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The relationship between sex and territorial behavior in the San Cristóbal lava lizard (*Microlophus bivittatus*)

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The relationship between sex and territorial behavior in the
San Cristóbal lava lizard (*Microlophus bivittatus*)

AN ALL COLLEGE THESIS

College of St. Benedict/St. John's University

In Partial Fulfillment

of the Requirements for Distinction

in the Department of Biology

By Meghan N. Koenig

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The relationship between sex and territorial behavior in the San Cristóbal lava lizard (*Microlophus bivittatus*)

Meghan Koenig

Abstract

The purpose of this study is to learn more about the territorial behavior of the San Cristóbal lava lizard (*Microlophus bivittatus*). It was hypothesized that, due to competition for mates, competition would be higher among individuals of the same sex than between individuals that were opposite sexes. This hypothesis was not supported by the data collected, as females were observed interacting more with other females than other males but males were observed interacting more with females than other males. This is likely a result of a sex ratio of two females to one male and the territory structure of the species.

Introduction

The purpose of this study is to investigate the relationship between sex and territorial behavior exhibited in the San Cristóbal lava lizard (*Microlophus bivittatus*) of the Galápagos Islands. The species of the Galápagos are under heavy protection due to their vulnerability, as extinctions are much more common in island populations than in mainland populations (Diamond, 1984; Vitousek, 1988; Flesness, 1989; Case et al., 1992; World Conservation Monitoring Centre, 1992; Smith et al., 1993). Since they evolved under conditions without humans or the presence of many predators they are not equipped to handle such disturbances. With little published on such a vulnerable species, it would be beneficial to study how they behave and react to threats.

The San Cristóbal lava lizard (*Microlophus bivittatus*) lives on San Cristóbal Island within the Galápagos Islands archipelago. This species exhibits territorial behavior in the form of head-bobbing, push-ups, chasing and fighting (personal observation). These behaviors

have also been observed in many other lizard species. This study is focused on whether gender, or sex (as it will be referred to throughout this thesis), has an influence on the territorial behavior displayed.

Characteristics:

The genus *Microlophus* consists mainly of other lava lizard and iguana species. The species name, *bivittatus*, derives from Latin—“bi” meaning “two” and “vitta” meaning “stripes” or “bands” (Figure 1). This is based off appearance, as adult males have black and white stripes over brownish-gray scales and adult females have a shade of yellow to light green stripes over brighter green scales (personal observation). Sexual dimorphism in adults, therefore, is apparent and suggests that visual cues may be important in sex recognition (Stebbins et al. 1967).



Figure 1. *Microlophus bivittatus* displays sexual dimorphism (Stebbins et al. 1967). An adult female is displayed on the left and an adult male is posed over her on the right. Image credit (Delso).

Females are known to develop orange patches on their throats when they become sexually mature. They will also develop orange on the sides of their bellies as a warning to males not to copulate with them as they already carrying eggs (Rowe, personal communication). This color reaches its full potential when carrying large, oviducal eggs (Stebbins et al. 1967). Males, on the other hand, will develop a faint shade of orange on their sides as well to attract a mate during breeding season, making the color development an ornament (Berglund et al. 1996). Sexual dichromatism, however, is not present in juveniles and it is difficult to tell whether individuals are male or female without examining them for their vent depth. Besides color differences in adults there is also a size difference between the sexes, males being larger (personal observation). In a previous study, male *Microlophus albemarlensis* were found to outweigh females by two or three times and averaged about 1/5 longer in body length. They also had more heavy-duty scales and longer spines of the vertebral crest (Stebbins et al. 1967). They may be able to live up to 10 years and large males can grow up to a

foot long, however, most of the population is about 6 inches long (igtoa.org).

Background on Biogeography and Evolutionary History of *Microlophus spp.*:

The Galápagos Islands are one of the most recent oceanic island formations (Christie et al, 1992). The archipelago is located about 960 km west from the coast of Ecuador. The “conveyor belt” mechanism for the island formation was proposed by Axelrod (1972) for many Pacific islands. The islands are constantly moving easterly on the Nazca Plate over a stationary volcanic plume (Cox 1983; Werner et al. 1999). This “conveyor belt” is likely to have been operating for 80 to 90 million years based on the ages of submerged seamounts found east of the hotspot (Christie et al. 1992). Due to the islands’ geography, the origins of many species on the islands, including lava lizards (Lopez et al. 1992), may predate the estimated ages of the current islands of the archipelago.



Figure 2. A topographic and bathymetric map of the Galápagos Islands. Islands in the east are oldest and islands in the west are the most recent. Image credit (Gaba, E), retrieved from Wikipedia.

Lava lizards, of the genus *Microlophus*, have 21 recognized species distributed along 5000 km of the western coast of South America and the Galápagos Islands. Twelve of these species are confined to the mainland and 9 are endemic to the Galápagos (Benavides, 2007). Several past studies have found that monophyly is supported in *Microlophus* (Frost, 1992; Harvey and Gutberlet, 2000; Frost et al., 2001). The genus is split into two groups, the *Occipitalis* group—of which the 9 Galápagos species are included—and the *Peruvianus* group. Benavides (2007) suggests that there were at least two independent colonization events. These colonizations resulted in separate radiations throughout the archipelago. The eastern radiation consists of *Microlophus habelii* of Marchena Island and *Microlophus bivittatus* of San Cristóbal Island. Colonization occurred on San Cristóbal Island and radiated to Marchena Island. There is strong support for the sister clade of this radiation to be the mainland's *Microlophus occipitalis* from the coast of Ecuador and Peru (Benavides, 2007). The western clade is mostly associated with what is referred to as the *Microlophus albemarlensis* complex, of which several other Galápagos lava lizard species are likely to be paraphyletic, and *Microlophus delanonis*. The *M. albemarlensis* complex consists of *Microlophus duncanensis*, *Microlophus pacificus*, and *Microlophus grayii*. These species spread across the rest of the archipelago after colonizing on Española. Their exact mainland origin has not yet been clearly defined, as a close relationship for this radiation has not been identified on the mainland yet. (Kizirian, 2004).

A likely reason for the colonization and distribution of species across the Galápagos is the ocean currents (Wright, 1983; Wright, 1984; Wyrski, 1967; Wyrski et al, 1976). There is presently no direct evidence supporting this hypothesis for the *Microlophus* genus; however

it has been documented (Censky et al, 1998) for other lizard groups. It would make sense for the *Microlophus* genus to have been transported by ocean currents given the fact that the Humboldt Current flows northwesterly at a speed of about 7 knots (Wright, 1983) in the fashion that the eastern radiation of lava lizards migrated from San Cristóbal to Marchena. In rainy seasons typical of El Niño it is theorized that freshwater systems of the islands flood and wash out mats of vegetation where they can be carried downstream to the ocean with stowaway lizards upon them (Censky et al. 1998). This would be a method by which the lizards could be carried to colonize individual islands (Wright, unpublished). This would also explain why the *M. albemarlensis* complex shows such weak divergence between islands (Kizirian, 2004).

A “progression rule” hypothesis also explains the path of colonization with the assumption that the oldest island was colonized from the mainland first and as new islands formed in the west by the volcanic hotspot, species continued colonizing along in an east-to-west fashion (Funk and Wagner 1995). Therefore, older species would inhabit older islands and younger species would inhabit younger islands. Most studies of the colonization events of the Galápagos’ species set the time frame from 4 to 5 million years ago, based on the estimated ages of the oldest islands (Cox, 1983). *Microlophus* has been estimated to have colonized between 2.45 (Wright 1983) to 3.4 million years ago (Lopez et al. 1992). Benavides et al (2008) estimated the time of divergence of the eastern radiation from its mainland sister species *M. occipitalis* between about 2.1 to 2.8 million years. The same study estimated *M. delanonis*’ ancestor to have colonized Española sometime between 3.7 and 1.4 million years ago and that the following dispersal of the western radiation occurred less than 1.4 million years ago, supporting the idea that the western radiation is much younger

than the eastern radiation. However, it was also found that some of the older islands were colonized much more recently than this “progression rule” would allow. Santa Fe Island, for example, which is 2.8 million years old was found to have been colonized less than 441 hundred thousand years ago (Benavides et al. 2008).

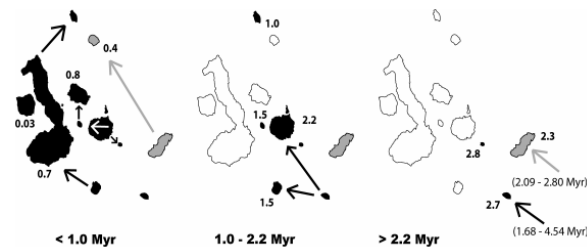


Figure 3. Map showing colonization timing in millions of years for the western and eastern radiations of lava lizards in the Galápagos Islands estimated by Benavides et al’s study in 2008. The panel starts on the left with the most recent colonization events and continues to the right with older events. Image credit (Benavides et al. 2008).

