Sexual Selection in San Cristóbal Lava Lizards (*Microlophus bivittatus*): A Test of Male Body Size Using Lizard Robots

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ABSTRACT: Intrasexual selection through male competition favoring larger male body size is the preferred explanation for the evolution and maintenance of male-biased sexual size dimorphism among polygynous species. Although sexual selection has been well studied in some groups of lizards, sexual selection in the nine species of lava lizards (*Microlophus* spp.) of the Galápagos has received little attention. The purpose of this research was to test the importance of male body size in the context of sexual selection by both sexes. Using three different sizes of robotic models capable of emulating the appearance and display patterns of male San Cristóbal Lava Lizards (*M. bivittatus*), we analyzed the responses that the models elicited among free-ranging lizards of the same sex (confrontation) and opposite sex (courtship). Results showed that body size of both male lizards and robotic antagonists influenced the number of displays performed by males. Male body size positively influenced the number of aggressive responses, scaling with the size of the opponent. The model representing larger lizards received higher display counts from males. Body size of robotic models, but not female lizards, influenced the number of displays performed by females. Females responded the most to the small and large models. Display intensity was not affected by any of the variables considered for either sex. Results from this study support the hypothesis that male-biased sexual size dimorphism in *M. bivittatus* is driven at least in part by both intrasexual and intersexual selection favoring larger male body size.

Key words: Body size; Display response; Galápagos; Lizard color; Robotic lizards; Sexual size dimorphism; Tropiduridae

THE THEORY of sexual selection predicts that individuals choose mates based on traits that maximize their fitness (Darwin 1871; Emlen and Oring 1977; Harrison et al. 2015). Body size is a key life-history trait that is potentially subject to both sexual and natural selection (Brown et al. 1993; Valle 2013). In species that show female defense polygyny, there may be strong sexual selection for large body size in males that increases access to mating opportunities (Emlen and Oring 1977; Clutton-Brock and Harvey 1978; Peters 1986; Clutton-Brock 1988; Andersson 1994). Intersexual selection through female mate choice may operate simultaneously with intrasexual selection on body size in polygynous species (Darwin 1871; Houde and Endler 1990). Mate choice also involves multiple intraspecific social communication repertoires that coincide with characteristics such as body size (Bradbury and Vehrencamp 2011). Behavioral repertoires may function to communicate fitness-related qualities of an individual to members of the same or opposite sex. In the case of males, ritualized threat displays may reduce the physical risks that are associated with combat and that could reduce fitness (Grether et al. 2013).

Galápagos lava lizards (*Microlophus* spp.) show sexual size dimorphism that favors males, and are sexually dichromatic, with females that develop nuptial coloration during the breeding season (Carpenter 1966, 1970; Stebbins et al. 1967; Clark et al. 2017; Rowe et al. 2020). Among lizards, female nuptial coloration signals hormonal status and reproductive quality. These cues, in turn, contribute to male decisions regarding courtship investment and mate choice (LeBas and Marshall 2000; Stuart-Fox and Goode 2014). Females displaying low-intensity nuptial coloration are fertile and

receptive to male courtship. In contrast, females displaying high-intensity nuptial coloration are gravid and behave more aggressively, deflecting male attention (Cooper and Greenberg 1992; Watkins 1997). Coloration may also play a role in communication between females, as females with intense nuptial coloration tend to be more tolerant of other high-intensity females than of males and low-intensity females (Moore 1983; E.J. Mancero, personal observation). Lava lizards also display species-specific social communication repertoires that involve head bobs, a form of up-and-down head movements, and push-ups, a form of head-and-body movements supported by the arms (Carpenter and Ferguson 1977; Clark et al. 2017, 2019; Macedonia et al. 2019). An identical display pattern is used in both aggressive (male–male) interactions and courtship (male–female) interactions; thus its meaning depends on the sex of the signaler and the receiver (Carpenter and Ferguson 1977).

