Ventral coloration and body condition do not affect territorial behavior in two *Sceloporus* lizards

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*Sceloporus* lizards are known to be defensive of their territories, which provide shelter, food, water, and mates. They often exhibit territorial behavior through visual displays of aggression, specifically with pushups. Along with aggression, this display can also expose the blue coloration on their ventral side, serving as an intraspecific communication between lizards that reveals information about their dominance, sex, and species membership. In this study, we compared how blue coloration and body condition affected territorial behavior in two *Sceloporus* lizards: the well-studied western fence (*Sceloporus occidentalis*) and the understudied sagebrush (*Sceloporus graciosus*), two closely related lizards with overlapping ranges in the San Jacinto Mountains. We also addressed whether these species would exhibit character displacement in their ventral coloration as a result of their sympatry. ImageJ and Adobe Photoshop were used for photo analyses to quantify the proportion and intensity of blue on each lizard’s ventral side. Territoriality was measured through number of pushups displayed and distance traveled. We found that both ventral coloration and body condition had no effect on the territoriality of either species, suggesting that territorial behavior is dependent on factors other than their ventral coloration.

**Keywords**: western fence lizard, sagebrush lizard, territory, blue pigmentation, *Sceloporus* lizard, pushups, body condition, territorial behavior

**INTRODUCTION**

Territorial behavior is a crucial aspect of animal ecology, as it can influence the fitness and reproductive success of many animals (Harris & Siefferman 2014). Although animals manifest territorial behavior in various ways, the definition of territoriality provided by Sheldahl and Martins is especially applicable to lizards: it is the relationship between aggression and the consistent use of a particular area (2000). Spiny lizards (*Sceloporus*) are no exception to this definition. This genus is one of the most diverse and species-rich clades of reptiles in North America, comprising upwards of 90 species (Leache 2010). Some spiny lizards exhibit strong fidelity to specific localities, where they have established their home ranges, and it is to defend these territories that spiny lizards display aggressive behavior (Davis & Ford 1983).

The aggression exhibited by spiny lizards can also impact how large their territory is...
Having larger territories yields an increase in the abundance of resources that animals have access to, like water and food availability and access to mates. However, an animal can only defend so much area; as its home range expands, the territory will become more difficult to defend (Davis & Ford 1983). This trade-off is a challenge that many spiny lizards cope with, and their territory size must be above a certain threshold in order to maximize their fitness (Davis & Ford 1983). In establishing and defending their territories, spiny lizards display a visual form of aggression: pushups, which are normally directed at another lizard (Sheldahl & Martins 2000). However, pushups can also be used to expose the unique color variations on the abdomen of male western fence lizards (*Sceloporus occidentalis*) and male sagebrush lizards (*Sceloporus graciosus*) as a mode of social signaling.

In several fence lizards, including the western fence lizard and the eastern fence lizard (*Sceloporus undulatus*), the vibrant patches of blue that males have on their throats and their abdomens are employed as a means of intraspecific communication (Cooper & Burns 1987; Langkilde et al. 2012). The ventral coloration can indicate individual quality traits to other lizards, such as social dominance (Langkilde et al. 2012) and agonistic prowess (Cooper & Burns 1987). Although the chromatic signaling of fence lizards has been well studied, it remains unclear how this signaling impacts their territoriality.

A previous study by Cooper and Burns demonstrated the importance of abdominal coloration in social responses of the western fence lizard, but it did not address whether males with more blue coloration exhibited more territoriality than males with less blue coloration (1987). Another study demonstrated that in wall lizards (*Podarcis muralis*), the blue pigmentation of the lizard abdominal surface affected its bite force (Lanuza et al. 2014). This study used bite force as a proxy for aggression. Although quantifying aggression in this way did demonstrate how differences in ventral coloration affect lizard aggression, the study did not look at other aspects of territorial behavior in wall lizards like pushups (Lanuza et al. 2014). Along with this knowledge gap, research on the ventral coloration of sagebrush lizards lacks, even though it has ventral color patterns similar to that of the western fence lizard.

