species. One likely possibility is that the epaulets increase detection of a male that is moving or displaying. Specifically, the luminance contrast of the black epaulet framed within a white surrounding margin (Supplemental Fig. S1) might elicit a visual grasp reflex: A shift in an observer's gaze when a moving object is detected on the periphery of the retina (Fleishman 1992). This possibility could be tested in a controlled lab setting like those featured in studies of the

visual grasp reflex in anoles (Fleishman and Persons 2001; Steinberg and Leal 2016; Gunderson et al. 2018).

In addition, the white-ringed oval black center of the epaulets could resemble the eye of a far larger individual. When a male *M. bivittatus* performs a signature display, the expansion and contraction of epaulet skin creates the illusion of an eye that repeatedly opens wide and then relaxes (see Supplemental Video S1, available online). Eyespots occur throughout the animal kingdom, and directing a viewer's attention toward them, as well as intimidating would-be predators (and perhaps rivals in our case), figure prominently among their proposed functions (see Stevens 2005 and Stevens and Ruxton 2014 for reviews). It should be possible to use robots to test whether the epaulets of adult male *M. bivittatus* have a deterrent effect on their primary avian predators, such as Lava Herons (*Butorides sundevalli*) and San Cristóbal Mockingbirds (*Mimus melanotis*), as well as San Cristóbal Snakes (*Pseudalsophis biserialis*), a diurnal visually hunting racer within a genus that preys most commonly on *Microlophus* sp. (Ortiz-Catedral et al. 2019). Previous studies of lizard coloration and/or markings have suggested (Macedonia et al. 2002, 2004) or demonstrated (Stuart-Fox et al. 2003; Husak et al. 2006) that conspicuous color patterns can increase attack rates from predators (but see Baird 2009). Thus, robotic males that display on a scheduled cycle, and whose epaulets are partially concealed until the torso is elevated, might provide insights into the potential antipredator function of this ornament in San Cristóbal Lava Lizards.

A third possibility for the function of *M. bivittatus* epaulets could be that they serve as a badge of status that honestly advertise the bearer's condition (Dawkins and Krebs 1978). It currently is unknown if epaulets can change in size dynamically with body condition or levels of circulating testosterone, both of which could have impacts on male territory size and quality. However, production of throat and abdominal color patches in male lizards previously have been linked to androgen secretion and have been viewed as a badge of social status (reviewed in Cooper and Greenberg 1992; Moore et al. 1998; Cox et al. 2005, 2008; Olsson et al. 2013; Stuart-Fox et al. 2021). For example, in a series of field experiments, Whiting et al. (2003) manipulated testosterone and independently enlarged, reduced, or eliminated the ventral color badge in Augrabies Flat Lizards (*Platysaurus broadleyi*). Males injected with testosterone were generally more aggressive and initiated more fights than did control lizards, but males with enlarged badges whose testosterone was not altered frequently won more contests than other treatment groups (Whiting et al. 2003). Progress in understanding the function of *M. bivittatus* epaulets might be made by following Whiting et al. (2003) in staging male–male contests where attributes of the male badge (epaulet) are manipulated with paint. Lastly, we feel it would be worth determining, via blood analysis combined with standardized epaulet measurements, if a positive correlation exists between epaulet area and circulating testosterone in *M. bivittatus* males.

To summarize, in our experiments we utilized conspecific-mimicking robots to test for the effects of epaulet presence/absence, size, and body location on male and female *M. bivittatus* viewers. Our results indicate that (1) male epaulets are a visual signal directed toward other males, (2) larger epaulets evoke stronger responses in conspecific males than do smaller epaulets, and (3) adult males distinguish familiar from unfamiliar body locations of the epaulets. We hope that in future experiments the function of *M. bivittatus* epaulets will be investigated from additional perspectives to gain a more thorough understanding of this enigmatic signal.

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Supplemental Material

Supplemental material associated with this article can be found online at https://doi.org/10.1655/Herpetologica-D-22-00026.S1–12.

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