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Color variation and habitat use in *Liolaemus silvai*

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Abstract. *Liolaemus* is a species-rich genus endemic to South America with relatively little known about the biology of most of the > 200 included species. One species, *L. silvai* is common in the coastal Atacama Desert and is sexually dimorphic. We studied their phenotypic variation in color and body size, as well as habitat use by capturing lizards active on the surface. To assess phenotypic variation, we categorized the color morph of each lizard based on visible coloration in their ventral throat region and their ventral body from the shoulder girdle to the hips. We also sexed each lizard, measured snout–vent length and body mass, and recorded incidences of tail breakage. For habitat use we measured perch height, distance from the rock edge to nearest vegetation, and the height of the rocks on which lizards were initially sighted. We assessed habitat selection by comparing perch characteristics to features available in the habitat by pairing capture rocks with the nearest rock in a random direction from the initial perch site. Male *L. silvai* were significantly larger than females, but color morph and tail break frequency were independent of sex. Lizards used rocks that were significantly closer to vegetation than random rocks available in the environment independently of sex or color morph. We document the same pattern for perch height. Future studies are needed to examine the exact role of vegetation for *L. silvai.*

Keywords. Atacama Desert; Habitat selection; Lizards; Phenotypic variation; Sexual dimorphism; Squamata.

INTRODUCTION

The genus *Liolaemus* is composed of more than 200 species distributed across southern South America (Uetz and Hosek, 2014). Other than basic natural history information and species descriptions, little is known about many of the species of the genus. *Liolaemus silvai* (Ortiz, 1989) is endemic to Chile, occurring in shrubby and rocky environments along the south-central coast (i.e., Huasco to Coquimbo; Troncoso-Palacios et al., 2015). The species is sexually dimorphic and exhibits highly variable coloration. Our study examined the natural history of *L. silvai,* focusing on phenotypic variation in color and body size, as well as habitat use, in a natural population. Based on our preliminary observations of *L. silvai* prior to data collection, we hypothesized that (1) *L. silvai* perched on rocks that were closer to vegetation than expected when compared to rocks present in the habitat and predicted that perch height would vary with color morph, (2) the proximity to vegetation of rock perches varied with sex, and (3) tail breakage affected perch choice relative to vegetation.

MATERIALS AND METHODS

We studied phenotypic variation and habitat use of *Liolaemus silvai* along an approximately 2 km stretch of the rocky intertidal zone and adjacent sandy desert centered on Peñablanca, ca. 40 km south of Huasco, Huasco Province, Atacama Region, Chile (28.6985°S, 71.3152°W; datum = WGS84). We captured lizards from 6–17 January 2020 between 09:00 and 18:30 and measured (snout–vent length [SVL, mm], tail length [mm], and mass[g]), sexed, and then marked each lizard using non-toxic paint pens. We determined sex by examining the cloacal area for the presence of pores that are evident in males (Troncoso-Palacios et al., 2015). The SVL of the smallest male with visible pores was 42 mm, so all individuals with SVL < 42 mm were categorized as juveniles. In addition, we recorded the number of breaks to the tail and total amount of regrowth from all breaks combined. To assess color variation, we visually determined color on the ventral body and chin of each lizard to be either orange, yellow or ambiguous (when the animal had both or no colors; Fig. 1). No lizard was captured more than once, and all were released within 3 h at their capture location.

Habitat use

To assess habitat use, we marked the initial position of each *Liolaemus silvai* and then classified the location as being either on a rock or on the ground. We measured the habitat after capturing, measuring, and releasing the lizard. We defined a minimum size for rocks because the substrate consisted of large boulders, sandy areas, and small pebbles. If the lizard was seen on a rock smaller than

