

Go big or go home: Divergence in morphology and behavior between island and islet
populations of the San Cristóbal lava lizard (*Microlophus bivittatus*)

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DEDICATION

To my dear family.

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ABSTRACT

Rapid divergence in body size is a well-documented phenomenon among island species, associated with macroevolutionary processes of diversification and adaptive radiation. The effect of insularity in determining larger body size as an optimal phenotype is primarily attributed to lower predation and greater intraspecific competition on islands. Our study examined interpopulation variation in morphology, social behavior and predator avoidance in Galápagos lava lizards endemic to San Cristóbal island (*Microlophus bivittatus*), and the nearby islet Isla Lobos. Islet populations have fewer competitors than those on the island, where native and introduced predators are abundant. We simulated interactions with predators and conspecifics by conducting stereotyped approaches and presentations of robotic models resembling males of equal and larger size. Arithmetic and geometric analyses of morphology describe islet males as larger than those in the island, with no significant variation in female size. Territorial displays were stronger towards larger robot models by islet males, and towards same-size robot models by island males. Female displays favored larger models in both locations. Predator avoidance was less pronounced on islet lizards, evidenced by shorter escape and flight distances than those of island lizards despite similar distance to refugia. Our results suggest that predation release, supported by strong male intrasexual selection, is a key component behind the evolution of divergent body sizes in this species.

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ABBREVIATIONS

Composite Response – CR

Escape distance – ED

Flight initiation distance – FID

Front limb length – FL

Generalized linear model – GLM

Hind limb length – HL

Mandibular length – ML

Mandibular width – MW

Million years ago – mya

Principal component – PC

Principal component analysis – PCA

Refuge distance – RD

Scaled mass index – SMI

Sexual dimorphism index SDI

Sexual size dimorphism – SSD

Snout-to-vent length – SVL

Tail length – TL

CHAPTER 1

INTRODUCTION

Distinctive biogeographical attributes of insular environments provide ample ecological opportunities to a scarce number of colonizing species, promoting the evolution of novel and often extreme phenotypes compared to continental relatives (Losos & Queiroz 1997; Whittaker & Fernández-Palacios 2007; Whittaker et al. 2008, 2017). Variation in body size following successful occupation of an insular niche is widely documented, reflecting the strong influence of this trait on the physiology, ecology and behavior of a species and its adaptive potential (Case 1978; Maurer et al. 1992; Lomolino 2005; Olden et al. 2007; Calsbeek & Cox 2010). A pattern named “The Island Rule” describes a tendency for insular species to evolve towards intermediate body sizes, where large species become smaller while smaller ones grow larger upon colonization (Foster 1964; Van Valen 1973; Lomolino 2005; Benítez-López et al. 2021). Originally described in mammals, this ecomorphological trend has received further attention on this taxon (Lomolino 1985; Damuth 1993; Lomolino et al. 2013) and others including birds (Grant 1965; Clegg & Owens 2002; Knapp et al. 2019), reptiles (Jaffe et al. 2011; Keehn et al. 2013), insects (Chown & Gaston 2010; Polet 2011), and most recently, plants (Biddick et al. 2019; Burns 2019). However widespread, empirical evidence for the generality of this pattern is strongly polarized given conflicting evolutionary responses among and within groups (Lomolino 2005; Meiri et al. 2005, 2008; Itescu et al. 2018). Phylogeny and autecology of individual species are proposed to explain variation in growth trajectory and optimal trait size, suggesting community composition and behavior as significant factors in determining the magnitude of morphological divergence in islands (Meiri et al. 2011; Biddick et al. 2019).

Species richness is notoriously low in island ecosystems, failing to support the resource

base required by predators to establish viable populations (Abbott 1980). Frequent encounters with predators select for survival strategies based around detection and escape, factoring trade-offs between habitat use and survival (Ydenberg & Dill 1986; Damas-Moreira et al. 2014). If predation risk decreases alongside predator richness, energy allocation will then shift away from vigilance (Greene 1988; López & Martín 1995). Low-risk conditions increase foraging success and survivorship, optimizing growth rates towards larger body size (Hamilton & Heithaus 2001; Vervust et al. 2007; Donihue et al. 2016). Greater investment in lifetime fitness and reproductive efforts is expected to increase population density, and thus intraspecific competition (Jirotkul 1999; Firman & Simmons 2008).

A larger body is advantageous in circumstances where the acquisition and maintenance of available resources is mediated by competition (Stamps & Krishnan 1994; Calsbeek & Smith 2007). This advantage extends to morphological correlates of body size, as proportional increases in head size and bite force are beneficial in prey selection and social dominance (Herrel et al. 1999, 2001, 2004). Ecological responses to these conditions are further biased by differences in life history among the sexes (O'Connell et al. 2019). Male-biased sexual size dimorphism (SSD) is a common feature of lineages characterized by male combat and territoriality (Watkins 1996; Cox et al. 2003, 2007; Blanckenhorn 2005; Toyama & Boccia 2021). Conversely, female-biased SSD correlates directly to greater reproductive investment and a tendency towards K-selection strategies (Andrews 1979; Cox et al. 2007).

The unique geology of the Galápagos Islands provides ideal conditions for deconstructing the influence of these factors on the evolutionary ecology of species and communities alike (Lomolino 1985; Harpp et al. 2014). Complex patterns of adaptive radiation are found in Galápagos lava lizards (*Microlophus spp.*), a genus of polygynous, territorial lizards that vary in

size, color and behavior (Benavides et al. 2009). Males and females perform species-specific signature displays consisting of stereotyped bobbing motions as a form of social communication, broadcasting territoriality or mate attraction (Carpenter 1977). Comparative analyses in this genus have established similar evolutionary trajectories for body size between island and mainland species, suggesting equal selection pressures in both environments (Toyama & Boccia 2021, 2022). However, ecomorphological variation in body size at the intraspecific level, where sex-specific selection is expected to be stronger, has not been explored for this group (Fairbairn & Preziosi 1994; Kaliontzopoulou et al. 2010). *Microlophus bivittatus*, a species endemic to San Cristóbal Island and its adjacent islet Isla Lobos, provides an excellent opportunity to examine the relationship between insular body size and patterns of natural and sexual selection acting upon it (Kizirian et al. 2004).

In this study, we described the morphological parameters of *M. bivittatus* from allopatric populations on an islet-island system and investigated the patterns and possible causes for differences found within this species. Both populations are distributed across almost identical elevation and latitude, avoiding confounding effects of other biogeographical patterns influencing body size (Rowe et al. 2019; Toyama & Boccia 2022). Generalist strategies, little differentiation from ancestral body plans and solitary colonization patterns seen in *Microlophus* oppose the assumption of interspecific competition having an impact on the evolutionary trajectory of this genus (Losos & Queiroz 1997; Poe et al. 2007; Benavides et al. 2009). While low primary productivity would be expected in the smaller islet, the presence of seabird communities may subsidize nutrient availability across the terrestrial food web (Snell et al. 1996; Pafilis et al. 2011).

We tested the hypothesis that predation release and sexual selection favor the evolution

of larger body size in island reptiles by analyzing behavioral responses to stimuli associated with these factors. We conducted simulations of stereotyped predation attacks and measured the characteristics of escape responses as an indicator of wariness. For sexual selection, our experimental design consisted of subjects being presented with a robot designed to mimic *M. bivittatus* male conspecifics performing stereotyped bobbing displays. Two treatments were used, one where the robot was scaled to the average size of local males, and another where it was scaled to a larger size. The number and intensity of behavioral displays performed in response to the robot provides an indicator of the level of aggression or receptivity to mating expressed by male and female subjects respectively. We expect the reduced area and isolation of Isla Lobos to result in lower abundance and richness of predators, and thus predict reduced wariness in the islet population of *M. bivittatus* compared to those on the island, promoting larger body sizes in the former. Similarly, we predict behavioral responses from both sexes to displaying male robots to be stronger in the islet population compared to the island one, favoring the larger treatment in both locations. If a more competitive environment is observed in the islet, we expect male body size to be further enhanced in this population. In accordance with Rensch's rule, which states that SSD increases with male body size in male-biased species, we predict SSD to be greater for the islet population compared to the island one (Rensch 1959; Cox et al. 2003).