San Cristóbal Lava Lizards (*Microlophus bivittatus*), part of the older of two evolutionary Galápagos lava lizard radiations (Kizirian et al. 2004), are endemic to San Cristóbal Island, and until recently remained largely unstudied. This lizard is an opportunistic omnivore that travels freely across the island and establishes temporary territories during the breeding season (February–April). Mating may occur year-round given the appropriate environmental conditions (Troya 2012; Lewbart et al. 2017; Moore et al. 2017; but see Hervías-Parejo et al. 2019). Males exhibit a color pattern of dark browns and grays punctuated by a white lateral stripe running the length of the torso on each side. Comparatively, females are patterned in muted browns and grays with a slight yellow tint, expressing intense patches of orange to red shades during the breeding season. Populations show healthy hematological parameters (e.g., % hematocrit, mean corpuscular hemoglobin concentration) and genetic diversity but

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are subject to high levels of predation because of introduced feral cats (Arguedas et al. 2018; Carrión and Valle 2018). Recent behavioral studies using robotic lizards have shown that visual communication in *M. bivittatus* is sensitive to alterations in display structure, response timing and extent of nuptial coloration, yet conspecific display recognition has not been shown in this species (Clark et al. 2016, 2017, 2019; Macedonia et al. 2019).

The role of sexual selection as an explanation for larger male body size, relative to females, has been assumed for Galápagos lava lizards (Snell et al. 1988). Female preference for larger males has been found in both territorial and nonterritorial species of lizards (Censky 1997; Kohlsdorf et al. 2006). Increased fighting ability and deterrence of other males are desirable traits associated with large male body size, allowing for females to conserve energy for growth and egg development (Abell 1997). In territorial and polygynous species such as *M. bivittatus*, the ability to acquire and defend high-quality territories plays a significant role in female mate choice (Candolin and Voigt 2001; Huyghe et al. 2005). Large-bodied males perform better in intraspecific competition for territory, increasing female encounter rate and reproductive success (Hews 1990; Baird et al. 1996; Candolin and Voigt 2001; Salvador and Veiga 2001; Kohlsdorf et al. 2006; Moore et al. 2009; but see Lappin and Husak 2005). Reproductive success as evidenced by paternity further confirms the importance of male body size in female choice (Abell 1997; Lewis et al. 2000; Hofmann and Henle 2006; Johnson et al. 2021; but see Morrison et al. 2002). To date, however, a causal link between sexual selection and large male body size in Galápagos lava lizards has yet to be demonstrated.

In our study, we used robotic models of male *M. bivittatus* to investigate the role of sexual selection on male body size. We tested the following two hypotheses: (1) body size of an aggressively displaying signaler (the "male" robot) and the body size of the recipient (a free-ranging male) affects the number and intensity of aggressive responses by the recipient, and (2) body size of a courting male (displaying "male" robot) affects the number and intensity of responses of a free-ranging female. We also investigated the role of female coloration, an apparent proxy of female mating status, on female responsiveness to a courting male.

MATERIALS AND METHODS
Robot Construction

We followed the protocol of Clark et al. (2016) for robot construction and use. We constructed adult male *M. bivittatus* models from foam and rubber in three different sizes: small (snout–vent length [SVL] = 65 mm), medium (average male body size, control; SVL = 79 mm), and large (SVL = 103 mm). We studied the display movement pattern of *M. bivittatus* from Carpenter (1966), translated the pattern into Arduino code, and uploaded it to an ArduinoONE card. We linked the ArduinoONE card to a mini servomotor (HS-225BB Mighty Mini Servo) that was powered by an adjustable battery with a 6-V output as a power source. Models were remotely controlled by a custom app running on a mobile phone (Samsung S6) sending signals to a BlueTooth module (HC-05) linked to the ArduinoONE card. This same mobile phone also served as

FIG. 1.—Components (top) and assembled form (bottom) of the *Microlophus bivittatus* robotic models. A color version of this figure is available online.

a camera during the study. All components were fixed to a wooden board for support, with the board itself fixed to the inside of a plastic container painted to resemble a lava rock. We placed the lizard model on top of the plastic container, which was secured to the wooden board inside it via magnets. The magnets were attached to small metal bearings placed on the front limbs and tail. We affixed a thin metal rod to the servomotor and passed it through the wooden board and plastic container to hook into a small metal ring in the model's neck, which facilitated the stereotyped bobbing display motion (Fig. 1).

Robot Presentation Protocol

We presented each male robotic lizard to free-ranging *M. bivittatus* lizards located along two different sampled sites, referred to as Site 1 (Sendero Tijeretas) and Site 2 (Playa La Lobería). Robot presentations took place at Site 1 along the path between the Galápagos National Park Interpretation Center (0°53′36.9″S, 89°36′32.8″W; datum = WGS84 for all coordinates) and the pier of Cerro Tijeretas (0°53′17.4″S, 89°36′30.0″W), and at Site 2 along the trail between the entrance to La Lobería beach (0°55′21.6″S, 89°36′56.6″W) and near the base of the cliff passing the beach (0°55′54.8″S, 89°36′30.6″W). All locations were dominated by volcanic rock substrate and native vegetation cover. Robot presentations were conducted daily from and between 0900 and 1700 h, in temperatures of 26–32°C under clear to partly cloudy skies, according to the time of day that lizards are most active (Stebbins et al. 1967). Robot presentations were conducted at Site 1 from 7 to 14 April 2017, and at Site 2 from 29 May to 4 June 2017.