Among the social signals conveyed by the ventral coloration of spiny lizards is species identification (Cooper & Burns 1987). The ranges of the western fence lizard and the sagebrush lizard are sympatric (overlapping) in several areas along the west coast, so it is possible that the ventral coloration of these species would be different from each other in sympatric regions as a result of character displacement. Character displacement is the phenomenon in which the differences among closely related species are more pronounced where those species co-occur. The differences are less pronounced where those species do not overlap. Previous studies have discovered this phenomenon in the sizes of closely related spiny lizards (Colwell & Gatz 1993). Furthermore, character displacement in the ventral coloration of sympatric western fence lizards and sagebrush lizards would make sense, given it would reduce the chance of hybridization between the species (Ferguson 1973). If there is character displacement in the ventral coloration of these lizards where
their ranges overlap, then it is possible that one species is more aggressive than the other and, thus, is more territorial.

We expected that the western fence lizard would have more ventral blue coloration than the sagebrush lizard based on our initial observations. If this held true, we also expected that the western fence lizard would be more aggressive and would display more territorial behavior than the sagebrush lizard. We also predicted that an increase in the body condition of a lizard would correspond to an increase in its territoriality, since healthier lizards are expected to have more blue and thus, should display more pushups and maintain larger territory sizes.

METHODS

2.1 Study System

This study was conducted at the James San Jacinto Mountains Reserve (33.80° N, 116.77° W), a 30-acre reserve located in Riverside County, where the ranges of the western fence lizard and the sagebrush lizard overlap. The reserve hosts unique rock formations and various plant communities such as riparian forests, oak woodlands, and montane chaparral. Spiny lizards prefer locations with high-intensity sunlight, and they can be found basking atop of rocks and tree logs with consistent sun exposure. On the reserve, the western fence and sagebrush lizards were some of the most common species of lizards and would be frequently found within close proximity of each other. Both species were caught in three different locations on the reserve: the Flux road, the cabin site, and the solar panels (Fig. 1). The Flux road and solar panels had a mix of forest and chaparral plant communities along with some rocks and human development. The vegetation included shrubs, trees, and logs/wood piles, which all provided shelter and basking areas for lizards. The cabin site consisted of forest and development, and lizards were found on top of trees, logs, cement walls, and fences.

![Figure 1. Location of capturing sites.](image-url) The three locations where western fence and sagebrush lizards were caught in the James San Jacinto Reserve in Riverside, CA. Each point represents one lizard that was captured in that area.
2.2 Capturing

Fieldwork took place from May 5–9, 2021. We captured a total of 24 spiny lizards: 15 western fence (10 male, 5 female) and nine sagebrush (6 male, 3 female). Both species of lizards were captured using a 5.5-foot fishing pole with a noose made of dental floss tied to the end of it. Each lizard was handled by its foreleg, and the researcher would use her forefinger and thumb to gently hold the individual. While being held, species and sex was identified. Each lizard was then photographed (iPhone XR) under the shadow of one researcher, and a ruler and blue notecard were placed in the background of the picture. The weight of the lizard was measured to the nearest hundredth of a gram. The lizards were then marked using white-out and a colored fabric paint before being released back to their catch site. Finally, a flag was placed where each lizard was originally seen.

2.3 Observational Study

Each of the three sites were revisited in hopes of coming across one of the 24 sampled lizards. As each site was approached, we used binoculars to keep our distance and look out for any marked lizards. As soon as a marked lizard was spotted, we stood at least 10 meters away from it and observed the lizard for seven minutes. During this time frame, we counted the number of pushups the lizard displayed, as we used this as a proxy for aggression. We then placed a flag at the furthest point it traveled to. We continued to return to the same site every two hours from 11 a.m. to 5 p.m. and placed a flag at new sites where marked lizards were re-spotted. This process was continued until a total of four flags were placed for each lizard, including the original flag from the time of capture. The distances from each flag to the original flag were measured and averaged to acquire the distance (cm) a lizard traveled. This measurement was established as a proxy for territory size as lizards rarely travel outside their home range.