Purpose

The purpose of this study is to further investigate if certain ecological factors are associated with the emergence of greater body sizes in island species, and the implications this has on adaptive radiations in islands. Specifically, we attempt to identify and characterize patterns in morphology across populations of the San Cristóbal lava lizard, *M. bivittatus*, living on the main island against a similar gigantic population living on a nearby islet. Our

experimental design will then examine the influence of environmental pressures associated with territoriality and predation on defining the optimal morphological traits in each population, according to predictions established by previous literature on island-mediated phenotypic divergence.

Scope

Conclusions gathered from this research on lizard populations in San Cristóbal, Galápagos can be applied to other members of the genus with geographically isolated island conspecifics. Carefully, these patterns can be considered for any group expressing phenotypic divergence as a result of insularity, including comparisons between populations or species from the continental landmass. Additionally, our results provide baseline ecological information relevant to conservation efforts in the Galápagos National Park.

Assumptions

1. We assume that all morphological and behavioral observations are representative of each sampling location as a whole
2. We assume that responses to stereotyped predation approaches using human models are representative of behavior in response to local live predators
3. We assume that a lack of changes in orientation and location of the lizard model attached to the robot does not influence interactions with conspecifics.

Hypothesis

We tested the hypothesis that predation release and sexual selection favor the evolution of larger body size in island reptiles by analyzing behavioral responses to stimuli associated with these factors. We established the following research questions to accomplish this objective: (1) Is there interpopulation divergence in the morphology of *M. bivittatus*? (2) Are there

interpopulation differences in the intensity of behavioral displays signaling territoriality and courtship in *M. bivittatus*? (3) Are there interpopulation differences in responses to an approaching predator? (4) In case of morphological divergence between populations, is it explained by the patterns observed in behavioral responses?

Significance

Conflicting reports on the generality of the island rule have been observed across various taxa (Meiri et al. 2008; Lokatis & Jeschke 2018; Biddick et al. 2019; Benítez-López 2021), including reptiles (Meiri 2007; Itescu et al. 2018). Previous literature on morphological divergence in insular lizards has focused predominantly on anoles (Schoener 1969; Lister 1976; Irschick et al. 1997; Thomas et al. 2009; Velasco et al. 2020). The effect of latitude and altitude as determinants of body size divergence is well established, pending analysis in other groups (Bock et al. 2009; Goodman et al. 2013). Toyama and Boccia (2021, 2022) take this into consideration for *Microlophus* at the interspecific scale across the range of the genus and determine a lack of differences in body size between continental and insular species, remarking the insufficient latitudinal variation in the Galápagos and suggesting further research on natural history. This study expands upon these results by taking similar considerations focused on the insular members of *Microlophus*, previously unexplored at the interpopulation scale.

Definitions

Display action patterns: Structural representation of the movements occurring during stereotypical bobbing displays.

Scaled mass index (SMI): Body condition in a population expressed as body mass divided

by body size and multiplied by mean body size of the group (SVL_0) to the power of the respective scaling exponent (b_{SMA}); $SMI = mass/SVL * SVL_0^{b_{SMA}}$.

Size dimorphism index (SDI): Dimorphism in a population expressed as the average body size of males divided by that of females, centralized around a mean of zero; $-(SVL_{male} / SVL_{female}) + 1$.

CHAPTER 2

Go big or go home: Divergence in morphology and behavior between island and islet populations of the San Cristóbal lava lizard (*Microlophus bivittatus*)

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ABSTRACT

Rapid divergence in body size is a well-documented phenomenon among island species, associated with macroevolutionary processes of diversification and adaptive radiation. The effect of insularity in determining larger body size as an optimal phenotype is primarily attributed to lower predation and greater intraspecific competition on islands. Our study examined interpopulation variation in morphology, social behavior and predator avoidance in Galápagos lava lizards endemic to San Cristóbal island (*Microlophus bivittatus*), and the nearby islet Isla Lobos. Islet populations have fewer competitors than those on the island, where native and introduced predators are abundant. We simulated interactions with predators and conspecifics by conducting stereotyped approaches and presentations of robotic models resembling males of equal and larger size. Arithmetic and geometric analyses of morphology describe islet males as larger than those in the island, with no significant variation in female size. Territorial displays were stronger towards larger robot models by islet males, and towards same-size robot models by island males. Female displays favored larger models in both locations. Predator avoidance was less pronounced on islet lizards, evidenced by shorter escape and flight distances than those of island lizards despite similar distance to refugia. Our results suggest that predation release, supported by strong male intrasexual selection, is a key component behind the evolution of divergent body sizes in this species.

Key words: Body Size; Escape Behavior; Galápagos; Island Biogeography; Island Gigantism; Island Rule; Sexual Selection; Sexual Size Dimorphism; Territoriality; Tropicoduridae.

INTRODUCTION

Distinctive biogeographical attributes of insular environments provide ample ecological opportunities to a scarce number of colonizing species, promoting the evolution of novel and often extreme phenotypes compared to continental relatives (Losos & Queiroz 1997; Whittaker & Fernández-Palacios 2007; Whittaker et al. 2008, 2017). Variation in body size following successful occupation of an insular niche is widely documented, reflecting the strong influence of this trait on the physiology, ecology and behavior of a species and its adaptive potential (Case 1978; Maurer et al. 1992; Lomolino 2005; Olden et al. 2007; Calsbeek & Cox 2010). A pattern named “The Island Rule” describes a tendency for insular species to evolve towards intermediate body sizes, where large species become smaller while smaller ones grow larger upon colonization (Foster 1964; Van Valen 1973; Lomolino 2005; Benítez-López et al. 2021). Originally described in mammals, this ecomorphological trend has received further attention on this taxon (Lomolino 1985; Damuth 1993; Lomolino et al. 2013) and others including birds (Grant 1965; Clegg & Owens 2002; Knapp et al. 2019), reptiles (Jaffe et al. 2011; Keehn et al. 2013), insects (Chown & Gaston 2010; Polet 2011), and most recently, plants (Biddick et al. 2019; Burns 2019). However widespread, empirical evidence for the generality of this pattern is strongly polarized given conflicting evolutionary responses among and within groups (Lomolino 2005; Meiri et al. 2005, 2008; Itescu et al. 2018). Phylogeny and autecology of individual species are proposed to explain variation in growth trajectory and optimal trait size, suggesting community composition and behavior as significant factors in determining the magnitude of morphological divergence in islands (Meiri et al. 2011; Biddick et al. 2019).

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signature displays consisting of stereotyped bobbing motions as a form of social communication, broadcasting territoriality or mate attraction (Carpenter 1977). Comparative analyses in this genus have established similar evolutionary trajectories for body size between island and mainland species, suggesting equal selection pressures in both environments (Toyama & Boccia 2021, 2022). However, ecomorphological variation in body size at the intraspecific level, where sex-specific selection is expected to be stronger, has not been explored for this group (Fairbairn & Preziosi 1994; Kaliontzopoulou et al. 2010). *Microlophus bivittatus*, a species endemic to San Cristóbal Island and its adjacent islet Isla Lobos, provides an excellent opportunity to examine the relationship between insular body size and patterns of natural and sexual selection acting upon it (Kizirian et al. 2004).

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METHODOLOGY

Study site and Subjects

San Cristóbal is the easternmost island in the Galápagos, estimated to have formed 2.3 mya and historically isolated from the rest of the archipelago (Benavides et al. 2009; Ali & Aitchison 2014). The main island has a surface area of 558 km² and a maximum elevation of 730m (Snell et al. 1996). Isla Lobos is an islet located 165m off the western coast of San Cristóbal, roughly a thousand times smaller at 0.66 km² of surface area (Snell et al. 1996). Biogeographical history of the islet has not been explored, but extrapolation based on rising sea levels suggests much more recent separation from the main island at several thousand years ago (Poulos et al. 2009). Ecosystems in the island range from humid highlands peaking at 730m and arid beach zones bordered by lava rocks, with the islet structured entirely as the latter only a few meters above sea level (Ali & Aitchison 2014). Sampling on the island centered around La Lobería beach (0°55'21.2"S, 89°37'02.1"W) and Cerro Tijeretas (0°53'25.5"S, 89°36'30.3"W), while sampling on the islet encompassed the whole islet (0°51'21.5"S, 89°33'57.8"W). Sampling occurred linearly in one direction along trails in each study site, preventing pseudoreplication by disregarding individuals from previously sampled areas. Data collection was performed between 0900 and 1700 h, in temperatures of 26–34°C under clear to partly cloudy skies, corresponding to the times lizards are most active (Stebbins et al. 1967).