TABLE 1.—The number (*n*) of robot presentation trials conducted with male or female San Cristóbal Lava Lizards (*Microlophus bivittatus*) in the field. Values represent the percentage (%) of trials where lizards responded to the displaying robot with a maximal response of head bobs (HBOs) or push-ups (PUPs). Note that PUP represent the highest level of response, as lizards often start responding with HBOs, which escalate to PUPs. The bottom row shows the percentages for each type of response calculated over all lizards, regardless of robot size.

	Males				Females			
		Responsive (%)				Responsive (%)		
Robot size	*n*	PUPs	HBOs	Total	*n*	PUPs	HBOs	Total
Large	24	33.33	25.00	58.33	16	31.25	25.00	56.25
Medium	23	17.39	8.70	26.09	22	9.09	9.09	18.18
Small	20	30.00	5.00	35.00	20	10.00	45.00	55.00
All	67	26.87	13.43	40.30	58	15.52	25.86	41.38

When a lizard was located, we carefully placed the robot in clear view of the subject at a distance of 1–2 m from it, and we stepped back to start the trial. If the lizard did not flee or show signs of disturbance after placement of the robot, we remotely activated the robot and started video recording. Trials (presentation of a displaying robot) were 3 min in duration, which is the time period when lizards are most responsive to robots (E.J. Mancero, personal observation). We discarded trials lasting less than 3 min (e.g., when lizards were disturbed by another lizard, or when the subject moved out of view before the end of the trial). Field conditions and lizard behavior did not allow for a repeated-measures design, such as a random sequential presentation of all three sized robots to each lizard. Instead, we presented a single robot to individual lizards and randomized the size of the robot used for each trial. To ensure the independence of behavioral observations, we sampled lizards systematically through the site with no return to previously sampled areas.

Measuring Size, Behavioral Responses, and Scoring Coloration

Because of permit restrictions that prevented the physical handling of the study species, we assessed lizard body size (SVL) by standing 1–2 m away from the side of the lizard subject and subsequently measuring the distance on the ground between the projection of the tip of the lizard's snout and the base of its tail (cloaca). In an identical approach with lizards of the same species and in the same location, lizards were captured and measured following body size assessment. Assessed and measured body sizes were strongly correlated ($r = 0.92$, $F_{1,88} = 487.7$, $P < 0.01$). The use of assessed body size was preferred over applying a correction factor (i.e., $SVL_{Measured} = 6.75 + 0.88 \ SVL_{Assessed}$, $P < 0.01$) in order to avoid introducing further uncertainty and because, on average, the assessed body size only slightly overestimated the measured body size (mean of differences = 2.17 mm, 95% confidence interval [CI] = 1.22–3.13 mm; P.L. Carrión and C.A. Valle, personal observations). We computed the relative body size (Δ mm) as the size difference between the robot and the lizard used in the trial.

We evaluated responses of the free-ranging lizards (head bobs [HBOs] and push-ups [PUPs]) from video recordings played frame by frame. The robot was considered to be a contender when in a trial with a male, and a potential mate when in a trial with a female. We counted the total number of display responses of the lizard to the robot (full series of stereotyped head bobs plus push-ups) per trial. We measured intensity of responses as the highest intensity of a display response during the trial among the three ascending

categories of response: unresponsive, head bobbing (up-and-down head movements), and push-ups (up-and-down movements of the entire body by flexion of the legs).

For the free-ranging females, we subjectively analyzed the intensity of nuptial coloration on the throat, sides, and back using coverage and saturation as criteria. Nuptial coloration patches were ranked as (1) absent, (2) apparent, and (3) intense.

Statistical Analyses

We modeled the body sizes of the lizards and the robotic models simultaneously as explanatory variables, controlling for each other's effects. Response variables analyzed in the model are display count, responsiveness (response versus no response), and display intensity. Female color intensity was included as an explanatory variable when analyzing data from female lizards. We ran statistical analyses separately for males and females given the sex differences in the context of signaling (Carpenter and Ferguson 1977).