2.4 Image Analysis

Images were analyzed using ImageJ software, v1.44 (SAS Institute, 2019). Each photo contained a ruler and the ventral side of a lizard. Processing every photo followed the same four steps (Fig. 2). First, using the “straight line” option, we drew a 1 cm line on the ruler in the photo and set the scale to an increment of one centimeter. Second, we drew a line from the tip of the lizard’s mouth to its vent to obtain its snout-vent length in centimeters. Third, we used the “freehand” selection tool and traced an outline of the lizard starting from the tip of the mouth, excluding its arms, legs, and tail, to obtain the lizard’s ventral surface area. Lastly, we traced around the individual patches of blue on the throat and the abdomen to measure the area of blue on each lizard’s ventral surface. The proportion of blue was calculated by adding together the area of each blue patch and dividing by the total ventral surface area.
Figure 2. Step by step process of ImageJ analysis. Each lizard photo was analyzed using the same four steps to obtain its snout-vent length, ventral body area, and the proportion of blue on its body.

2.5 Photoshop Analysis

The intensity of blue coloration was analyzed using Adobe Photoshop 2020, v21.2.4 (Adobe Inc. (2019). Adobe Photoshop. Retrieved from https://www.adobe.com/products/photoshop.html). Each lizard’s photo was taken with the same blue notecard in the background. Using the “eyedropper” tool, we randomly picked two points from the background, particularly from the top and bottom of the photo, found the blue values of those points, and averaged them to establish a background value. We used this process to find the blue value in the background of all photos, and we standardized the backgrounds to account for differences in lighting. Using the “eyedropper” tool again, we found and averaged the blue value on the throat and the abdomen and used this value as an indicator of blue intensity.

2.6 Statistical Analysis

All statistical analyses were conducted using JMP statistical software v16.0 (JMP *, Version 16. SAS Institute Inc., Cary, NC, 1989-2019.). We ran two t-tests to compare the proportion of blue and the intensity of blue in the western fence lizard and the sagebrush lizard. We also ran mixed model linear regressions to test how the proportion of blue and the intensity of blue on the ventral surface of a lizard affect the number of pushups displayed and the distance traveled. Each test was done separately for the western fence and sagebrush lizards and accounted for sex as an additional x-variable. To obtain an index for body condition, a linear regression was done to test the relationship between weight and length, and the residual values were gathered (Lanuza et al. 2014). Positive residual values meant that the lizard had a greater weight in proportion to its length and therefore, was in a better body condition. Negative residual values meant that the lizard had a lower weight in proportion to its length and therefore, was in a worse body condition. Mixed model linear regressions were then used to test the effect of body condition on number of pushups displayed and distance traveled separately for each species and also accounted for sex differences by including sex as a variable.
RESULTS

There was no difference in the proportion of blue or the intensity of blue between the western fence lizard and the sagebrush lizard (n_{proportion blue} = 24, t_{proportion blue} = -1.20, p_{proportion blue} = 0.12; n_{blue intensity} = 24, t_{blue intensity} = -0.44, p_{blue intensity} = 0.34). Overall, there were also no relationships between our measures of lizard condition and territorial behavior. The proportion of blue did not affect the number of pushups nor the distance traveled (Table 1). The intensity of blue also did not affect the number of pushups nor the distance traveled (Table 1). While longer lizards were shown to be heavier (N= 24, R^2 = 0.63, p < 0.01; Fig. 3), their resulting body conditions had no effect on the number of pushups or distance traveled (Table 1; Fig. 4). These results were true regarding both species and both sexes of all lizards.

Figure 3. Relationship between length and weight in the western fence and sagebrush lizards found at the James San Jacinto Reserve. Longer lizards tend to have a greater weight (N = 24, R^2 = 0.63, p < 0.01) and its residuals (the distance between the data points and the line of best fit) are used as an index for body condition. Points above the line are lizards that have better body condition and points below the line are lizards that have worse body conditions.