Habitat:

Most of the *Microlophus* species endemic to the Galápagos live in the lowlands of the islands where it is dryer than the misty and foggy highlands. Lava lizards become less abundant with elevation (Stebbins, et al., 1967).

Diet and Predation:

Lava lizards are predators and their diets consist mainly of arthropods, particularly ants, although they have also been documented to eat vegetation such as leaves, flowers and berries (Schluter, 1984). They have also been seen congregating around other animals that attract insects such as sea lions (Orr, 1965) and marine iguanas (Stebbins et al. 1967) to catch flies, a display of mutualism. They are preyed upon by feral cats (Kruuk 1979; Kramer 1984; Konecny 1987), the Galápagos Hawk, egrets, herons, short-eared owls and snakes (Snell et al.

1988). The lizards avoid predation by fleeing to hiding spots under rocks and vegetation (Werner 1978) which is a common tactic among lizards (Greene 1988).

Behavior:

The lizards arise with the sun in the morning and are most active around midmorning, about 9:00 or 10:00 am (Stebbins et al. 1967; Koenig, personal observation). On sunny days they retreat to cracks in the lava rocks or shady areas and bury themselves in sand at midday when the temperature becomes too hot for them. This midday retreat from the sun has been reported in many other species of lizards that live in temperate zones (Mayhew 1964). On overcast or cloudy days, however, they can be seen all throughout the day lounging on rocks and attempting to absorb what little thermal radiation from the sun that they can (Stebbins et al. 1967; Koenig, personal observation). The lizards bed down in soil, sand and leaf litter after the sun sets. They bury themselves in typical iguanid fashion, diving in head first and kicking with the hind legs alternately and moving the head laterally until buried. They shift bed sites often but can sometimes be seen using the same site repeatedly (Stebbins et al. 1967).

Mating Behavior and Sexual Selection:

Mating for lava lizards is rather rough on the females, hence the display of orange on their sides to warn off males that they are already carrying eggs (Rowe, personal communication). This is a tactic used in many other lizard species as well since females will often reject males following copulation (Crews, 1973c). Males will pursue a female that is ready to mate and catch her by biting her on the back of the neck, a leg, or the tail. The male will carry her off, quickly mate and leave (Stebbins et al. 1967). Mating behavior is often observed through posturing of individuals. Females will

go into a rejection pose that resembles that of the typical territorial stance with the body raised up off the ground (Stebbins et al. 1967; Fitch 1940; Stebbins and Robinson 1946; Blair 1960). A sexually receptive female will typically stay in place, arch her neck and allow the courting male to bite her there as observed in *Anolis carolinensis* by Crews' (1973c). Behavior such as this has been observed in *M. bivittatus* females on San Cristóbal Island (Koenig, personal observation). Males also seem to sniff at the vent region of females—where the outlet for the reproductive tracts are located—which could mean that males can recognize non-receptive females by odor and appearance (Stebbins et al. 1967). This is possible, since pheromones have been observed as important for mate recognition in some other lizard species (Mason, 1992).

Charles Darwin (1871) defined sexual selection as "the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction." There are two proposed ways a female lizard may choose a mate, one that is based on provision of resources by males and the other that is based on phenotypical features or behaviors of males. The debate between which way is more important for female lizards in choosing a mate is largely unresolved for most species (Tokarz, 1995). Several studies have shown evidence that female lizards may choose their mates based on their ability to provide resources rather than directly on his phenotype (Davies, 1991; Emlen and Oring, 1977; Halliday, 1983; Howard, 1978; Maynard Smith, 1987; Partridge and Halliday, 1984; Searcy, 1979; Thornhill and Alcock, 1983). Male lizards do not directly give food to females, however, so the ability to provide resources for the female is based on the resources located within that male's territory (Andrews, 1985).

An interesting issue comes up for species in which female lizards choose males phenotypically because of the structure of male territories. Females, which tend to be mostly sedentary, may have few opportunities to interact with males to choose the best candidate to mate with, since male territories tend to enclose female home ranges and the territory owner usually excludes other males (Stamps, 1983). It is argued by Trivers (1985) that these females are still able to advertise their sexual receptivity to males with connecting territories. This is seen in *Anolis garmani*, where females commonly chose very prominent places to display their sexual maturity and where 5% of the observed copulations took place with an invading male instead of with the territory holder (Trivers, 1976, 1985).

There are several characteristics that may be important for a female lizard when choosing a mate, including body size, body shape, display behavior, and coloration (Tokarz, 1995). Body size is positively correlated with age which indicates survivorship, a positive feature for a mate if one is looking to pass on good genes (Halliday, 1992; Halliday and Verrell, 1988). In most polygynous lizard species larger males have larger territories, access to more females and copulate with females more frequently than smaller individuals (Andrews, 1985; Dugan, 1982; Ruby, 1981, 1984; Stamps, 1983; Trillmich, 1983; Trivers, 1976).

Display behavior is also important in lizards since they appear to be the most visual display based reptiles (Carpenter and Ferguson, 1977). Males will display by shifting body stance, changing color, head bobbing, doing push-ups, extending their dewlaps—a large and sometimes colorful flap of skin in the throat region (Bels, 1990; von Geldern, 1919)—or moving their tail (Carpenter, 1967, 1978). Head bobbing is a behavioral display that has been

recognized as distinctive at the individual level (Bels, 1986; Berry, 1974; Crews 1975b; Greenberg and Jenssen, 1982; Jenssen, 1971; Jenssen and Hover, 1976; Martins, 1991; Rothblum and Jenssen, 1978) and at the species level (Carpenter, 1986). Head bobbing is not only used in courtship rituals, but also in aggressive contexts (Martins, 1991).

Of course, male lizards can also display mating preferences. In a study done by Cooper (1985) on the keeled earless lizard, *Holbrookia propinqua*, females from outside a male's home range were transported there and it was found that males courted and attempted to mate with non-resident females significantly more than resident females. This led Cooper (1985) to suggest that males in *H. propinqua* are capable of individual recognition.

There are a couple of advantages to *H. propinqua*, or any lizard species, showing a preference to mate with unfamiliar females. Cooper (1985) proposed that by showing the male's vigor and health, it might encourage a nonresident female to stay within his territory. It could also increase the male's reproductive success by having a nonresident female full of eggs with his genes leave the area to find a new territory (Cooper, 1985).

Reproduction:

Females of *M. bivittatus* will carry one to 4 eggs per clutch, although 4 is rare. They bury their eggs in loose sand (Stebbins et al. 1967; Koenig, personal observation). A sex ratio of 2 females to each male has been observed in *M. albemarlensis* (Stebbins et al. 1967). This favors polygamy in lava lizards and the more successful males have been noted to have harems. One male's home range included 11 adult females, while 2 or 3 females per male is more common (Stebbins et al. 1967). This shows that the dominating males of an area have more access to females.

Territoriality:

It has frequently been observed in studies that sexual selection and the development of sexual dimorphism often favors aggressive tactics in males to maintain high social status and dominate other mates (Caro and Bateson 1986; Moore 1991; Gross 1996). Competition for mates among males is usually reflected in the defense of territories (sensu Wilson 1975; Stamps 1983b, 1994). Therefore, territoriality is a major behavior present in *Microlophus*. In *M. albemarlensis* it has been recorded as being more common among males than females (Stebbins et al. 1967). Another study on collared lizards (*Crotaphytus collaris*) showed much higher rates in patrol of territories and advertisement displays of males than females in intrasexual interactions, as well as a marked difference in approach of encounters and intensity of behaviors between them (Baird et al. 2001). Time of year is also a factor, however, as frequencies of agonistic behaviors, or any activity that relates to fighting (Barrows 2001), in female collared lizards fluctuated during the season, depending on nest construction and development of eggs (Sloan and Baird 1999).

Lava lizards will defend their territories by bobbing their heads, performing push-ups, chasing and engaging in combat with trespassers (Koenig, personal observation). It is important to realize the difference between territory and home range. Territory is any area that is defended by an individual, while home range is not defended and is where the animal spends most of its time (Burt, 1943). A male lava lizard's home range averaged at 423 m² and females averaged at 145 m² in Stebbins' et al. study (1967). They will challenge others in a pose in which the sides are flattened and the neck crest—the spines that run with the vertebral column—will be elevated and the body is held off the ground and broadside

toward the other individual. A fully agitated male ready to fight will turn a pale grey that makes him conspicuous against the dark surrounding lava rock (Stebbins et al. 1967). A similar color change in *M. bivittatus* was observed during this study (see Figure 4). The normally brownish scales turn light grey and the vertebral crests rise high. Some flecks of yellow or rust red, especially on the neck crest and dorsal region, also appear with the shift in color. (Koenig, personal observation). When lava lizards fight they go into the challenging position and slap at each other with their tails. Females have also been witnessed fighting in this way (Stebbins et al. 1967; Koenig, personal observation).