We used zero-inflated Poisson regression to analyze display count data, as is recommended in the presence of outliers and zeros, as was the case with this variable (Zeileis et al. 2008). Responsiveness is a binary categorical variable influenced by several independent predictors, making binary logistic regression an ideal choice for analyzing the relationship between these variables (King 2008). Because of its ordinal nature, we analyzed display intensity using ordinal logistic regression with a cumulative link (see Christensen 2019). Type III analysis was used to account for the effect of the explanatory variable on each other (Dmitrienko 2017). We conducted all tests using RStudio (v4.1.2; R Core Team 2021) and SAS (v9.4; SAS Institute Inc., Cary, NC).

RESULTS

We presented the male robotic lizards to 67 male and 58 female free-ranging lava lizards. Overall, 40% of males and 41% of females responded to the displaying robots; the rest remained unresponsive (Table 1). Sexes did not differ in responsiveness to the displaying robots (Pearson's chi-squared test $\chi^2 = 0.015$, df = 1, $P = 0.90$). However, among actively responding lizards, the intensity of response (i.e., PUP vs. HBO) differed between the sexes ($\chi^2 = 4.79$, df = 1, $P = 0.03$); males responded more frequently with PUPs and females with HBOs.

Male Analyses

The number of responses (display count) of male lizards to a displaying robot (the contender) was positively
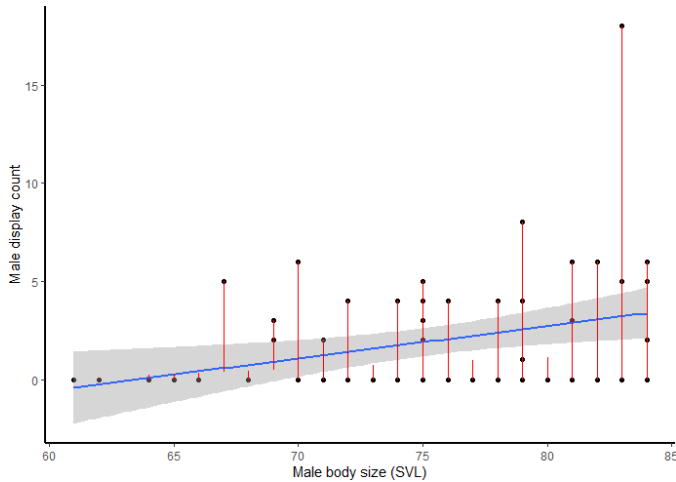
FIG. 2.—The number of responses of male *Microlophus bivittatus* lizards to confrontation displays from robotic lizards according to male body size (SVL). Black dots represent individuals. Gray shading indicates the error associated with the regression. A color version of this figure is available online.

correlated with male body size (Fig. 2; $r = 0.32$, Poisson regression coefficient $= 0.09$, SE $= 0.02$, Z $= 4.64$, $P < 0.01$) when controlling for robot size. A Type III analysis showed that both male body size ($\chi^2 = 24.47$, df $= 1$, $P < 0.01$) and robot size (Fig. 3; $\chi^2 = 20.39$, df $= 2$, $P < 0.01$) were significant predictors of male display count. Multiple comparisons between the three different robot sizes ($\alpha = 0.05/3 = 0.017$) revealed no significant difference between the ability of small-sized robots and medium-sized robots to predict male display count when controlling for male body size (Poisson regression coefficient $= 0.43$, SE $= 0.29$, Z $= 1.5$, $P = 0.13$). Large-sized robots, on the other hand, were significantly different than small-sized (Poisson regression coefficient $= 0.58$, SE $= 0.21$, Z $= 2.7$, $P < 0.01$) and
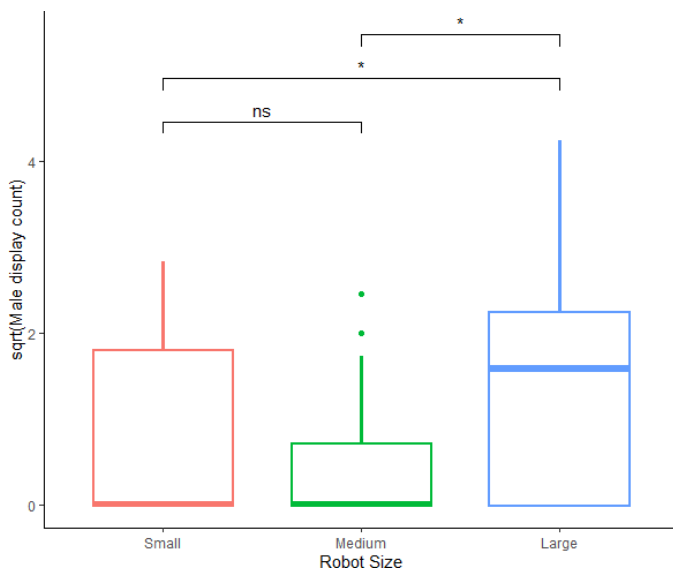