Microlophus bivittatus is a small tropidurid lizard, polygynous and territorial, endemic to San Cristóbal island and Isla Lobos. This species is diurnally active and common at low elevations, frequently alternating between rock faces and shaded areas to regulate body temperature (Rowe et al. 2019). Similar to other members of the genus, *M. bivittatus* performs species-specific signature bobbing displays singularly or in “volleys” of a few sequential

displays (Macedonia et al. 2019). A second type of structurally distinct bobbing display is unique to *M. bivittatus*, consisting of a brief two-bob motion. These displays are performed briefly before locomotion or reorientation, always singularly (Macedonia et al. 2019, Clark et al. 2023). Diet consists of various invertebrates such as moths and crickets and plant material including fruits of palo santo trees (*Bursera graveolens*), contributing to seed dispersal (Moore et al. 2017; Hervias-Parejo et al. 2019). Natural predators include lava herons (*Butorides sundevalli*), chatham mockingbirds (*Mimus melanotis*) and the eastern Galápagos racer (*Pseudalsophis biserialis*) (Ortiz-Catedral et al. 2019; Clark et al. 2023). The addition of cats (*Felis domesticus*) to the predator community is exclusive to San Cristóbal, with lizards making the most of their diet (Carrion & Valle 2018).

Robot Construction

Robotic models simulating the appearance and display action patterns of male *M. bivittatus* lizards were used to elicit behavioral responses from males and females. Display action patterns for *M. bivittatus* described by Carpenter (1966) were adapted into Arduino code and uploaded to an Arduino® UNO R3 programmable computer board. This board was then connected to a HiTec HS-225BB Mighty Mini servomotor (HITEC RCD USA, Inc.) and powered by 9-V-2ADC Li-ion battery (SHANQIU Mini UPS, Model FX5-12, Shenzhen Feixing Technology Co., Ltd.). All components were then fixed to a rigid 3D printed surface attached to the inside of an opaque plastic box.

Lizard models resembling adult male *M. bivittatus* were constructed using 3D modeling software (Meshmixer v3.5, Autodesk, Inc., San Francisco, CA, USA). Based on prior reports of mean and maximum body sizes of males from both sites, we scaled the models to body sizes corresponding to: (1) average San Cristóbal Island male (SVL = 70 mm); (2) average Isla Lobos

male/large San Cristóbal Island male (SVL = 100 mm); (3) and large Isla Lobos male (SVL = 120 mm). Models were then 3D printed using NinjaFlex® TPU filament and painted to resemble live conspecifics. Finished models were attached to the top of the plastic container and secured in place with screws (Fig. 1). Stereotyped motion corresponding to bobbing displays is achieved by attaching one end of a thin metal push rod to the servomotor and the other to the lizard model, transferring movement accordingly.

Robot Presentation Protocol

Robot presentation trials were conducted from 4–11 March and 27 July–9 August 2022 on a total of 183 free-ranging *M. bivittatus* lizards, 48 males and 41 females from San Cristóbal and 67 males and 27 females from Isla Lobos. Trials consisted of three push-up displays performed by lizard model atop the robot followed by a 30.0s pause, reiterated for a total of 6 minutes. Two lizard models corresponding to the average and above-average size of local males were used in each site. Each subject was shown only one model per trial. Upon spotting a lizard, we carefully approached it and placed the robot directly across the subject at a distance of ~2m. We then set up a cell phone camera (Samsung S21+5G) and began recording the interaction on a high-resolution video format (H.264) upon activating the robot. Trials where subjects were disturbed by another lizard or fled more than 5m away from the robot were not considered valid.

Determination of Morphological Variables

Following robot presentation trials, lizards were collected manually by noose, sexed and measured individually to the nearest 1mm using Adoric 0–6" Electronic Micrometer digital calipers and a transparent plastic ruler. To ensure the independence of behavioral observations, the lower dorsum of sampled individuals was marked inconspicuously using a black Sharpie™ marker after measuring. Morphological variables measured in this study include: Snout-to-vent

length (SVL), front limb length from shoulder joint to wrist (FL), hindlimb length from hip joint to ankle (HL), mandibular length from the tip of the lower mandible to the point of articulation with the skull (ML), and mandibular width at widest point including soft tissue (MW) and tail length from base to tip (TL). Tails were visually inspected for signs of prior autotomy and regeneration. For the March sample ($n = 98$), mass was assayed to the nearest 1g using a 50g Pesola spring scale.

Determination of Display Behavior

Display data was gathered from individual video recordings, counting the number of distinct signature and two-bob displays performed during robot presentation trials. An array of non-bobbing displays was observed across subjects, indicating varying degrees of engagement with the robot model. We followed the protocol for computing a composite response (CR) score established by Clark et al. (2015, 2023) to account for these behaviors. Non-bobbing displays are ranked by aggression, as described by Carpenter (1977), and assigned point values accordingly. Each behavior is only counted once per trial and added into a cumulative score. We incorporated the following displays and point values into our analysis: (1) Tongue touch: Tongue briefly pressed against substrate. 1 point. (2) Tail lash: Undulating movement of the tail. 2 points. (3) Rapid reorientation: Sudden shift of body orientation above 30°. 3 points. (4) Gular expansion: Outward expansion of the gular fold. 3 points. (5) Displacement jump: Abrupt upward movement, body and feet briefly off the substrate. 4 points. (6) Lateral presentation: Reorientation maximizing lateral view, sides compressed and arms fully extended. 4 points. (7) Challenge display: Signature display performed with a heavily arched back, compressed sides and expanded gular fold. 5 points.

Determination of Escape Behavior

Simulated predation events were conducted from 27 July–9 August 2022 on a total of 98 free-ranging *M. bivittatus* lizards, 33 males and 13 females from San Cristóbal Island and 36 males and 16 females from Isla Lobos. In order to simulate a predation event, adult lizards were surveyed from a 5–10m distance across the study area. Once a lizard was located, the researcher approached it at a slow, constant speed of 0.5m/s (Stone et al. 1994; Cooper Jr. 1997).

Approaches continued until the lizard abandoned its position and moved away. Once the lizard had ceased its movement, reference points corresponding to (1) Final location of the researcher, (2) Initial location of the lizard, (3) Final location of the lizard and (4) Nearest refuge, defined as a rock crevice or otherwise inaccessible microhabitat, were marked with reflective tape. The flight initiation distance (FID; Horizontal distance between the researcher and the initial location of the lizard), escape distance (ED; Horizontal distance between the initial and final locations of the lizard), and refuge distance (RD; Horizontal distance between the initial location of the lizard and the location of the nearest refuge) were determined by measuring the distance between these tape marks (Cooper Jr. 2006). All approaches were performed by the same researcher wearing the same clothing, always from the front and maintaining visual contact with the subject (Burger & Gochfeld 1990, 1994).

Statistical Analyses

Subadult individuals were identified and excluded from the final sample by removing the lower 25th percentile defined by the smallest SVL value observed for each sex at each site (Losos et al. 2003). The values for all morphological measurements were ln-transformed prior to analysis. TL values were excluded from analysis owing to the variation in length observed for regenerated tails. We performed Principal component analysis (PCA) on all measurements to

visualize the morphological space occupied by each group and identify a size component of variation and allometric relationships.

We assessed the degree of sexual dimorphism by calculating a size dimorphism index (SDI) according to Lovich and Gibbons (1992). The value for SDI in each population was defined as the average body size of males divided by that of females, centralized around a mean of zero; $SDI = -(SVL_{\text{male}} / SVL_{\text{female}}) + 1$. We estimated body condition in each population, for each sex, by using the scaled mass index (SMI) proposed by Peig and Green (2009, 2010). For each group, a scaling exponent (b_{SMA}) is obtained from the slope of a standardized major axis regression of ln-transformed body mass on ln-transformed body size. Individual index values are then calculated from body mass divided by body size and multiplied by mean body size of the group (SVL_0) to the power of the scaling exponent; $SMI = \text{mass}/SVL * SVL_0^{b_{\text{SMA}}}$. We examined differences in tail status between sites using a GLM with binomial error structure, using SVL, sex, site, and interaction between sex and site as predictors.