Figure 4. An agitated male lava lizard (*Microlophus bivittatus*) that has changed color. Note the yellow and orange colors on the dorsal crest and belly. Photo credit: Meghan Koenig.

Based on the collective information gathered on territorial behavior differences in males and females in closely related species of lizards, such as *Microlophus albemarlensis* and the collared lizard (*Crotaphytus collaris*), I hypothesize that, due to competition for mates, competition within the same sex will be greater than between males and females. If my hypothesis is true, then same sex (intrasexual) territorial interactions will be observed more

frequently than interactions between males and females (intersexual). I arrive at this hypothesis because (1) collared lizards (*Crotaphytus collaris*) show much higher rates in patrol of territories and advertisement displays of males in intrasexual interactions (Baird et al. 2001), (2) male lava lizard home ranges and other closely related species' territories are much larger than that of females' (Stebbins et al. 1967; Andrews, 1985; Dugan, 1982; Ruby, 1981, 1984; Stamps, 1983; Trillmich, 1983; Trivers, 1976) and (3) the sex ratio of 2 females to each male observed in *M. albemarlensis*, a closely related species, favors a polygynous mating system. This, in turn, causes the construction of a male hierarchy, in which more successful males have harems of females (Stebbins et al. 1967). If the same mating system exists within the San Cristóbal lava lizard, this leads me to believe that there would be more competition between females for access to the male in their home range. It also hints that males would most likely exhibit more territorial behavior towards other males in order to defend their territory and the females within it.

Methods

The study site:



Figure 5. San Cristóbal Island of the Galápagos Archipelago. Puerto Baquerizo Moreno is shown circled in green at the southwestern end of the island. (Photo retrieved from Bing maps).

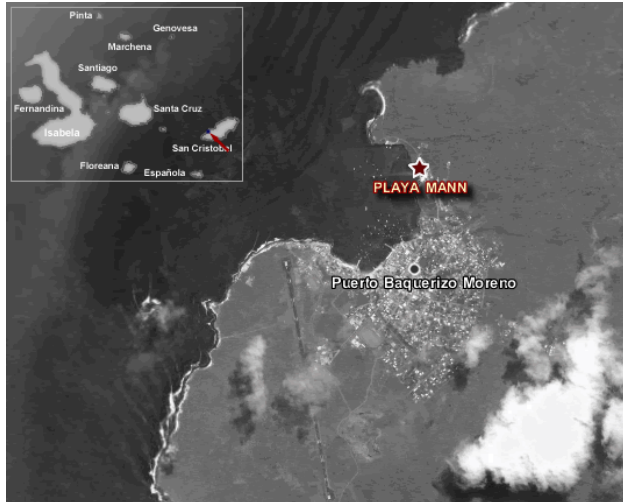


Figure 6. Playa Mann is shown with the red star and lettering. It is located just north of Puerto Baquerizo Moreno on San Cristóbal Island. (Photo retrieved from ecostravel.com).

Observations took place in one location at Playa Mann in Puerto Baquerizo Moreno on the south-western point of the island San Cristóbal within the Galápagos Archipelago (Figures 5, 6). They took place between July 20th 2015 and August 17th 2015. The observation area was 12 meters by 20 meters and consisted of a few piles of lava rocks on which the observer could sit and watch interactions, a sandy stretch that continued from the beach, some short grass, a rock wall and some other lava rocks strewn about the area (shown in figures 7 and 8). This area was where there seemed to be the most lava lizards seen while touring the small portion of the island.

The climate of this particular region of the island is arid. As you go up in elevation, towards the highlands, the moisture increases. This study took place during July and August, which are normally part of the island's dryer, cooler months. However, it was an El Niño year and, therefore, the typical climate was not necessarily represented during this period of time. Some days were overcast, rainy and cool and others were hot and sunny. Plant life in this area consisted mostly of shrub like plants,

grasses and some cacti. The substrate was made up of sand and lava rock. The topography of the observation site was mostly flat with a slight incline from the beach to the road past the stone wall shown in Figure 7.



Figure 7. This shows the observation area from behind the area on which I sat to observe. There was a strip of sand with smaller lava rocks scattered across the area, a patch of dense vegetation to the right and a stone wall on the outer border of the area. (Photo credit: Meghan Koenig).



Figure 8. This is a picture of the observation process. If you look very closely, there is a lava lizard on the rock about a foot away from my foot. Sea lions were also frequent visitors. (Photo credit: Sarah Power).

The study area was frequently visited by sea lions (*Zalophus wollebaeki*), marine iguanas (*Amblyrhynchus cristatus*) and even the

occasional group of tourists or locals walking through. The lizards did not usually seem bothered by marine iguanas or sea lions. However, when people walked through it disrupted their activities and they typically hid away under rocks for a few minutes before resuming their typical behavior. I am uncertain as to whether my presence affected their behavior or not. I restricted my movements to only necessary ones, such as recording observations on a notepad. The fact that I had a couple of female lizards chase each other right across my feet on one occasion leads me to believe they did not notice me if I did not move. It is also possible that they became habituated to my presence.

Data Collection:

I observed the lizards for 2 hours every day, from 9-11 am, when they were observed as most active. They were categorized by sex, male (M) and female (F), however some juveniles were hard to categorize as they had not yet developed adult characteristics. In order to keep data accurate juvenile interactions were discarded. The interactions that were recorded were categorized as male-female (M-F), female-male (F-M), male-male (M-M), and female-female (F-F). The individual placed first in order of interaction name was the individual that initiated the interaction or conflict—this only mattered with opposite sex interactions, however. Since we were concerned with the aggressive territorial behaviors of both sexes it

was important to distinguish which sex was confronting the other in male-female or female-male interactions. The territorial behaviors observed were then categorized as head-bobbing (1), push-ups (2), and chasing (3).

Statistical analyses:

Data was analyzed using chi-squared tests of independence. A total of 21 chi-squared tests were performed in order to see if there was a difference between varying factors in the data. One of these varying factors is whether the sex ratio in *M. bivittatus* follows that of its close relative *M. albemarlensis* (2 females to 1 male). If we assume the sex ratio to be 1 female to 1 male then expected values should be assigned in equal value throughout the interaction groups. However, if the sex ratio is assumed to be 2 females to 1 male it becomes necessary to give expected values proportional to that ratio. The expected values for the 2:1 sex ratio tests were calculated by assigning “points” to each interaction group, with one point for each male and two points for each female involved. Thus, the interaction group M-F and F-M would both be worth three points, M-M would be two points, and F-F would be worth four points. The total number of interactions were then divided up proportionally to each interaction group based on the amount of points they had to assign the expected values.

Results

Push-ups were the most frequent behavior observed, with the F-M group being the exception as when females displayed to males they used head-bobbing more frequently (Figure 9). Head-bobbing appears to be the most evenly spread out among the interaction groups out of the territorial behaviors observed. Chasing and push-ups were observed at much more variable frequencies (Figure 9). In

addition to head-bobbing, push-ups and chasing, fighting was also observed. Males were observed fighting other males on 4 occasions and females were observed fighting other females on 2 occasions. The sample size was too small to perform a chi-squared test on this behavior. A chi-squared test between the total amounts of times each behavior was observed returned a significant p-value (Table 2: $p \ll 0.001^*$). Chi-squared tests were also performed on the total of times each behavior was observed in an interaction group. Assuming that there is one female for every male (sex ratio of 1:1), there was not a significant difference between the interaction groups and the amount of times they used head-bobbing as a territorial display (Table 3: $p = 0.051$). However, there is a significant difference for this behavior if a sex ratio of two females to one male is assumed (Table 3: $p \ll 0.001^*$). When testing for a difference between the total observations of push-ups for each interaction group, both chi-squared tests for the different sex ratios returned significant p-values (Table 4: $p \ll 0.001^*$ and $p \ll 0.001^*$). The chasing behavior was also found to be significantly different across the interaction groups for both the 1:1 and the 2:1 sex ratio (Table 5: $p \ll 0.001^*$; $p \ll 0.001^*$).