FIG. 3.—Male *Microlophus bivittatus* responses to confrontation displays from three sizes of robotic lizards. Each boxplot shows the distribution of the (square-root transformed) number of displays performed during male trials towards each size of the robotic model. A color version of this figure is available online.
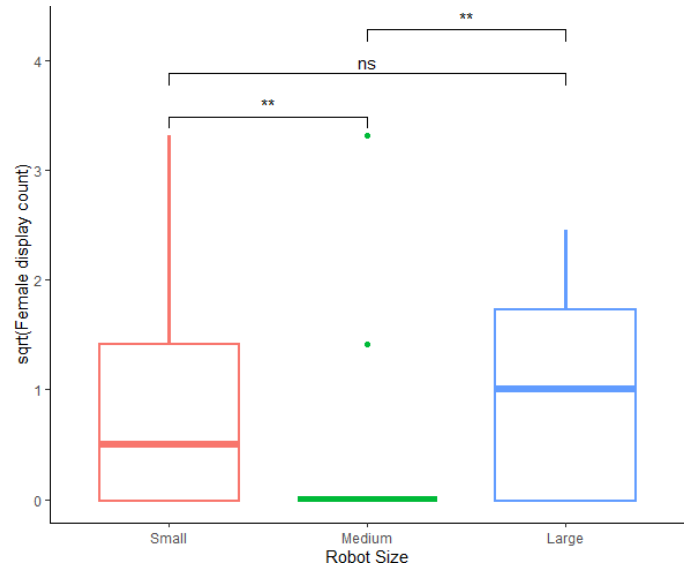

FIG. 4.—Female *Microlophus bivittatus* responses to courtship displays from three sizes of robotic lizards. Each boxplot shows the distribution of the (square-root transformed) number of displays performed during female trials towards each size of the robotic model. A color version of this figure is available online.

medium-sized robots (Poisson regression coefficient $= 1.02$, SE $= 0.26$, Z $= 3.97$, $P < 0.01$) in predicting male display count when controlling for male body size.

There was no significant effect of male body size on overall responsiveness (responsive versus nonresponsive) towards robot displays (binary logistic regression coefficient $= 0.09$, SE $= 0.05$, Z $= 1.8$, $P = 0.07$) when controlling for robot size. A Type III analysis shows that neither male body size ($\chi^2 = 3.24$, df $= 1$, $P = 0.07$) nor robot size ($\chi^2 = 3.67$, df $= 2$, $P = 0.16$) were significant predictors of male responsiveness, when controlling for each other's effects.

Male display intensity towards a displaying robot was not influenced by male size (ordered logit coefficient $= 0.08$, SE $= 0.05$, $t = 9.04$, $P = 0.07$) when controlling for robot size. A Type III analysis showed that neither male body size ($\chi^2 = 3.28$, df $= 1$, $P = 0.07$) nor robot size ($\chi^2 = 2.3$, df $= 2$, $P = 0.32$) were significant predictors of male display intensity, when controlling for each other's effects.

Female Analyses

The number of responses (display count) of female lizards to a displaying robot (a potential mate) was not positively correlated with female body size ($r = 0.32$, Poisson regression coefficient $= -0.06$, SE $= 0.04$, Z $= -1.62$, $P = 0.11$) when controlling for all other predictors. A Type III analysis showed that both robot size (Fig. 4; $\chi^2 = 8.69$, df $= 2$, $P = 0.01$) and the intensity of female nuptial coloration on the sides of the lizard ($\chi^2 = 8.39$, df $= 2$, $P = 0.02$) were significant predictors of female display count. On the other hand, neither female body size (Pearson's chi-squared test $\chi^2 = 2.81$, df $= 1$, $P = 0.09$), throat nuptial coloration ($\chi^2 = 2.59$, df $= 2$, $P = 0.27$), nor back nuptial coloration ($\chi^2 = 4.75$, df $= 2$, $P = 0.09$) were significant predictors of female display count.