Figure 4. Linear regression of body condition on number of pushups in the western fence lizards found at the James San Jacinto Reserve. Body condition (whether a lizard was above or below a weight proportional to its length) had no effect on the number of pushups displayed in the seven-minute observation period (N= 9, t= -0.65, p= 0.55).

Table 1. The effects of the proportion of blue, blue intensity, body condition, and sex on number of pushups displayed and distance traveled (cm) in western fence and sagebrush lizards.
DISCUSSION

Our results suggest that the western fence lizard and the sagebrush lizard do not exhibit character displacement in their ventral blue coloration, since they have the same proportion of blue and the same intensity of blue. This was a surprise since ventral coloration is known to indicate certain traits to other lizards, including species identification. Since these lizards have similar blue pigmentation, we can infer that they identify members of the same species in ways other than signals from ventral coloration. Also, there was no difference in the territorial behaviors between the western fence lizard and the sagebrush lizard. This indicates that one species is not more territorial than the other, which was another surprise. We began this study expecting that the western fence lizard would demonstrate more territoriality than the sagebrush lizard because it has been so well studied in terms of its territorial behaviors, and because the sagebrush lizard has been a relatively untouched model species to study territoriality compared to other lizards in the genus. Since the blue coloration and the territoriality of these species are not different, we can expect that the lizards are niche partitioning in other ways. This is a probable explanation as to why the species remain so similar in terms of their ventral coloration and territorial behavior, despite their overlapping ranges.

For both the western fence lizard and the sagebrush lizard, we found no effect of the proportion of ventral blue coloration on the number of pushups displayed, nor was there an effect on the distance lizards traveled. The intensity of blue pigmentation returned similar results, as it also did not affect the number of pushups displayed nor the distance lizards traveled. These results suggest that in both the western fence lizard and the sagebrush lizard, the ventral coloration does not affect territorial behavior. Cooper and Burns concluded that the hue of ventral coloration is likely unimportant in the social behaviors of the eastern fence lizard (Sceloporus undulatus), which supports our conclusions on the effects of ventral coloration on territoriality of the western fence lizard and the sagebrush lizard (1987). Furthermore, Lanuza and others had similar results to those of our study; they demonstrated that color morph did not affect the bite force of wall lizards (2014). Yet, they incorporated the ultraviolet light-reflective blue value of the lizard abdomens into their study and demonstrated that these values affected lizard bite force, even though color morph did not. This would be an interesting future direction for research on spiny lizards, as it is possible that the ultraviolet light-reflective blue pigmentation value would also affect territoriality in lizards in this genus, despite the results we obtained using the proportion of blue and blue intensity.

We also found that for both the western fence lizard and the sagebrush lizard, body condition did not affect the number of pushups displayed nor the distance the lizards traveled. This suggests that fatter, healthier lizards are not more territorial than thinner, less healthy lizards. Again, these results align with those obtained by Lanuza and others, as they also demonstrated that body condition does not affect bite force of wall lizards (2014). This result supports our conclusion that body condition has no effect on the territoriality of spiny lizards.
However, lizards may demonstrate territoriality in other ways than the variables we observed. For a more comprehensive study on aggressive behavior, pushups in combination with lateral compression and ventral extension of the dewlap can be used to study territoriality in spiny lizards, as Cooper and Burns did in their study (1987). Furthermore, an observation window that spans longer than seven minutes would better generalize the territorial behavior of each lizard (Sheldahl & Martins 2000). Future research should also consider obtaining territory size through area if feasible. Plotting more points over a longer time and using those to estimate the area of home range, rather than distance traveled as a proxy, would provide a more accurate representation of the territoriality of each lizard (Sheldahl & Martins 2000).

Here we have demonstrated that the western fence lizard and the sagebrush lizard do not exhibit character displacement in their ventral coloration, and we also showed that the coloration these species have does not affect their territorial behavior. This finding should encourage future research on the social behaviors that are elicited by the blue pigmentation of spiny lizards. Despite the fact that this pigmentation is generally considered an indicator of dominance in spiny lizards, it remains unclear whether there are ways in which the coloration affects territoriality in these species.

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REFERENCES