Females were observed displaying territorial behaviors to other females more frequently than any other interaction group. On the other hand, females displaying to males was the least common interaction group observed (Figure 10). The chi-squared test between the total amounts of times each interaction group was observed engaging in territorial behaviors assuming a sex ratio of 1:1 was significant (Table 6: $p \ll 0.001^*$). In addition, the chi-squared test for the same values assuming a sex ratio of 2:1 was also significant (Table 6: $p \ll 0.001^*$).

The total number of times a male initiated an interaction was higher than the total number of times a female initiated an interaction and females received more interactions than males did (Table 1). A chi-squared test on the difference between the number of times males versus females initiated an interaction was insignificant (Table 7: $p = 0.2$) assuming that the sex ratio is 1:1. However, in the chi-squared test assuming the ratio is 2 females to 1 male there was a significant difference between the amount of times males and females initiated (Table 7: $p \ll 0.001^*$). Chi-squared tests were also performed on the total amount of times males and females received interactions. For both sex ratios there was a significant difference (Table 8: $p \ll 0.001^*$; $p \ll 0.001^*$).

Same sex interactions appear to be more frequent than opposite sex interactions when females initiated a territorial display, however males appear to initiate more opposite sex interactions than they do same sex interactions (Figure 10). A chi square test assuming a 1:1 sex ratio on same sex versus opposite sex interactions for males found a significant difference (Table 9: $p \ll 0.001^*$). A complementary chi-squared test for females also found a significant difference (Table 10: $p \ll 0.001^*$). The chi-squared tests for same sex versus opposite sex interactions for both males and females assuming a 2:1 sex ratio had to be broken down by each behavior for effective display of data. The males were found to display head-bobbing and chasing in same sex and opposite sex interactions at a significantly different rate (Table 11: $p \ll 0.001^*$; Table 13: $p \ll 0.001^*$). However, there was not a significant difference between the rates at which they displayed push-ups in same sex and opposite sex contexts (Table 12: $p = 0.475$). For females, use of the head-bobbing behavior was found to be significantly different between same sex and opposite sex interactions (Table 14: $p = 0.023^*$). In addition, push-ups and chasing were found to be significantly different in same sex and opposite sex contexts (Table 15: $p \ll 0.001^*$; Table 16: $p \ll 0.001^*$).

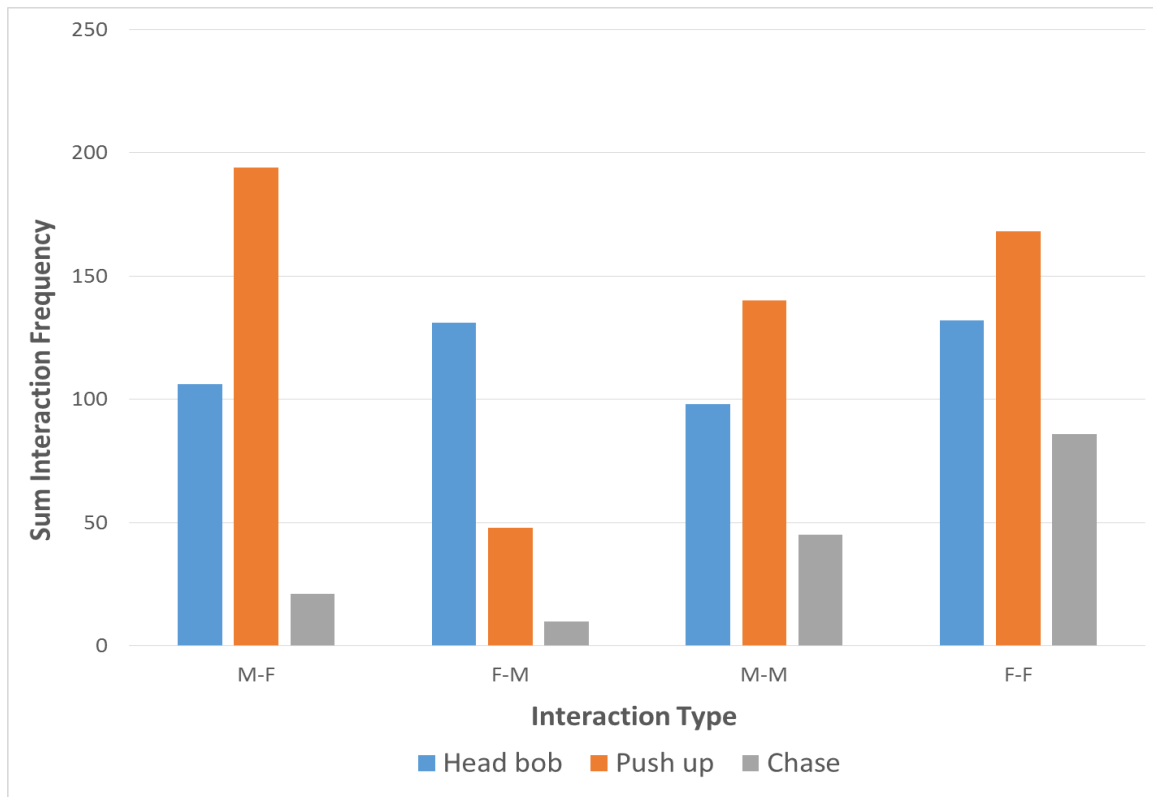


Figure 9. The total number of territorial behaviors observed and the interaction group involved (M-F, F-M, M-M, F-F). Observations occurred from July 20th to August 17th of 2015 from 9 am to 11 am at Playa Mann on San Cristóbal Island in the Galapagos Islands, Ecuador.

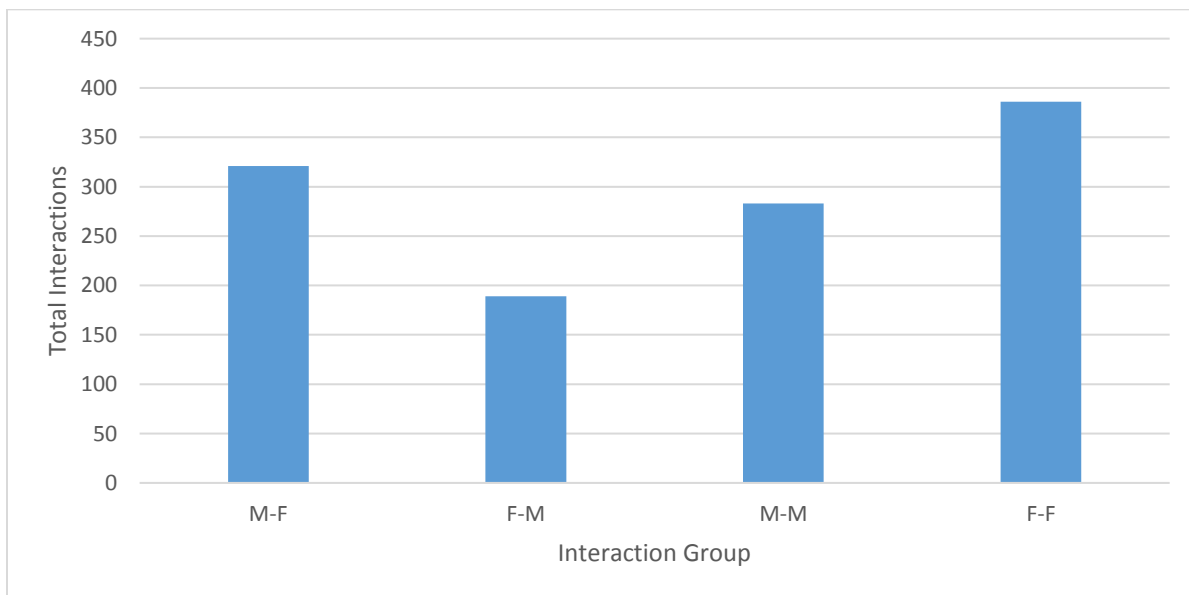


Figure 10. The total number of all territorial behavior interactions observed and the interaction group involved (M-F, F-M, M-M, and F-F). Observations occurred from July 20th to August 17th of 2015 from 9 am to 11 am at Playa Mann on San Cristóbal Island in the Galapagos Islands, Ecuador.