Multiple comparisons between the three different robot sizes ($\alpha = 0.05/3 = 0.017$) reveal no significant difference
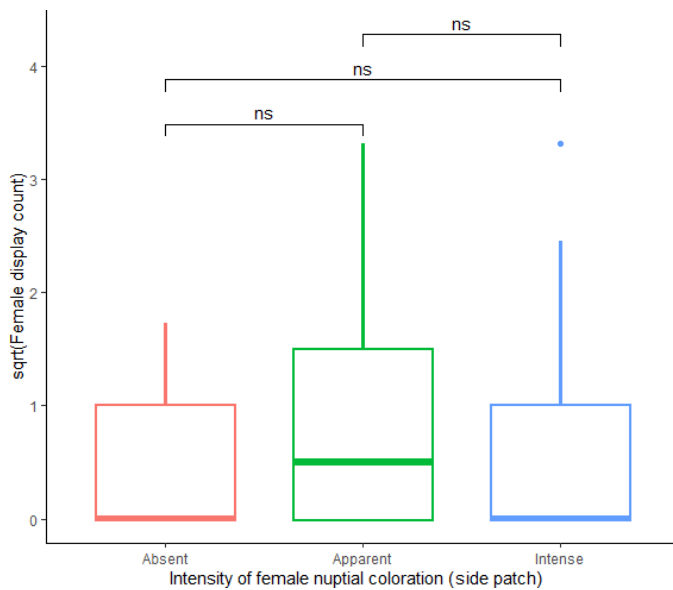
Fig. 5.—Female *Microlophus bivittatus* responses to courtship displays from robotic lizards according to the intensity of female nuptial coloration on side patches. Each boxplot shows the distribution of the (square-root transformed) number of displays performed during female trials grouped by each level of intensity of female side patch nuptial coloration. A color version of this figure is available online.

between the ability of small-sized robots and large-sized robots in predicting female display count (Fig. 4; Poisson regression coefficient = −0.08, SE = 0.29, Z = −0.27, P = 0.79). Medium-sized robots, on the other hand, were significantly different than small-sized (Poisson regression coefficient = −0.94, SE = 0.37, Z = 2.52, P = 0.01) and large-sized robots (Poisson regression coefficient = −0.86, SE = 0.34, Z = 2.52, P = 0.01) in predicting female display count.

Multiple comparisons between the three levels of side nuptial coloration intensity ($\alpha = 0.05/3 = 0.017$) reveal no significant difference between the ability of absent side nuptial coloration and intense side nuptial coloration in predicting female display count (Fig. 5; Poisson regression coefficient = 0.52, SE = 0.53, Z = 0.98, P = 0.33). Similarly, apparent side nuptial coloration was close to, but ultimately was not significantly different from, absent side nuptial coloration (Poisson regression coefficient = 1.05, SE = 0.48, Z = 2.21, P = 0.03) and intense side nuptial coloration (Poisson regression coefficient = 0.53, SE = 0.27, Z = 2.03, P = 0.04) in predicting female display count.

There was no significant effect of female body size (binary logistic regression coefficient = −1.36, SE = 0.1, Z = −1.3, P = 0.18) or any other predictor on responsiveness (responsive versus nonresponsive) towards robot displays. A Type III analysis showed that female body size ($\chi^2 = 1.81$, df = 1, P = 0.18), robot size ($\chi^2 = 5.07$, df = 2, P = 0.08), side nuptial coloration ($\chi^2 = 1.28$, df = 2, P = 0.53), throat nuptial coloration ($\chi^2 = 1.15$, df = 2, P = 0.56), and back nuptial coloration ($\chi^2 = 2.14$, df = 2, P = 0.34) were not significant predictors of female responsiveness.

Female display intensity towards a displaying robot was not influenced by female size (ordered logit coefficient = −0.16, SE = 0.96, t = 7.03, P = 0.09) or any other predictor. A Type III analysis showed that female body size ($\chi^2 = 2.87$, df = 1, P = 0.09), robot size ($\chi^2 = 4.39$, df = 2, P = 0.11), side nuptial coloration ($\chi^2 = 2.09$, df = 2, P = 0.35), throat nuptial coloration ($\chi^2 = 2.7$, df = 2, P = 0.26), and back nuptial coloration ($\chi^2 = 1.01$, df = 2, P = 0.6) were not significant predictors of female responsiveness.