We explored morphological variation in shape by following Butler and Losos (2002), adjusting for body size by using Mosimann's geometric mean method (Mosimann 1970). We defined the SIZE variable as the fifth root of the product of SVL, FL, HL, MW and ML for each individual. Values for the morphological shape of each trait were the ln-transformed ratio of each trait to SIZE. For example, the size-adjusted value for FL is defined as: $\ln(\text{FL}/\text{SIZE}) = \ln(\text{FL}) - \ln(\text{SIZE})$. We performed PCA on size adjusted traits to visualize relationships on shape morphology by each group. We modeled two-way ANOVAs using site, sex and an interaction of site and sex as predictors, with each of the size-adjusted traits as a response variable.

Data corresponding to robot trials were analyzed separately for males and females, based on contextual differences in territorial behavior (Carpenter and Ferguson 1977). We analyzed

differences in territorial behavior between sites in a GLM with poisson error structure, using SVL, model size, site and the interaction between model size and site as predictors. Counts of signature displays, two-bob displays, and CR scores were analyzed separately as response variables. Finally, we analyzed wariness by modeling two-way ANOVAs using site, sex and an interaction of site and sex as predictors, taking the ln-transformed geographical measurements of FID, ED and RD as response variables. We conducted all tests using RStudio (R Core Team 2022).

RESULTS

Body Size and Sexual Size Dimorphism

Average size of measured traits in adult *M. bivittatus* males was greater in Isla Lobos compared to San Cristóbal, whereas average size of female traits was similar in both locations (Table 1). Consequently, SDI was higher in Isla Lobos than in San Cristóbal, at 0.48 and 0.22 respectively. A principal component analysis described 93.5% of the variability found in ln-transformed measurements by the first PC with an eigenvalue of 4.67, with high contributions (< -2.15) by all variables (Fig. 2). SVL had a significant effect on the probability of having a damaged or regenerated tail ($z = 2.08$, $sd = 0.03$, $P < 0.01$), unlike site ($z = -0.04$, $sd = 0.65$, $P = 0.97$), sex ($z = -1.7$, $sd = 0.98$, $P = 0.09$) and interaction effects between site and sex ($z = 1.68$, $sd = 0.91$, $P = 0.09$). Scaled mass index differed between sites for males ($W = 243$, $P < 0.01$), but not for females in Isla Lobos ($W = 68$, $P = 0.45$).

A principal component analysis described 67.18% of the variability found in size adjusted morphological variables in terms of the first two PCs with eigenvalues higher than 1 (Fig. 3). PC1 explained 42.4% of the variability with higher contributions from AL (-1.78) and LL (-1.73), as well as ML (1.12) and MW (1.91). PC2 explained 24.77% of the variability with higher contributions from SVL (-2.01) and ML (1.43). Comparisons of size adjusted morphological variables revealed differences in snout-to-vent-length between sites, and in mandibular length and width between sites and sexes, with a significant effect of site and sex (Table 2).

Intrasexual selection

Behavioral response patterns were similar between males and females across both sites. The probability of performing signature displays towards a robot increased at larger body sizes,

for both territorial ($z = -2.1$, $sd = 1.43$, $P < 0.05$) and courtship interactions ($z = 2.23$, $sd = 0.05$, $P < 0.05$; Fig. 4). Interaction effects between model size and site were relevant for male signature displays ($z = -2.7$, $sd = 0.55$, $P < 0.01$), with higher odds of response displays towards the large robotic model observed in Isla Lobos males. The probability of female response displays differed with model size, with greater odds of response towards the large robotic model. No variable analyzed had an effect on the number of two-bob displays performed. Composite Response scores followed a similar pattern, with the exception of significant interaction effects between model size and sex for males (Table 3).

Predator avoidance

Female lizards exhibited greater FID ($F_1 = 6.14$, $P < 0.05$) and RD ($F_1 = 9.37$, $P < 0.01$) than males, with no differences in ED ($F_1 = 2.27$, $P = 0.14$). We observed greater FID ($F_1 = 16.65$, $P < 0.01$) and ED ($F_1 = 19.52$, $P < 0.01$) in the San Cristobal population, with no differences in RD ($F_1 = 2.36$, $P = 0.13$). Interaction effects between sex and site were not observed for FID ($F_1 = 0.48$, $P = 0.49$), ED ($F_1 = 1.45$, $P = 0.23$), or RD ($F_1 = 0.13$, $P = 0.72$; Fig. 5).

DISCUSSION

This study examined the effect of insularity on morphological divergence in the San Cristóbal lava lizard, testing whether habitat-specific life history changes best explain this phenomenon. We found the population on Isla Lobos expressed greater body size, restricted to males. This population presented more intense male competition and decreased predator wariness compared to the main island. Collectively, our results suggest that predation release and increased territoriality influence the divergent evolution of insular morphology at the interpopulation level, with a stronger effect on male individuals. Sex-specific ecomorphological and behavioral variation in island systems is documented across various lacertid groups (Petren & Case 1997; Poe et al. 2007; Cooper Jr. et al. 2009; Raia et al. 2010; Runemark et al. 2014; Anaya-Meraz & Escobedo-Galván 2020; Avramo et al. 2021). Previous analyses comparing insular and continental species of *Microlophus* found no evidence of this pattern (Toyama & Boccia 2021). Sensitivity to environmental variation may be more pronounced at the population level, elucidating the basis of macroevolutionary patterns of phenotypic divergence observed in island systems (Clegg & Owens 2002; Kaliontzopoulou et al 2015).

Male *M. bivittatus* are larger on the islet, and in better condition. Evolutionary changes in body size require balancing the benefits of growth against increased energy requirements and risk of predation (Lima & Dill 1990; Lima 1998). Changes in body shape accumulate at a slower rate than those in size, correlating to finer aspects of these tradeoffs such as growth patterns and foraging efficiency (Losos 1990; Butler & Losos 2002; Erickson et al. 2012). The magnitude of selective forces stabilizes at a different, more lenient level on insular ecosystems, allowing the expression of extreme phenotypes (Lande 2007). Island biogeography predicts that surface area and distance to the nearest landmass determines community assembly, with larger and closer

islands supporting greater species richness (Whittaker and Fernández-Palacios 2007; Zhu et al. 2020). As a result, large carnivores, mammals in particular, are seldom naturally occurring on islands (Lomolino 1994; Fox & Fox 2000). Release from predation pressure leads to increased opportunities for foraging, territorial defense and mating, facilitating the development of island gigantism (Blanckenhorn 2000). Lizards under these conditions quickly diverge in phenotypic and behavioral traits, establishing themselves at a high trophic level (Meiri 2008; Runemark et al. 2014).

We observed intense predator avoidance for both sexes in the island population relative to the islet one, evidenced by greater flight initiation and escape distances despite no difference in refuge distance between sites. Male lizards on both sites tolerated closer approaches and stayed closer to refuges in relation to females. The loss of adaptations against predators is expected to occur under lower predation regimes, as those expected in island ecosystems (McNab 1994, van Damme & Castilla 1996; Rödl et al. 2007). In contrast with morphological changes, behavior can be quickly adapted to respond to novel threats and the ability to recognize them (Lima 1998; Berger et al. 2001). Urbanization and repeated introductions of invasive species are the main drivers of extinction in modern island ecosystems (Simberloff 1995; French et al. 2008) Domestic cats (*Felis silvestris catus*), in particular, have destroyed local assemblages through lethal and sub-lethal influence (Medina et al. 2011, 2014). Introduced cats in the Galápagos archipelago exert significant pressure on native species, and are likely responsible for the near extinction of various species on Floreana (Grant et al. 2005). On San Cristóbal, *M. bivittatus* is the most widely consumed item in the diet of feral cats (Carrion & Valle 2018). Male lizards engage in more conspicuous behaviors than females, increasing predation and the costs of maintaining body condition (Snell et al. 1988; Pressier & Orrock 2012). Constant

exposure to the threat of predation reduces foraging opportunities and growth rates, leading to earlier maturation at suboptimal body size (Downes 2001). The frequency of tail breaks was identical between sites for both sexes, obscuring the exact causes of autotomy. Predator absence supports longevity, with older individuals attaining larger sizes and accumulating wounds from aggressive intraspecific interactions (Vervust et al. 2009).