Table 1. Sum totals of territorial lava lizard (*Microlophus bivittatus*) interactions based on sex observed at study site, Puerto Baquerezo Moreno, San Cristóbal, Galápagos Islands, Ecuador (2015).

| | Initiating | Receiving |
|----------------------------|------------|-----------|
| Sum of male interactions | 624 | 486 |
| Sum of female interactions | 580 | 718 |

Statistical analysis:

Table 2. Are behaviors being displayed at different rates? The sum of each territorial behavior observed in the San Cristóbal lava lizard (*Microlophus bivittatus*), the expected values for the chi-squared test and the resulting p-value. Data was collected from July 20th to August 17th 2015 at Playa Mann in Puerto Baquerezo Moreno, San Cristóbal, Galápagos Islands, Ecuador.

| | Observed | Expected | p-value |
|--------------|----------|----------|----------|
| Head-bobbing | 467 | 393 | <<0.001* |
| Push-ups | 550 | 393 | |
| Chasing | 162 | 393 | |

Table 3. Is head-bobbing occurring at different rates throughout the interaction groups? The sum of each interaction group performing head-bobbing as a territorial behavior observed in the San Cristóbal lava lizard (*Microlophus bivittatus*), the expected values for the chi-squared tests and the resulting p-values. Expected values were calculated using a one to one ratio (1:1) of females to males and a two to one ratio (2:1) of females to males. Data was collected from July 20th to August 17th 2015 at Playa Mann in Puerto Baquerezo Moreno, San Cristóbal, Galápagos Islands, Ecuador.

| | Observed | Expected (1:1) | Expected (2:1) | p-value (1:1) | p-value (2:1) |
|-----|----------|----------------|----------------|---------------|---------------|
| M-F | 106 | 119 | 119 | 0.051 | <<0.001* |
| F-M | 131 | 119 | 119 | | |
| M-M | 98 | 119 | 79.33 | | |
| F-F | 132 | 119 | 158.67 | | |

Table 4. Are push-ups occurring at different rates throughout the interaction groups? The sum of each interaction group performing push-ups as a territorial behavior observed in the San Cristóbal lava lizard (*Microlophus bivittatus*), the expected values for the chi-squared tests and the resulting p-values. Expected values were calculated using a one to one ratio (1:1) of females to males and a two to one ratio (2:1) of females to males. Data was collected from July 20th to August 17th 2015 at Playa Mann in Puerto Baquerizo Moreno, San Cristóbal, Galápagos Islands, Ecuador.

| | Observed | Expected (1:1) | Expected (2:1) | p-value (1:1) | p-value (2:1) |
|-----|----------|----------------|----------------|---------------|---------------|
| M-F | 194 | 137.5 | 137.5 | <<0.001* | <<0.001* |
| F-M | 48 | 137.5 | 137.5 | | |
| M-M | 140 | 137.5 | 91.67 | | |
| F-F | 168 | 137.5 | 183.33 | | |

Table 5. Is chasing occurring at different rates throughout the interaction groups? The sum of each interaction group performing chasing as a territorial behavior observed in the San Cristóbal lava lizard (*Microlophus bivittatus*), the expected values for the chi-squared tests and the resulting p-values. Expected values were calculated using a one to one ratio (1:1) of females to males and a two to one ratio (2:1) of females to males. Data was collected from July 20th to August 17th 2015 at Playa Mann in Puerto Baquerizo Moreno, San Cristóbal, Galápagos Islands, Ecuador.

| | Observed | Expected (1:1) | Expected (2:1) | p-value (1:1) | p-value (2:1) |
|-----|----------|----------------|----------------|---------------|---------------|
| M-F | 21 | 40.5 | 40.5 | <<0.001* | <<0.001* |
| F-M | 10 | 40.5 | 40.5 | | |
| M-M | 45 | 40.5 | 27 | | |
| F-F | 86 | 40.5 | 54 | | |

Table 6. Is each interaction group interacting at different rates? The sum of all behaviors observed in each interaction group in the San Cristóbal lava lizard (*Microlophus bivittatus*), the expected values for the chi-squared tests and the resulting p-values. Expected values were calculated using a one to one ratio (1:1) of females to males and a two to one ratio (2:1) of females to males. Data was collected from July 20th to August 17th 2015 at Playa Mann in Puerto Baquerizo Moreno, San Cristóbal, Galápagos Islands, Ecuador.

| | Observed | Expected (1:1) | Expected (2:1) | p-value (1:1) | p-value (2:1) |
|-----|----------|----------------|----------------|---------------|---------------|
| M-F | 321 | 294.75 | 294.75 | <<0.001* | <<0.001* |
| F-M | 189 | 294.75 | 294.75 | | |
| M-M | 283 | 294.75 | 196.5 | | |
| F-F | 386 | 294.75 | 393 | | |

Table 7. Are males and females initiating interactions at different rates? The sum of each behavior initiated by males and females in the San Cristóbal lava lizard (*Microlophus bivittatus*), the expected values for the chi-squared tests and the resulting p-values. Expected values were calculated using a one to one ratio (1:1) of females to males and a two to one ratio (2:1) of females to males. Data was collected from July 20th to August 17th 2015 at Playa Mann in Puerto Baquerezo Moreno, San Cristóbal, Galápagos Islands, Ecuador.

| | Observed | Expected (1:1) | Expected (2:1) | p-value (1:1) | p-value (2:1) |
|-------------------|----------|----------------|----------------|---------------|---------------|
| Males initiated | 624 | 602 | 401.33 | 0.2 | <<0.001* |
| Females initiated | 580 | 602 | 802.67 | | |

Table 8. Are males and females receiving interactions at different rates? The sum of each behavior received by males and females in the San Cristóbal lava lizard (*Microlophus bivittatus*), the expected values for the chi-squared tests and the resulting p-values. Expected values were calculated using a one to one ratio (1:1) of females to males and a two to one ratio (2:1) of females to males. Data was collected from July 20th to August 17th 2015 at Playa Mann in Puerto Baquerezo Moreno, San Cristóbal, Galápagos Islands, Ecuador.

| | Observed | Expected (1:1) | Expected (2:1) | p-value (1:1) | p-value (2:1) |
|------------------|----------|----------------|----------------|---------------|---------------|
| Males received | 486 | 602 | 401.33 | <<0.001* | <<0.001* |
| Females received | 718 | 602 | 802.67 | | |

Table 9. Are males displaying to males at different rates than they display to females? (Assuming 1:1 ratio) The sum of each territorial behavior performed by males observed in the San Cristóbal lava lizard (*Microlophus bivittatus*), the expected values for the chi-squared tests and the resulting p-values. Data was collected from July 20th to August 17th 2015 at Playa Mann in Puerto Baquerezo Moreno, San Cristóbal, Galápagos Islands, Ecuador.

| | Head-bobbing | Push-ups | Chasing | p-value |
|-----|--------------|----------|---------|----------|
| M-F | 106 | 194 | 21 | <<0.001* |
| M-M | 98 | 140 | 45 | |

Table 10. Are females displaying to females at different rates than they display to males? (Assuming 1:1 ratio) The sum of each territorial behavior performed by females observed in the San Cristóbal lava lizard (*Microlophus bivittatus*), the expected values for the chi-squared tests and the resulting p-values. Expected values were calculated using a one to one ratio (1:1) of females to males and a two to one ratio (2:1) of females to males. Data was collected from July 20th to August 17th 2015 at Playa Mann in Puerto Baquerezo Moreno, San Cristóbal, Galápagos Islands, Ecuador.

| | Head-bobbing | Push-ups | Chasing | p-value |
|-----|--------------|----------|---------|----------|
| F-M | 131 | 48 | 10 | <<0.001* |
| F-F | 132 | 168 | 86 | |

Table 11. Are males using the head-bobbing behavior at different rates with females than they are with other males? (Assuming 2:1 ratio) The sum of head-bobbing displays by males observed in the San Cristóbal lava lizard (*Microlophus bivittatus*), the expected values for the chi-squared tests and the resulting p-values. Expected values were calculated using a two to one ratio (2:1) of females to males. Data was collected from July 20th to August 17th 2015 at Playa Mann in Puerto Baquerizo Moreno, San Cristóbal, Galápagos Islands, Ecuador.

| | Head-bobbing | Expected | p-value |
|-----|--------------|----------|----------|
| M-F | 106 | 147.6 | <<0.001* |
| M-M | 98 | 98.4 | |

Table 12. Are males using the push-up behavior at different rates with females than they are with other males? (Assuming 2:1 ratio) The sum of push-up displays by males observed in the San Cristóbal lava lizard (*Microlophus bivittatus*), the expected values for the chi-squared tests and the resulting p-values. Expected values were calculated using a two to one ratio (2:1) of females to males. Data was collected from July 20th to August 17th 2015 at Playa Mann in Puerto Baquerizo Moreno, San Cristóbal, Galápagos Islands, Ecuador.

| | Push-ups | Expected | p-value |
|-----|----------|----------|---------|
| M-F | 194 | 200.4 | 0.475 |
| M-M | 140 | 133.6 | |