DISCUSSION

Social behavior in lizards is primarily driven by visual displays and chemical signaling (Ord et al. 2001; Mason and Parker 2010; Hews and Martins 2013). Experimental studies of several species of lava lizards in the Galápagos Islands have shown that robotic lizards displaying conspecific patterns stimulated behavioral responses (Clark et al. 2016, 2017, 2019; Macedonia et al. 2019). Therefore, we interpret that lava lizard responses to robots emulating a male lava lizard both physically and behaviorally correspond to either a displaying opponent (when the lizard was a male) or to a displaying potential mate (when the lizard was a female) and discuss our results accordingly. Furthermore, placement of a displaying robot close to a free-ranging male lizard emulated the intrusion of a male lizard into a resident male's territory or home range. Recent studies have shown that resident males are prone to initiate and win a fight (Olsson 1992; McMann 1993; Olsson and Shine 2000; Hardy and Kemp 2001; Umbers et al. 2012).

Display counts, measured as the number of full sequences of head bobs plus push-ups, are considered to be a proxy for the time and energy a male lizard invests in aggressive responses, as well as the time and energy that a female lizard invests in a prospective mate (Clark et al. 2015). Similarly, display intensity is a proxy of both the level of expressed aggressiveness and territoriality in males and the level of expressed interest in females (Carpenter and Ferguson 1977; Jenssen 1977; Ord et al. 2001; Watt and Joss 2003). Sex differences in the frequency and intensity of display behavior may be explained by sex differences in habitat use, life history, and the particular information being conveyed (Radder et al. 2006). Display intensity also indicates the disposition of a male to engage in risky behavior against a contender, as more intense displays are more likely to escalate into physical fights (e.g., see Tokarz 1995). Accordingly, we found that the likelihood that San Cristóbal Lava Lizards will reply with head bobs remained relatively constant for males of all sizes, whereas push-up responses were mainly performed by the largest males.

Male Response

We found that aggressive male responses towards an opponent, as evidenced by display count, were dependent on body size. Large male size of both the male lizard and the robotic opponent were associated with a relatively high number of responses, indicating that increased aggression and territoriality of larger males is further driven by contenders of similar proportions. It seems, then, that time and energy invested by males during aggressive responses, as well as the risk they may incur, increased along with body size. As the likelihood of winning a confrontation usually correlates positively with male body size (e.g., Olsson 1992; Zucker and Murray 1996; Schuett 1997), the relatively large males would be expected to prevail during confrontations with smaller males. Our findings are consistent with both

theoretical (e.g., Andersson 1994; Calsbeek and Sinervo 2004) and empirical work in reptiles (e.g., Marler and Moore 1988; Olsson 1992; Zucker and Murray 1996; Schuett 1997; McMann 2000; Tokarz et al. 2003).

We cannot rule out a possible confounding effect of male's resident status on their aggressive responses to displaying robots. Male residency status is expected to increase aggressiveness, but its effect is expected to interact with body size, increasing aggressiveness especially among the less aggressive smaller males when facing an opponent (e.g., see Umbers et al. 2012). Such an interaction between residence status and body size would weaken the effect of body size. However, the fact that we found an effect of body size on male display counts despite any role of residency status indicates that the effect of body size was sufficiently strong as to override any effect of residency.

In contrast to display counts, neither responsiveness nor display intensity was influenced by the size of either competitor. Reptiles perform specific movements to a multitude of social contexts with or without the need for a specific receiver (Leal and Rodríguez-Robles 1997; Jenssen and Nunez 1998). Males of other species do not alter display intensity or frequency based on the configuration of other males' signals; it is possible that head bobs in males are used to acknowledge the presence of another male rather than an invitation for further aggression (Macedonia and Stamps 1994; Tokarz et al. 2003). The lack of information regarding visual communication on *M. bivittatus* is likely to play a role in these results, as there may be signal patterns that have not yet been described (Carpenter 1977).