Gigantism expressed as an increase in body size in islet males has led to greater SSD for this population, a pattern consistent with Rensch's rule previously undocumented in this genus. Allometric relationships observed under Rensch's rule are hypothesized to emerge from the interaction between a genetic basis for body size shared by the sexes and continuous selection for larger male body size, leading to greater phenotypic plasticity compared to that of females (Fairbairn & Preziosi 1994; Abouheif & Fairbairn 1997; Fairbairn 1997; Baker & Wilkinson 2001; Fairbairn et al. 2007). Intraspecific competition is the main contributor to SSD, mediated by interspecific competition preventing divergence across the sexes (Greenberg & Olsen 2010). Habitat-specific variation in SSD aligns with the evolutionary trajectory of sexual selection, often enhancing patterns already present (Butler et al. 2000; Stephens & Wiens 2009; Meiri et al. 2014). Adaptation to local conditions determining resource availability and associated growth and mortality rates influences differences in the magnitude of SSD observed across populations (Fairbairn & Preziosi 1994, Fairbairn 2005, Teder & Tammaru 2005). Marine iguanas provide an example of sexual selection favoring large male size at the species level, yet male size at the population level is ultimately determined by local patterns of algae growth (Wikelski & Trillmich 1997; Wikelski et al. 1997). Differences in size and shape of the head are influenced by resource partitioning in addition to sexual selection (Stamps 1983). For instance, the diet and morphology of mainland congener *M. stolzmanni* varies considerably for both sexes, with

generalist males and specialist females (Beuttner & Koch 2019).

Patterns of behavioral display responses to robotic male conspecifics differed between the sexes on each population. Male signature displays were biased towards above-average sized models on the islet, as were female signature displays regardless of site. Island males were less territorial towards larger conspecific models compared to average sized ones. Previous studies on *M. bivittatus* describe male aggression and female choice favoring larger male body sizes, with greater investment in this trait reflecting the increased priority of intrasexual competition (Snell et al. 1988; Toyama & Boccia 2021; Mancero et al. 2022). Evolutionary shifts in territorial behavior are associated with female density and home ranges, augmenting SSD (Cox et al. 2003, 2007). Intraspecific differences in home ranges correspond to the cost of maximizing access to females under local conditions (Perry & Garland Jr. 2002). While higher density is a staple of island ecosystems, populations on smaller islands exhibit a greater aggregate density than those on larger island or mainland environments based on the lower species richness found within (Rodda & Dean-Bradley 2002). Higher rates of intrasexual competition are expected as a result of density compensation (MacArthur et al. 1972).

Our results do not allow us to ascertain if changes in morphology and behavior correspond to phenotypic plasticity or variation in the genetic basis for this trait. Genetic drift and geographical isolation may contribute to the emergence and maintenance of larger male size in the islet (Jordan & Snell 2008; Troya 2012). *Microlophus* endemic to the Galápagos exhibit a characteristic “one species one island” distribution attributed to single founder events (Stone et al. 2003). Furthermore, rapid development of morphological differences may be responsible for hindering recolonization efforts by congeners in this group as seen on the mainland ancestor *M. occipitalis* (Watkins 1996). For example, nuptial coloration in female *M. duncanensis* is over

developed in relation to females from species on neighboring islands (Benavides et al. 2009). Overexpression of this trait discourages mating efforts in males, this may put new founders at a disadvantage and increase reproductive isolation (Clark et al. 2017).

Our study illustrates the effects of both sexual and natural selection acting upon body size. Differences in perceived predation risk and top-down control account for the plasticity of morphology and behavioral responses expressed by different populations of *M. bivittatus*. Varying degrees of intrasexual competition increase the fitness of larger male body size, and the lack of predation pressure relaxes selection against it. Differences in dietary niche and ontological processes between sites present an alternate hypothesis for the patterns found in this research. Future studies that illuminate the extent of ecological and genetic systems influencing morphology and associated behaviors are critical for a greater understanding of the processes driving the evolution of divergent body sizes in insular environments.

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FIGURE CAPTIONS

Figure 1. Robotic models of male *Microlophus bivittatus*.

Figure 2. Variation of body size-adjusted morphological traits in San Cristóbal females, San Cristóbal males, Isla Lobos females, and Isla Lobos males of *M. bivittatus*, as described by the first two principal components of a principal component analysis (PCA) on morphological variables.

Figure 3. Variation of body size-adjusted morphological traits in San Cristóbal females, San Cristóbal males, Isla Lobos females, and Isla Lobos males of *M. bivittatus*, as described by the first two principal components of a principal component analysis (PCA) on size-adjusted morphological variables.

Figure 4. Inter-population comparison of predicted values of square root transformed counts of signature displays to lizard models resembling conspecifics of average and above average size by male and female *M. bivittatus* from Isla Lobos (IL) and San Cristóbal (SC).

Figure 5. Standard boxplots showing the inter-population comparisons between flight initiation distance, escape distance and refuge distance by male and female *M. bivittatus* from Isla Lobos (IL) and San Cristóbal (SC).

TABLES

TABLE 1.— Mean \pm SD (n) of snout-vent length (SVL), front limb length (FL), hindlimb length (HL), mandibular length (ML), mandibular width (MW), and size dimorphism index (SDI¹) for male and female *M. bivittatus* from San Cristóbal Island and Isla Lobos.

Variables (mm)	San Cristóbal Island		Isla Lobos	
	Males ($n = 31$)	Females ($n = 36$)	Males ($n = 50$)	Females ($n = 20$)
SVL	73.11 \pm 6.41	60.06 \pm 3.22	92.22 \pm 10.42	62.35 \pm 4.63
FL	24.11 \pm 2.29	20.19 \pm 1.51	29.29 \pm 3.31	20.3 \pm 1.86
HL	38.41 \pm 3.5	31.09 \pm 1.95	46.31 \pm 4.99	31.9 \pm 2.07
ML	17.74 \pm 1.47	14.73 \pm 1.01	20.51 \pm 1.97	14.69 \pm 0.8
MW	11.10 \pm 1.16	8.95 \pm 0.74	12.8 \pm 1.83	8.54 \pm 0.98
SDI ¹		0.22		0.48

¹ Lovich and Gibbons (1992).

TABLE 2.— Two-way ANOVA results for comparisons between size-adjusted measurements of snout-vent length (SVL), front limb length (FL), hindlimb length (HL), and mandibular length (ML), and mandibular width (MW) of *M. bivittatus*. Statistically significant *p* values shown in bold.

Variable	Effect	F	P
ln(SVL/SIZE)	Sex	1.94	0.16
	Site	54.58	<0.01
	Site*Sex	2.57	0.11
ln(FL/SIZE)	Sex	2.08	0.15
	Site	0.84	0.35
	Site*Sex	0.62	0.43
ln(HL/SIZE)	Sex	0.59	0.45
	Site	3.4	0.07
	Site*Sex	0.87	0.35
ln(ML/SIZE)	Sex	12.03	<0.01
	Site	7.04	<0.01
	Site*Sex	4.13	<0.05
ln(MW/SIZE)	Sex	4.75	<0.05
	Site	17.88	<0.01
	Site*Sex	0.33	0.57

TABLE 3.— Poisson regression results for comparisons between square root transformed counts of signature displays, two-bob displays and composite response (CR) scores of *M. bivittatus*. Statistically significant *p* values shown in bold.

Variable	Effect	Males			Females		
		sd	z	P	sd	z	P
Signature Displays	SVL	1.43	2.08	<0.05	0.05	2.23	<0.05
	Model Size	0.34	1.53	0.13	0.85	2.08	<0.05
	Site	0.42	2.5	<0.05	0.81	1.88	0.06
	Model Size*Site	0.55	-2.7	<0.01	0.94	-1.41	0.16
Two-bob Displays	SVL	0.02	0.95	0.34	0.07	-1.02	0.31
	Model Size	0.46	0.98	0.33	0.85	-0.68	0.5
	Site	0.61	0.55	0.58	0.68	-0.39	0.7
	Model Size*Site	0.74	-0.97	0.33	0.96	0.57	0.57
Composite Response Score	SVL	0.01	0.12	0.91	0.05	0.57	0.57
	Model Size	0.28	1.85	0.06	0.6	0.8	0.43
	Site	0.35	0.76	0.45	0.58	-0.18	0.86
	Model Size*Site	0.43	-2.2	<0.05	0.71	0.36	0.72

FIGURES

FIGURE 1.