Table 13. Are males chasing females at different rates compared to chasing other males? (Assuming 2:1 ratio) The sum of chasing occurrences by males observed in the San Cristóbal lava lizard (*Microlophus bivittatus*), the expected values for the chi-squared tests and the resulting p-values. Expected values were calculated using a two to one ratio (2:1) of females to males. Data was collected from July 20th to August 17th 2015 at Playa Mann in Puerto Baquerizo Moreno, San Cristóbal, Galápagos Islands, Ecuador.

| | Chasing | Expected | p-value |
|-----|---------|----------|----------|
| M-F | 21 | 39.6 | <<0.001* |
| M-M | 45 | 26.4 | |

Table 14. Are females using the head-bobbing behavior at different rates with males than they are with other females? (Assuming 2:1 ratio) The sum of head-bobbing displays by females observed in the San Cristóbal lava lizard (*Microlophus bivittatus*), the expected values for the chi-squared tests and the resulting p-values. Expected values were calculated using a two to one ratio (2:1) of females to males. Data was collected from July 20th to August 17th 2015 at Playa Mann in Puerto Baquerizo Moreno, San Cristóbal, Galápagos Islands, Ecuador.

| | Head-bobbing | Expected | p-value |
|-----|--------------|----------|---------|
| F-M | 131 | 112.7 | 0.023* |
| F-F | 132 | 150.28 | |

Table 15. Are females using the push-up behavior at different rates with males than they are with other females? (Assuming 2:1 ratio) The sum of push-up displays by females observed in the San Cristóbal lava lizard (*Microlophus bivittatus*), the expected values for the chi-squared tests and the resulting p-values. Expected values were calculated using a two to one ratio (2:1) of females to males. Data was collected from July 20th to August 17th 2015 at Playa Mann in Puerto Baquerezo Moreno, San Cristóbal, Galápagos Islands, Ecuador.

| | Push-ups | Expected | p-value |
|-----|----------|----------|----------|
| F-M | 48 | 92.7 | <<0.001* |
| F-F | 168 | 123.6 | |

Table 16. Are females chasing males at different rates compared to chasing other females? (Assuming 2:1 ratio) The sum of chasing occurrences by females observed in the San Cristóbal lava lizard (*Microlophus bivittatus*), the expected values for the chi-squared tests and the resulting p-values. Expected values were calculated using a two to one ratio (2:1) of females to males. Data was collected from July 20th to August 17th 2015 at Playa Mann in Puerto Baquerezo Moreno, San Cristóbal, Galápagos Islands, Ecuador.

| | Chasing | Expected | p-value |
|-----|---------|----------|----------|
| F-M | 10 | 41.1 | <<0.001* |
| F-F | 86 | 54.8 | |

Discussion

The first set of chi-squared tests analyzes all territorial behaviors displayed to determine if there is a difference between the observed values. When testing all the behaviors together, each behavior was observed at significantly different rates (Table 2: $p \ll 0.001^*$). This indicates that the lava lizards are displaying each territorial behavior at a different rate. This is visually evident when you compare the behaviors in Figure 9. It is possible that some behaviors are used more often than others based on their energetic costs. For instance, chasing takes more energy than head-bobbing, so this could be a possible explanation for the differences in frequencies seen across the behaviors. An interesting anomaly in the frequencies of behaviors performed is in the push-ups in the female to male interaction group. Push-ups are the most frequent behavior displayed in all the interaction groups except for in the female to male group, in which head-bobs were the most frequent. It is possible, however only a speculation, that females use head-bobs in response to a male's presence because of the interest to mate, since head-bobbing can be used in courtship (Martins 1991). Perhaps they do not use push-ups because it is connected to status somehow as well and the "alpha" male is above them in status, or perhaps they do not see males as a territorial threat.

Each behavior was then analyzed independently to determine if there was a difference between the rates each behavior was being displayed within each interaction group. There was no difference between the use of head-bobbing across the interaction groups when assuming a sex ratio of one female to each male (Table 3: $p = 0.051$). A possible reason for this is the ambiguity of the head-bobbing behavior in the first place, since it has been found to be used in both territorial and courtship contexts (Martins 1991). However, when we assume that a sex ratio of two females to each male is applicable, there is a significant difference (Table 3: $p \ll 0.001^*$). Statistically significant values for the push-up behavior for either sex ratio situation (Table 4: $p \ll 0.001^*$; $p \ll 0.001^*$) suggests that push-ups are

being displayed differently across the interaction groups as well. Finally, chasing was also displayed at significantly different rates (Table 5: $p < 0.001^*$; $p < 0.001^*$). Reflecting on this information, Figure 9 does show the varying totals for each behavior within each interaction group and they do differ quite a bit.

Each interaction group was observed displaying territorial behaviors at significantly different rates for both sex ratio options (Table 6: $p < 0.001^*$; $p < 0.001^*$). This informs us that the difference seen in the total number of interactions for each group (Figure 10) is significant and not due to random chance. Females interacted with other females more often than any other interaction group. A likely reason for the high rates of female to female interactions is a structure in the lava lizards' territories in which an alpha male's territory encompasses multiple smaller female territories. In this case, the females would compete with other females more simply because there are more females to compete with around them and not just because they are competing for the male as a mate.

The second set of chi-squared tests focuses on the initiation and reception of territorial displays by males and females. There was not a significant difference between the amount of times males initiated and females initiated a territorial interaction under the assumption of a 1:1 sex ratio (Table 7: $p = 0.2$). Under the assumption of a 2:1 sex ratio, however, there was a significant difference (Table 7: $p < 0.001^*$). Following that, there was a significant difference between the amount of times males received territorial displays and the amount of times females received them under either sex ratio (Table 8: $p < 0.001^*$; $p < 0.001^*$). A possible explanation for the difference between the results in the 1:1 sex ratio scenario is that even though females did not initiate as many territorial interactions with males as males did with them, they more than made up for it by interacting very frequently with other females. The conflicting results between the 1:1 and 2:1 ratios for the initiation test are most likely due to the higher concentration of females in the study area, and further supports that there was a large "alpha" male territory encompassing multiple females' territories. There were many females within the study area in which the "alpha" male was very active, while other males tended to stay on the edge of the observation area.

The final set of chi-squared tests is most relevant to my hypothesis because it determines whether there is a real, significant difference between the way intrasexual and intersexual interactions are occurring in *M. bivittatus*. When assuming a sex ratio of one female to one male, males were found to display each type of behavior at a significantly different rate to other males as compared to females (Table 9: $p < 0.001^*$) and females were also found to display each behavior at a significantly different rate to other females as compared to males (Table 10: $p < 0.001^*$). The observed values in Table 10 indicate that the group with the most frequent territorial interactions was the female to female group. This indicates that intrasexual competition is higher among females. However, the data within Table 9 indicates that males actually interacted less with other males than they did with the females for head-bobbing and push-up displays. This would suggest that intersexual competition is actually greater for males, leading me to reject my hypothesis. Chasing is the exception to this statement, as males chased other males more frequently than they chased females. I suggest that this difference is another effect of the territory structures that I have mentioned before. The other males tended to stay on the outer rim of the observation area, which seemed to be the edge of the alpha male's territory, and did not venture into that territory often. When they did the alpha male would chase them away. So it seems as if the males are more aggressive with each other, if one considers chasing to be more aggressive than head-bobbing and push-ups, than they are with the females within their territory. Perhaps, if future studies

were to consider how aggressive each territorial behavior is by factoring in energetic costs there would be higher levels of aggression found in intrasexual interactions than intersexual interactions for males. One could, then, conclude whether competition is greater in intrasexual or intersexual contexts for males. Again, many assumptions are being made in this explanation.

If we assume a sex ratio of two females to one male when we perform the same tests on the same data, we get similar results. Females were found to use each behavior significantly more on other females than they did with males (Table 14: $p = 0.023^*$; Table 15: $p \ll 0.001^*$; Table 16: $p \ll 0.001^*$). This once again suggests that intrasexual competition is greater amongst female individuals of *M. bivittatus*, but the male interactions complicate the results yet again. Males interacted significantly more with females than they did with other males when using head-bobs as a territorial display (Table 11: $p \ll 0.001^*$), but push-ups were not significant between the same sex and opposite sex interactions (Table 12: $p = 0.475$). Perhaps this indicates that males are not responding to females as competitors, but rather as potential mates. Head-bobbing can be used in defense of territories and in courtship behavior (Martins 1991), so males could be using that behavior more with females just because they are attempting courtship. Meanwhile, they are using push-ups and chasing only for territory defense, which appear to be much less frequent behaviors used in intersexual interactions compared to intrasexual interactions when compared in Figure 9.