Why are larger male lava lizards more aggressive towards an intruder despite all the potential costs and risks? Among lizards with territorial polygyny (e.g., Marler and Moore 1988; McMann 2000), like lava lizards of the Galápagos where a male's territory overlaps the territory of several females (Rowe et al. 2020), a male's mating opportunities would be expected to correlate with territory size, territory quality, or both. Furthermore, and although it is unknown for Galápagos lava lizards, in some lizard species the chance of owning a larger and higher quality territory is also positively correlated with male body size (e.g., Marler and Moore 1988; McMann 2000). Thus, for a larger male holding a large and high-quality territory, it is expected that all other transient and resident neighboring males would represent a threat to his territory ownership and mating opportunities. The payoff of displaying for an extended period of time and risking a fight will be disproportionately higher for these larger males. Smaller males are expected to hold low-quality territories with poor female presence. As larger males establish greater home ranges, it is expected that smaller males behave as floaters in the outskirts of such territories, interacting primarily with larger competitors. Quick and nonaggressive signaling behavior from smaller males could reduce the risk of physical injury resulting from relatively unequal confrontations (Ord et al. 2001; Kohlsdorf et al. 2006).

Female Response

Female San Cristóbal Lava Lizards displayed the most to both the larger and smaller male robot compared to the medium-sized male robot, suggesting a preference for both large and small males, either because of their size or some correlates to male body size. Among polygynous territorial lizards, females are likely to choose mates based on resources that males hold rather than on a male's physical traits (e.g., see Kiester 1979; Ruby 1981, 1984; Trillmich 1983; Stamps 1987a,b; Hews 1990). Although territory ownership dynamics have not been well established for San Cristóbal Lava Lizards, males might precede females in establishing home ranges and territories during each mating season (C.A. Valle, personal observation). Such a pattern would confer females ample opportunity for mate choice, because they might be able to sample several territorial males and establish their territory within that of either a preferred mate or a preferred territory, similar to lekking species. Furthermore, if male body size correlates with territory quality (Cooper and Vitt 1989; Anderson and Vitt 1990), then large male body size could be a quick but reliable indicator of a male's territory quality.

On the other hand, if large male body size also correlates positively with social dominance (Fox 1983; Tokarz 1985) and the ability to acquire and maintain the best territories through aggressive competition with other males, then male body size might also be an indicator of male genetic quality. By choosing a large male, females might benefit from both a high-quality mate and resources for reproduction.

There may also be advantages to preferring smaller males. Smaller males without a territory contribute paternity to clutches in a number of species (Cooper and Vitt 1993; Olsson et al. 1996). Smaller males may be young and unfamiliar to the females and thus likely to be more genetically distant than other local males, becoming attractive mates by siring more viable offspring via a decreased risk of endogamy (Olsson et al. 1996). Reproductive success is not entirely restricted to large males, with the number of offspring sired by males in both extremes of the body size spectrum being fairly similar (Hoffman and Henle 2006; Johnson et al. 2021). These demographic patterns may allow for populations to adapt quickly to changes in selection pressures favoring one type of male over the other, ensuring genetic diversity in the event of a population crash.

The effect of coloration on female responsiveness to courting male robots remains unclear. Female coloration among lizards has been ascribed a reproductive-status–signaling function (Vinegar 1972; Yedlin and Ferguson 1973; Cooper 1986, 1988; Zucker 1989; Watkins 1997; Cuadrado 2000; Hager 2001; Weiss 2002; Baird 2004). Only one aspect of nuptial coloration, the extent of red pigmentation on the side of females, had an effect on female display count, although post hoc pairwise tests found no effect of side patch intensity on display count. Also, there was no effect of nuptial coloration on female display intensity. Female coloration expression among lizards develops (i.e., increased patch size and color intensity) during the reproductive season and peaks before mating, and then fades and retracts (Weiss 2002). Thus, the likelihood that females expressing the same color pattern could be sexually receptive or nonreceptive could account for the difference in response to a displaying male. Levels of ornamentation have different effects on male and female lizards. Males may prefer less ornamented females (Swierk and Langkilde 2013), yet highly ornamented females with low cortisol may risk avoidance or even aggression by males, but may produce eggs richer in protein (Ensminger et al. 2018). Watkins' (1997) hypothesis

that female coloration signals a postmating lack of sexual receptivity cannot be ruled out as another possible explanation.

In conclusion, we argue that female San Cristóbal Lava Lizards are selecting both larger and smaller males because of the quality of the male's genetic makeup and, in the case of large males, high-quality territories ensure optimal resources for reproduction. The extent of male body size as a measure of reproductive success deserves further investigation, particularly in the context of DNA data and paternity. This study sheds light on the importance of untangling the effect of body size from associated morphological, hormonal, and genetic factors, with *M. bivittatus* acting as an ideal model for understanding the dynamics of mate choice and population demographics of lava lizards.

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