FIGURE 2.

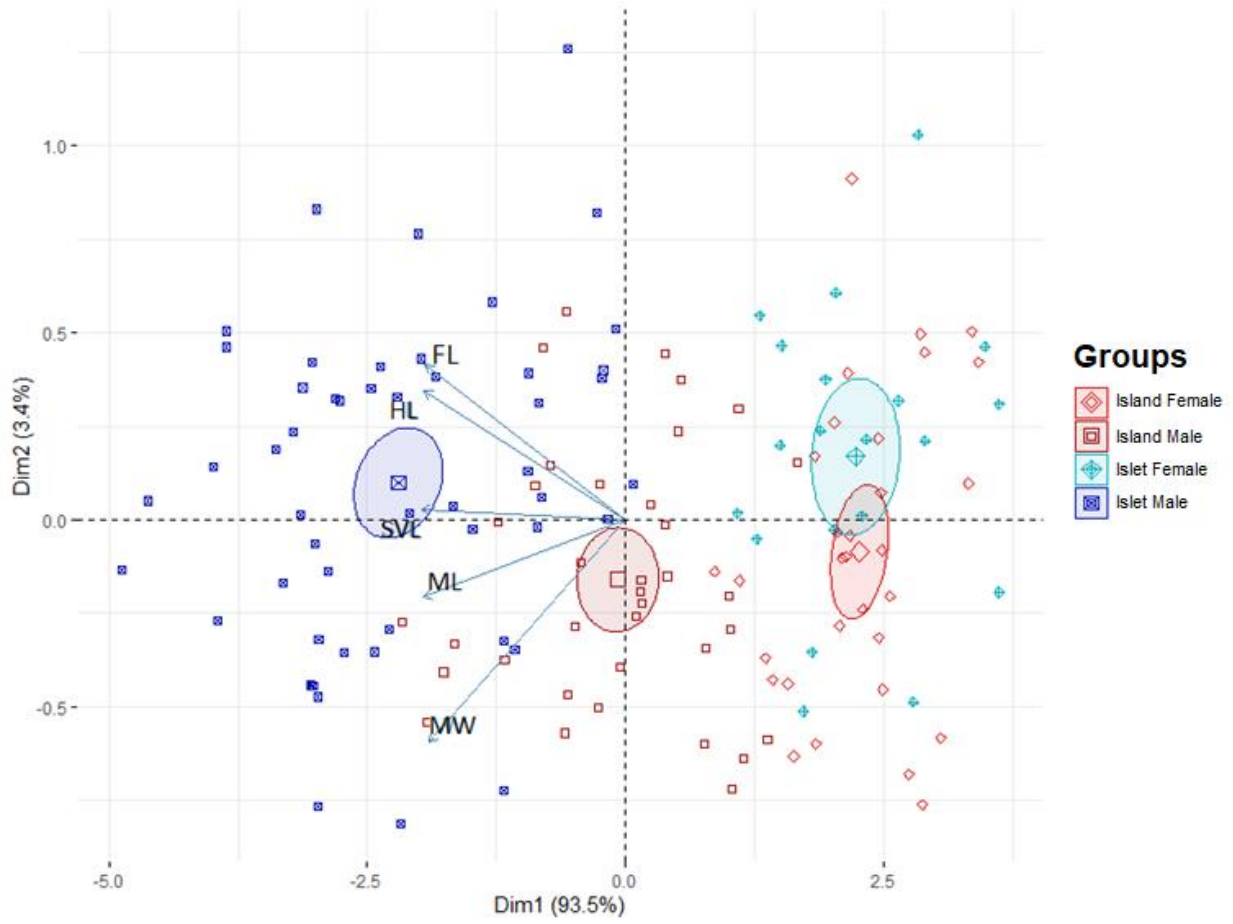


FIGURE 3.

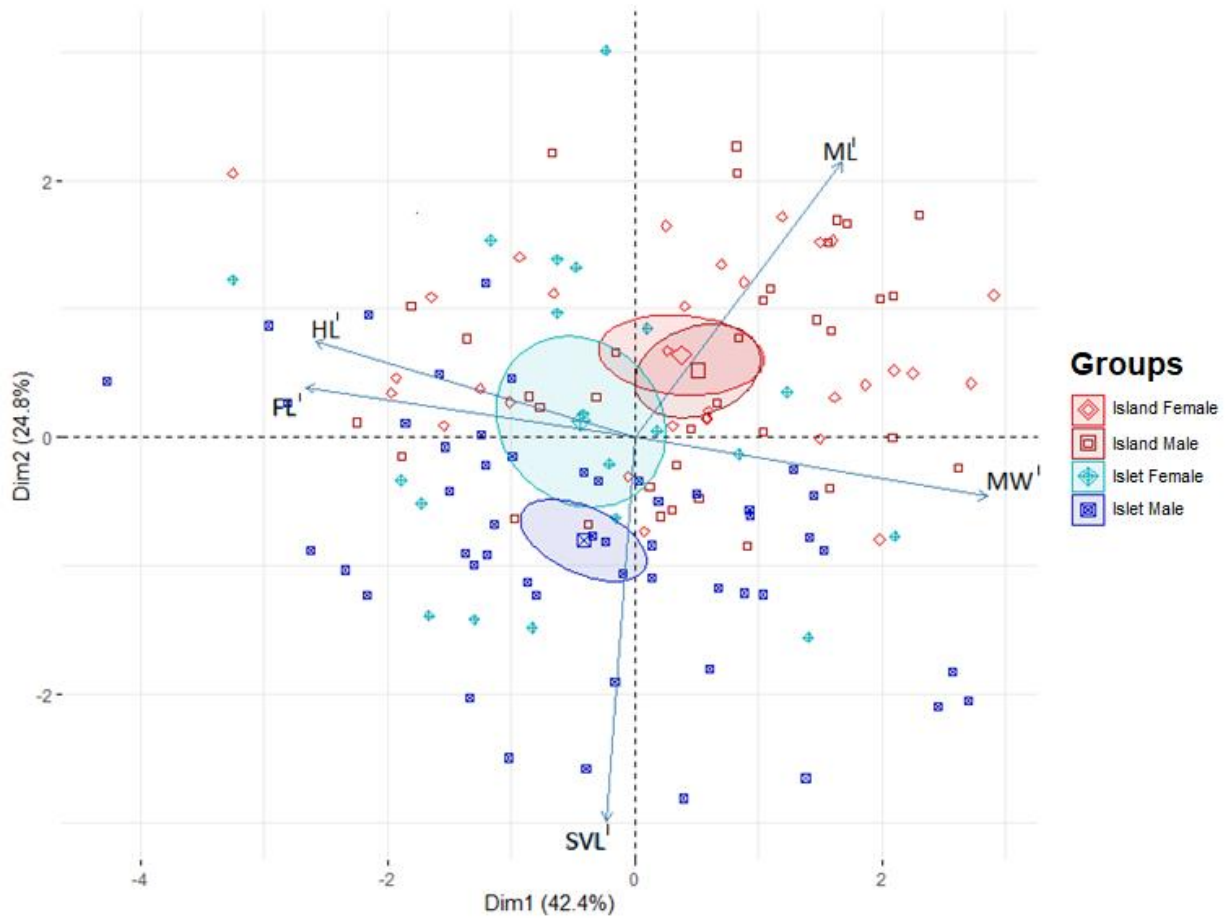


FIGURE 4.