There are confounding factors within this study that should be given consideration before any conclusions are made. The sample size is unfortunately small, considering only 19 days of data were collected. In addition, only one small area was observed. It would increase validity in future studies to increase the sample size and the number of sample sites. Furthermore, it is quite possible individuals behave very differently depending upon dominance and status. There seemed to be an “alpha” male that initiated often with both the females and the males in the area. In that case, the presence of outliers would skew this data. There was, unfortunately, no way to mark individuals so that each one could be identified during data collection and analyzed separately because of strict laws regarding wildlife in the Galapagos Islands and need of a research permit.

Another factor that could be skewing the data for this study is the possibility of females having smaller territories within alpha male’s territory. This would mean they would be interacting much more frequently with each other rather than males that have been excluded from the male’s territory. At the same time, the main male of the study would be interacting mostly with the females within his territory, which makes it almost impossible to distinguish whether his behavior is mating behavior or territorial behavior.

On that note, it is certainly possible that courtship behavior was being mistaken for territorial behavior in the case of opposite sex interactions. It is difficult to differentiate between mating displays and territorial disputes between males and females. For instance, head-bobbing is used in other species in both territorial and courtship contexts (Martins 1991). As mentioned earlier, this could be the reason that head-bobbing displays were not significantly different across the interaction groups in this study. In addition, I observed males try to grab females with their jaws and even appear to sniff at the vent region on several occasions, which is typical mating behavior (Stebbins et al. 1967; personal observation). I also occasionally observed a female digging in the sand around mid-morning, which doesn’t seem necessary for predation, since they hunt above the sand, or thermal homeostasis, since it was not late enough in the morning to be too hot for them. It is most probable that she was digging for a place to lay eggs. This

is supported by the fact that several females were flashing very bold orange colors on their bellies, which serves the purpose of warning males that they are gravid and not sexually receptive (Rowe, personal communication). Even though this study did not take place during their strict mating season, February to April (Rowe, personal communication), it is still possible that some mating behavior was being observed. For example, *Cryptoblepharus*, a tropical skink in Australia, has been found to breed year-round (James and Shine 1985). It is possible that *M. bivittatus* may continue to mate later in the year, especially in El Niño years due to the warmer temperatures, as in this study.

In conclusion, the results of this study are simply too confounding and contradictory between results for the males and females to safely say that intrasexual competition is greater than intersexual competition. There is much to be learned about the territory structure and defense, as well as mating behavior, in the San Cristóbal lava lizard.

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References

- Andrews, R. M. 1985. Mate choice by females of the lizard, *Anolis carolinensis*. J. Herpetol. 19: 284-289.
- Axelrod, D. I. 1972. Ocean floor spreading in relation to ecosystematic problems. Pp. 15-76 in R. R. Allen and F. C. James, eds. Symposium on ecosystematics. Univ. Arkansas Press, Fayetteville, AR.
- Baird, T. A., C. L. Sloan, and D. K. Timanus. 2001. Intra- and inter-seasonal variation in the socio-spatial behavior of adult male collared lizards, *Crotaphytus collaris* (Reptilia, Crotaphytidae). Ethology 106: 1-19.
- Barrows, Edward. 2001. Animal Behavior Desk Reference. Florida: CRC Press LLC. Pg. 10.
- Bels, V. L. 1986. Analysis of the display-action-pattern of *Anolis chlorocyanus* (Sauria: Iguanidae). Copeia. 1986:963-970.
- 1990. The mechanism of dewlap extension in *Anolis carolinensis* (Reptilia: Iguanidae) with histological analysis of the hyoid apparatus. J Morphol 206:225-244.
- Benavides, Edgar; Baum, Rebecca; McClellan, David; and Jack W. Sites, Jr. 2007. Molecular Phylogenetics of the Lizard Genus *Microlophus* (Squamata: Tropiduridae): Aligning and Retrieving Indel Signal from Nuclear Introns. Syst. Biol. 56 (5): 776-797.

- Benavides, Edgar; Baum, Rebecca; Snell, Heidi M.; Snell, Howard L.; and Jack W. Sites, Jr. 2008. Island Biogeography of Galápagos Lava Lizards (Tropiduridae: *Microlophus*): Species Diversity and Colonization of the Archipelago. *Evolution* 63-6: 1606-1626.
- Berglund, A. A. Bisazza, and A. Pilastro. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biol. J. Linn. Soc.* 58:385-399.
- Berry, K. H. 1974. The ecology and social behavior of the chuckwalla (*Sauromalus obesus obesus*). *Univ. Calif. Publ. Zool.* 101:1-60.
- Blair, W. F. 1960. The rusty lizard: a population study. University of Texas, Press.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* Vol 24: 346-352.
- Caro, T. M., and P. Bateson. 1986. Organization and ontogeny of alternative tactics. *Anim. Behav.* 34:1483-1499.
- Carpenter, C. C. 1967. Aggression and social structure in iguanid lizards. Pp 87-105. In W. W. Milstead (Ed), *Lizard Ecology: A Symposium*. University of Missouri Press, Columbia.
- 1978. Ritualistic social behaviors in lizards. Pp. 253-267. In N. Greenberg and P.D. Maclean (Eds), *Behavior and Neurology of Lizards*. NIMH US Department of Health, Education and Welfare (DHEW), Rockville, Maryland Publ. No. (ADM) 77-491.
- 1986. An inventory of the display-action-patterns in lizards. *Smithson. Herpetol. Info. Serv.* 68:1-18.
- Carpenter, C. C. and J. W. Ferguson. 1977. Variation and evolution of stereotyped behavior in reptiles. Pp. 335-554. In C. Gans and D. W. Tinkle (Eds), *Biology of the Reptilia*, Volume 7. Academic Press, London.
- Censky, Ellen J., Karim Hodge and Judy Dudley. 1998. Over-water dispersal of lizards due to hurricanes. *Nature*. Vol 395, 556.
- Christie, D. M., R. A. Duncan, A. R. McBirney, M. A. Richards, W. M. White, K. S. Harp, and C. G. Fox. 1992. Drowned Islands Downstream from the Galápagos Hotspot Imply Extended Speciation Times. *Nature* 355: 246-248.
- Cooper, W. E., Jr. 1985. Female residency and courtship intensity in a territorial lizard (*Holbrookia propinqua*). *Amphibia Reptilia* 6: 63-69.
- Cox, A. 1983. Ages of the Galápagos Islands. Pp. 11-24 in R. I. Bowman, M. Berson, and A. E. Leviton, eds. *Patterns of evolution in Galápagos organisms*. Pacific Division of the American Association for the Advancement of Science, San Francisco, CA.
- Crews, David. 1973. Coition-induced inhibition of sexual receptivity in female lizards (*Anolis carolinensis*). *Physiology and Behavior*. Vol. 11, 4, p. 463-468.
- 1975. Psychobiology of Reptilian Reproduction. *Science*. Vol. 189, p. 1059-1065.

- Darwin, C. 1871. The descent of man. The Great Books of the Western World. 1871;49:320.
- Davies, N. B. 1991. Mating systems. Pp. 263-294. In J. R. Krebs and N. B. Davies (Eds.), Behavioral Ecology: An Evolutionary Approach, 3rd Edition. Blackwell Scientific Publications, Oxford, UK.
- Delso, Diego. *San Cristóbal Lava Lizard (Microlophus bivittatus), Punta Pitt, San Cristóbal Island, Galápagos Islands, Ecuador*. 2015. Web. 8 Oct. 2015.
- Dugan, B. 1982. The mating behavior of the green iguana, *Iguana iguana*. Pp. 320-341. In G. M. Burghardt and A. S. Rand (Eds). Iguanas of the World: Their Behavior, Ecology and Conservation. Noyes Publication, Park Ridge, New Jersey.
- Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science. Vol. 197, 4300, p. 215-223.
- Fitch, H. S. 1940. A field study of the growth and behavior of the fence lizard. Univ. Calif. Publ. Zool. 48: 149-168.
- Frost, D. 1992. Phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). Am. Mus. Novitates 3033: 1-68.
- Frost, D. R., M. T. Rodrigues, T. Grant, and T. A. Titus. 2001. Phylogenetics of the lizard genus *Tropidurus* (Squamata: Tropiduridae: Tropidurinae): Direct optimization, descriptive efficiency, and sensitivity analysis of congruence between molecular data and morphology. Mol. Phylogenet. Evol. 21: 352-371.
- Funk, V. A. and W. L. Wagner. 1995. Biogeographic patterns in the Hawaiian Islands, Pp 379-419 in W. L. Wagner and V.A. Funk, eds. Hawaiian biogeography: evolution on a hot spot Archipelago. Smithsonian Institution Press, Washington, DC.
- Greenberg, N. and T. A. Jenssen. 1982. Displays of captive banded iguanas (*Brachylophus fasciatus*). Pp. 232-251. In G. M. Burghardt and A. S. Rand (Eds). Iguanas of the World: Their Behavior, Ecology and Conservation. Noyes Publication, Park Ridge, New Jersey.
- Greene, H. W. 1988. Antipredator mechanism in reptiles. In Biology of the Reptilia, Vol. 16 (C. Gans and R. B Huey, eds), pp. 1-152. Alan R. Liss, NY, USA.
- Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within the sexes. *Trends Ecol. Evol.* 11: 92-98.
- Halliday, T. R. 1983. The study of mate choice. Mate choice. Vol. 1, p. 462.
- 1992. Sexual selection in amphibians and reptiles: Theoretical issues and new directions. Pg. 81-95 in K. Adler (Ed.) Contributions to Herpetology, No. 9. Society for the Study of Amphibians and Reptiles, Oxford, Ohio.
- Halliday, T. R. and P. A. Verrell. 1988. Body size and age in amphibians and reptiles. J. Herpetol. 22:253-265.
- Harvey, M. B., and R. L. Gutberlet, Jr. 2000. A phylogenetic analysis of tropidurine lizards (Squamata: Tropiduridae), including new characters of squamation and epidermal microstructure. Zool. J. Linn. Soc. 128: 189-233.

Howard, R. D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. *Evolution*. Vol. 32, No. 4, pg. 850-871.

International Galápagos Tour Operators Association (IGTOA). Wildlife of the Galápagos. 2016.
http://www.igtoa.org/travel_guide/wildlife#lava_lizard

James, Craig and Richard Shine. 1985. The seasonal timing of reproduction: a tropical-temperate comparison in Australian lizards. *Oecologia*. Vol. 67, No. 4, pg. 464-474.

Jenssen, T. A. 1971. Display analysis of *Anolis nebulosis* (Sauria: Iguanidae). *Copeia* 1971:197-209.

Jenssen, T. A. and E. L. Hover. 1976. Display analysis of the signature display of *Anolis limifrons* (Sauria: Iguanidae). *Behavior* 57: 227-240.

Kizirian, D., A. Trager, M. A. Donnelly, and J.W. Wright. 2004. Evolution of the Galápagos Island lizards (Iguania: Tropiduridea: *Microlophus*). *Mol. Phylogenet. Evol.* 32: 761-769.

Konecny, M. J. 1987. Food habits and energetics of feral house cats in the Galápagos Islands. *Oikos* 50: 24-32.

Kramer, P. 1984. Man and other introduced organisms. Pages 253-258 in R. J. Berry, editor. *Evolution in the Galápagos Islands*. Academic Press, London, England.

Kruuk, H. 1979. Ecology and control of feral dogs in Galápagos. Technical Report to Charles Darwin Research Station, Galápagos, Ecuador.

Lopez, T. J., E. D. Hauselman, L. R. Maxson, and J. W. Wright. 1992. Preliminary analysis of phylogenetic relationships among Galápagos Island lizards of the genus *Tropidurus*. *Amphibia-Reptilia* 13: 327-339.

Martins, E. P. 1991. Individual and sex differences in the use of the push-up display by the sagebrush lizard (*Sclerophorus graciosus*). *Anim Behav.* 41: 403-416.

Mayhew, Wilbur W. 1964. Taxonomic status of California populations of the lizard genus *Uma*. *Herpetologica*. Vol. 20, No. 3, p. 170-183.

Maynard Smith, J. 1987. Sexual selection: a classification of models. *Sexual selection: Testing the alternatives*. Pg. 9-20.

Moore, M. C. 1991. Application of the organization-activation theory to alternative male reproductive strategies: a review. *Horm. Behav.* 25:154-179.

Orr, R. 1965. Barrington Island. *Pacific Discovery* 18: 23-27.

Partridge, L., Halliday, T. 1984. Mating patterns and mate choice.

Rothblum, L. and T. A. Jenssen. 1978. Display repertoire analysis of *Sclerophorus undulates hyacinthinus* (Sauria: Iguanidae) from southwestern Virginia. *Anim Behav* 26:130-137.

Rowe, John. Alma College in Michigan. Personal communication in 2015.

- Ruby, D. 1981. Phenotypic correlates of the male reproductive success in the lizard *Scleroporos jarrovi*. Pg. 96-107. In R. D. Alexander and D. W. Tinkle (Eds). *Natural Selection and Social Behavior: Recent Research and New Theory*, Chiron Press, New York.
- . 1984. Male breeding success and differential access to females in *Anolis carolinensis*. *Herpetologica*. 40:272-280.
- Schluter, D. 1984. Body size, prey size and herbivory in the Galápagos lava lizard, *Tropidurus*. *Oikos* 43: 291-300.
- Searcy, W. A. 1979. Female choice of mates: a general model for birds and its application to Redwinged Blackbirds (*Agelaius phoeniceus*). *Am. Nat.* 114:77-100.
- Sloan, C. A. and T. A. Baird. 1999. Is heightened post-ovipositional aggression in female collared lizards (*Crotaphytus collaris*) nest defense? *Herpetologica* Vol. 55: 516-522.
- Snell, Howard L.; Jennings, Randy D.; Snell, Heidi M.; and Sylvia Harcourt. 1988. Intrapopulation variation in predator-avoidance performance of Galápagos lava lizards: the interaction of sexual and natural selection. *Evolutionary Ecology*, 1988, 2: 353-369.
- Stamps, J. A. 1983b. Territoriality and the defense of predator-refuges in juvenile lizards. *Anim Behav* 31: 857-870.
- 1994. Territorial behavior: testing the assumptions. In *Advances in the study of behavior*. Vol. 23, edited by P. J. B. Slater, J. S. Rosenblatt, C. T. Snowden, and M. Milinski, 173-232. Academic, San Diego.
- Stebbins, R. C. and H. B. Robinson. 1946. Further analysis of a population of the lizard *Sceloporus graciosus gracillis*. *Univ. Calif. Publ. Zool.* 48: 149-168.
- Stebbins, Robert C.; Lowenstein, Jerold M.; and Nathan W. Cohen. 1967. A Field Study of the Lava Lizard (*Tropidurus albemarlensis*) in the Galápagos Islands. *Ecology*. Vol. 48, No. 5, pp. 839-851.
- Thornhill, R. and J. Alcock. 1983. *The evolution of insect mating systems*. Harvard University Press, Cambridge, Massachusetts.
- Tokarz, R. R. 1995. Mate choice in lizards: a review. *Herpetological Monographs*. Vol. 9, p. 17-40.
- Trillmich K. G. K. 1983. The mating system of the marine iguana (*Amblyrhynchus cristatus*). *Z. Tierpsychol.* 63: 141-172.
- Trivers, R. L. 1976. Sexual selection and resource accruing abilities in *Anolis garmani*. *Evolution*. 30: 253-269.
- 1985. *Social Evolution*. Benjamin/Cummings Publishing Co., Inc., Menlo Park, California.
- von Geldern, C. E. 1919. Mechanism in the production of the throat-fan in the Florida chameleon, *Anolis carolinensis*. *Calif. Acad. Of Sci.*
- Werner, D. I. 1978. On the biology of *Tropidurus delanonis*, Baur (Iguanidae). *Z. Tierpsychol.* Vol 47, 337-95.

Werner, R. K., Hoernle, P. Van Den Bogaard, C. Ranero, R. von Huene and D. Korich. 1999. Drowned 14-m. y-old Galápagos archipelago off the coast of Costa Rica: implications for tectonic and evolutionary models. *Geology* 27: 499-502.

Wilson, E. O. 1975. *Sociobiology: the new synthesis*. Harvard University Press, Cambridge, Mass.

Wright, J. W. 1983. The evolution and biogeography of the lizards of the Galápagos Archipelago: Evolutionary genetics of *Phyllodactylus* and *Tropidurus* populations. Pp. 123-155 in R. I. Bowman, M. Berson, and A. E. Leviton, eds. *Patterns of evolution in Galápagos organisms*. Pacific Division of the American Association for the Advancement of Science, San Francisco, CA.

Wright, J. W. 1983. The evolution and biogeography of the lizards of the Galápagos Archipelago: Evolutionary genetics of *Phyllodactyllus* and *Tropidurus* populations. Pages 123-155 in *Patterns of evolution in Galápagos organisms* (R. I. Bowman, M. Berson, and A. E. Levinton, eds.) AAAS Symposium Volume, San Francisco, California.

Wyrтки, Klaus. 1967. Circulation and water masses in the eastern equatorial Pacific Ocean. *Journal of Oceanology and Limnology*. Vol. 1, No. 2, p. 117-147.