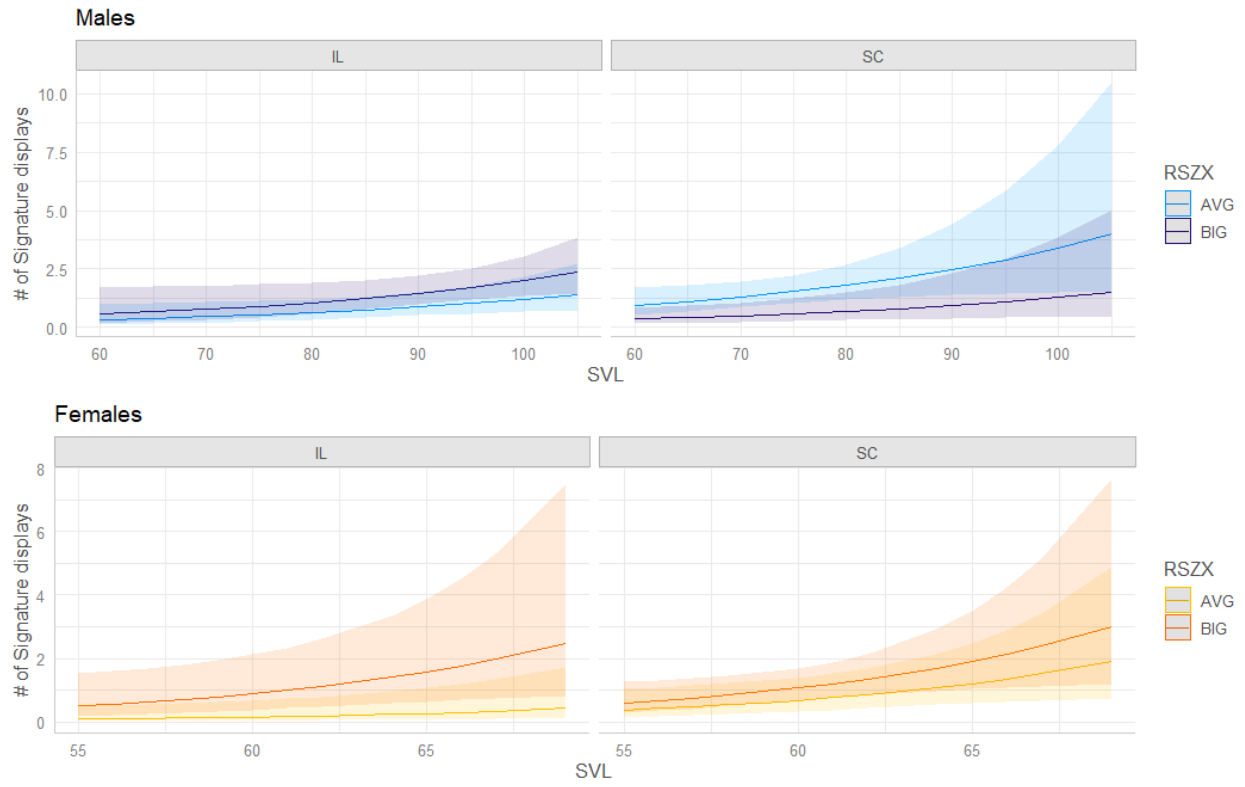
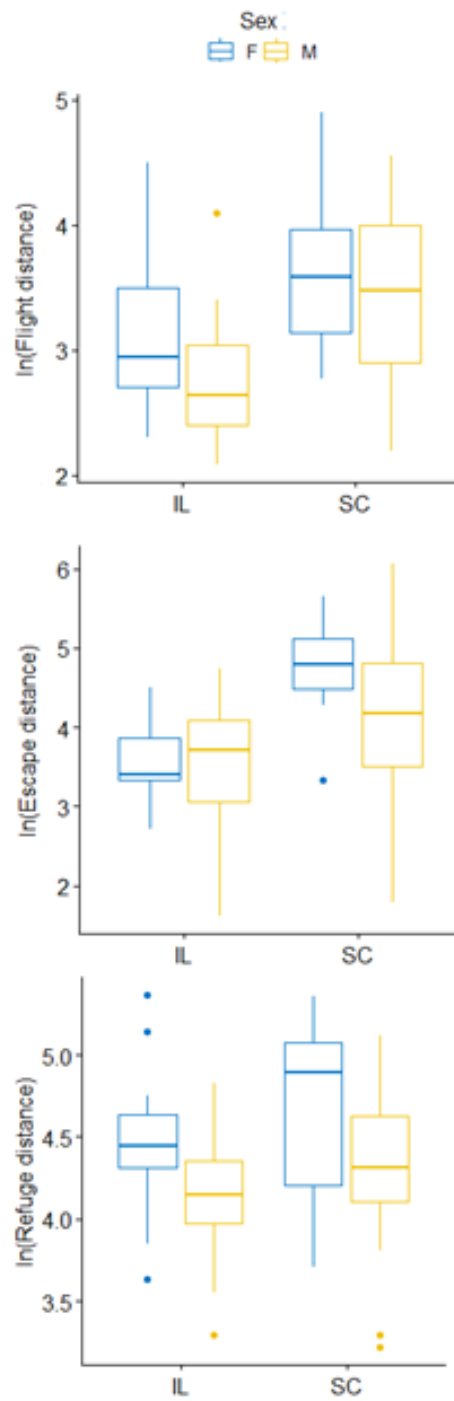


FIGURE 5.



CHAPTER 3

EXTENDED REVIEW OF LITERATURE

Insular biogeography and ecology

Biogeography is the study of the geographical distribution of organisms, and the effects variations in biological features arise from gradients in the physical composition of a landscape (Brown & Gibson 1983). Across various taxonomic scales and groups, patterns emerging from variation in geographical dimensions influence fundamental evolutionary processes of immigration, extinction and evolution (Lomolino 2000). Oceanic islands, atolls and archipelagos make up 5% of the earth's surface, where geographic isolation facilitates the development of unique biological patterns (Brown & Lomolino 1989). Discrete spatial structures with varying degrees of homogeneity found on insular systems constitute a microcosm of nearby continental landmasses, elucidating the mechanisms driving the expression of key biological processes (Warren et al. 2015).

MacArthur & Wilson (1963, 1967) developed a unifying Equilibrium Theory of Island Biogeography Theory (ETIB), describing the low species richness of island systems resulting from surface area and distance to the mainland filtering colonizers. Island diversity is assumed to emerge from the equilibrium between the immigration and extinction rates in the system, greater species richness affects this balance resulting in lower immigration and greater extinction (MacArthur & Wilson 1967). Extinction rate depends on island area, where larger islands are an easier to locate and colonize by successful propagules (MacArthur 1984; Ricklefs & Bermingham 2007; Losos & Ricklefs 2009). Similarly, habitat complexity and heterogeneity increases with surface area, providing ample niche space for immigrating species (Liu et al.

2018). Groups with higher dispersal abilities are able to readily establish themselves over longer distances, overriding the common “stepping stone” model of consecutive short migrations (Nathan 2006).

Further studies on this equilibrium find it to be dynamic, owing to multiple sources of colonizers routed across varying dispersal filters (Heaney 2000). Migration history is a key factor in determining the ecological relationships and adaptive potential of arriving species (Fukami et al. 2010). Early colonizers are suggested to rapidly capitalize on untapped resources, hindering the successful establishment of new arriving lineages (Carine et al. 2004; Silvertown 2004). Larger, more diverse areas are able to host greater population densities, fostering competitive displacement (Gravel et al. 2011). Community assemblage is further influenced by geographic origin, as emerging volcanic islands accumulate species quickly as colonization increases with virtually no extinction, in contrast to rapid extinction in islands breaking off from established landmasses (Whittaker & Fernández-Palacios 2007). While immigration determines the initial structure of the ecological community and its dynamics, niche partitioning and subsequent specialization to local conditions increase the significance of evolutionary changes (Santos et al. 2016).

Over longer evolutionary timescales, speciation rapidly factors in the balance determining the composition and endemism of local assemblages (Heaney 2000; Losos & Schluter 2000; Rosindell & Phillimore 2011). The original model for ETIB did not delve on evolutionary dynamics, but recognized the contribution of speciation over “radiation zones” in isolated archipelagos to overall species richness (MacArthur & Wilson 1963). Whittaker et al. (2008) incorporated these concepts into a framework named the General Dynamic Model of oceanic island biogeography (GDM), establishing variation in geological processes and features

as drivers of immigration, extinction and speciation. Geological ontogeny becomes a significant predictor of evolutionary trajectories, where older islands tend towards larger surface area and habitat complexity, increasing carrying capacity and population sizes (Whittaker et al. 2008; Rosindell & Phillimore 2011; Warren et al. 2015). High isolation and low turnover of competitors facilitates access to empty niches and local adaptation, increasing opportunities for *in situ* cladogenetic differentiation (Losos & Schluter 2000). Anagenetic patterns are common at intermediate distance from the main landmass, where consistent immigration of the source population stabilizes local variation (Rosindell & Phillimore 2011). Despite the assumption of smaller islands failing to meet an area threshold for differentiation, sufficient unsaturated niche space allows for cladogenetic and anagenetic processes to occur (Gillespie & Baldwin 2010).

Character release and insularity

Character release is a phenomenon described as rapid phenotypic variation in allopatric species as an adaptive response to ecological opportunities (MacArthur & Wilson 1967). Development of key innovations, dispersal to new environments and removal of antagonist species constitute major sources of ecological opportunity (Simpson 1944, 1953). These opportunities emerge as environmental changes relax a source of selective pressure acting on a given trait, creating ecological release (Yoder et al. 2010). Phenotypic expression of these traits is centered around an optimal mean, determined by local conditions (Schluter 2000). Divergence in natural selection readjusts the phenotypic mean, opposing stabilizing selection maintaining ancestral phenotypes (Lahti et al. 2009; Nosil 2012; Schluter 2000). Dispersal into a new environment can trigger strong directional selection on specific traits maximizing survival under novel conditions, potentially driving a reduction in stabilizing selection across all other traits (Yoder et al. 2010). Moreover, sporadic fluctuations in directional selection can coalesce into

stabilizing selection over longer time scales (Hansen 1997; Grant & Grant 2002).

Insular systems are ideal for exploring this phenomenon, given ample environmental variation between islands, each selecting for different trait means to maximize exploitation of available niche space. (Roughgarden 1972; Schluter 2000; Stroud & Losos 2016). Rapid accumulation of adaptive traits at the population level expands the niche width of a species, with individual specialization driving variation even further (Barrett & Schluter 2008; Baker et al. 2022). Individuals exploring new regions of niche space are subject to divergent selection for morphology and behavior maximizing performance, and thus fitness (Yoder et al. 2010; Calsbeek and Irschick 2007; Herrel et al. 2008). Conversely, intermediate phenotypes are to adapt sufficiently and are selected against (Schluter 2000). Traits associated with habitat use and mate recognition are further influenced by sexual selection, enhancing variation and reproductive isolation within a population (Panhuis et al. 2001; Turelli et al. 2001). The combined effect of these changes affects the rate of in situ diversification and speciation, shaping community assembly on island ecosystems (Aleixandre et al. 2013; Biddick et al. 2019).

EXTENDED METHODOLOGY

Measurements

Lizards were collected manually by noose, sexed and measured individually to the nearest 1mm using Adoric 0–6" Electronic Micrometer digital calipers and a transparent plastic ruler. To ensure the independence of behavioral observations, the lower dorsum of sampled individuals was marked inconspicuously using a black Sharpie™ marker after measuring. Morphological variables measured in this study include: Snout-to-vent length (SVL), front limb length from shoulder joint to wrist (FL), hindlimb length from hip joint to ankle (HL), mandibular length from the tip of the lower mandible to the point of articulation with the skull (ML), and mandibular width at widest point including soft tissue (MW) and tail length from base to tip (TL). Tails were visually inspected for signs of prior autotomy and regeneration. For the March sample ($n = 98$), mass was assayed to the nearest 1g using a 50g Pesola spring scale.

Use of conspecific robots

Robotic models simulating the appearance and display action patterns of male *M. bivittatus* lizards were used to elicit behavioral responses from males and females. Display action patterns for *M. bivittatus* described by Carpenter (1966) were adapted into Arduino code and uploaded to an Arduino® UNO R3 programmable computer board. This board was then connected to a HiTec HS-225BB Mighty Mini servomotor (HITEC RCD USA, Inc.) and powered by 9-V–2ADC Li-ion battery (SHANQIU Mini UPS, Model FX5-12, Shenzhen Feixing Technology Co., Ltd.). All components were then fixed to a rigid 3D printed surface attached to the inside of an opaque plastic box.

Lizard models resembling adult male *M. bivittatus* were constructed using 3D modeling software (Meshmixer v3.5, Autodesk, Inc., San Francisco, CA, USA). Based on prior reports of

mean and maximum body sizes of males from both sites, we scaled the models to body sizes corresponding to: (1) average San Cristóbal Island male (SVL = 70 mm); (2) average Isla Lobos male/large San Cristóbal Island male (SVL = 100 mm); (3) and large Isla Lobos male (SVL = 120 mm). Models were then 3D printed using NinjaFlex® TPU filament and painted to resemble live conspecifics. Finished models were attached to the top of the plastic container and secured in place with screws (Fig. 1). Stereotyped motion corresponding to bobbing displays is achieved by attaching one end of a thin metal push rod to the servomotor and the other to the lizard model, transferring movement accordingly.

Robot presentation trials were conducted from 4–11 March and 27 July–9 August 2022 on a total of 183 free-ranging *M. bivittatus* lizards, 48 males and 41 females from San Cristóbal and 67 males and 27 females from Isla Lobos. Trials consisted of three push-up displays performed by lizard model atop the robot followed by a 30.0s pause, reiterated for a total of 6 minutes. Two lizard models corresponding to the average and above-average size of local males were used in each site. Each subject was shown only one model per trial. Upon spotting a lizard, we carefully approached it and placed the robot directly across the subject at a distance of ~2m. We then set up a cell phone camera (Samsung S21+5G) and began recording the interaction on a high-resolution video format (H.264) upon activating the robot. Trials where subjects were disturbed by another lizard or fled more than 5m away from the robot were not considered valid.

Display data was gathered from individual video recordings, counting the number of distinct signature and two-bob displays performed during robot presentation trials. An array of non-bobbing displays was observed across subjects, indicating varying degrees of engagement with the robot model. We followed the protocol for computing a composite response (CR) score established by Clark et al. (2015, 2023) to account for these behaviors. Non-bobbing displays are

ranked by aggression, as described by Carpenter (1977), and assigned point values accordingly. Each behavior is only counted once per trial and added into a cumulative score. We incorporated the following displays and point values into our analysis: (1) Tongue touch: Tongue briefly pressed against substrate. 1 point. (2) Tail lash: Undulating movement of the tail. 2 points. (3) Rapid reorientation: Sudden shift of body orientation above 30°. 3 points. (4) Gular expansion: Outward expansion of the gular fold. 3 points. (5) Displacement jump: Abrupt upward movement, body and feet briefly off the substrate. 4 points. (6) Lateral presentation: Reorientation maximizing lateral view, sides compressed and arms fully extended. 4 points. (7) Challenge display: Signature display performed with a heavily arched back, compressed sides and expanded gular fold. 5 points.

Simulated predation approaches

Simulated predation events were conducted from 27 July–9 August 2022 on a total of 98 free-ranging *M. bivittatus* lizards, 33 males and 13 females from San Cristóbal Island and 36 males and 16 females from Isla Lobos. In order to simulate a predation event, adult lizards were surveyed from a 5–10m distance across the study area. Once a lizard was located, the researcher approached it at a slow, constant speed of 0.5m/s (Stone et al. 1994; Cooper Jr. 1997). Approaches continued until the lizard abandoned its position and moved away. Once the lizard had ceased its movement, reference points corresponding to (1) Final location of the researcher, (2) Initial location of the lizard, (3) Final location of the lizard and (4) Nearest refuge, defined as a rock crevice or otherwise inaccessible microhabitat, were marked with reflective tape. The flight initiation distance (FID; Horizontal distance between the researcher and the initial location of the lizard), escape distance (ED; Horizontal distance between the initial and final locations of the lizard), and refuge distance (RD; Horizontal distance between the initial location of the lizard

and the location of the nearest refuge) were determined by measuring the distance between these tape marks (Cooper Jr. 2006). All approaches were performed by the same researcher wearing the same clothing, always from the front and maintaining visual contact with the subject (Burger & Gochfeld 1990, 1994).

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