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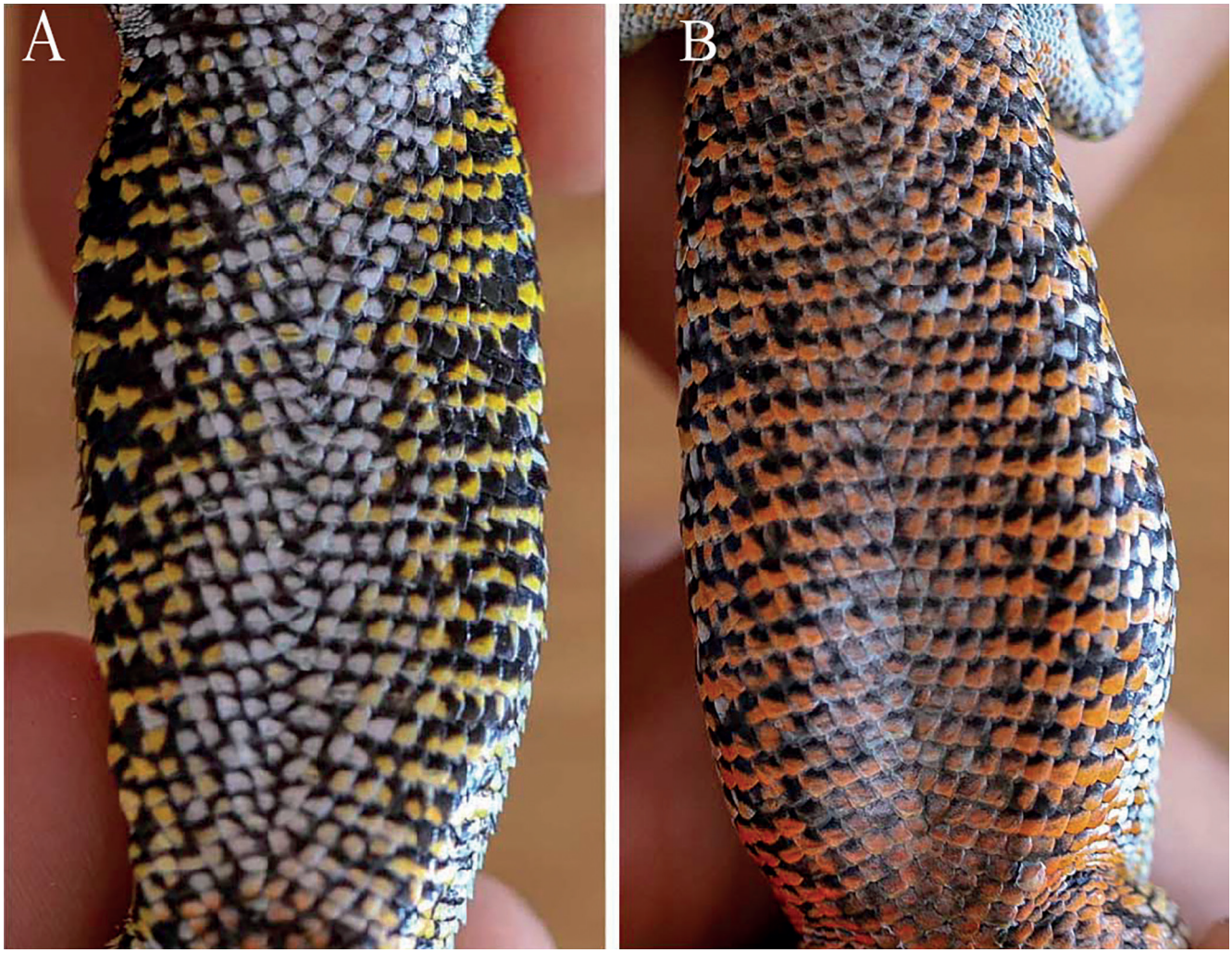

Figure 1. Examples of *Liolaemus silvai* determined to be **(A)** orange (snout–vent length [SVL] = 68 mm) and **(B)** yellow (SVL = 69 mm).

12 × 18 cm or on the ground, we did not record rock measurements. For each rock location, we measured the maximum height of the rock, the height at which the lizard was perched when sighted (= vertical distance from the ground to the lizard's initial position), and the distance from the rock's edge to the closest vegetation. In many cases, vegetation was attached to or growing under the rock where the lizard was initially sighted, in which case we scored distance to the closest vegetation as 0 cm. When lizards were spotted on a rock wall (> 300 × 300 cm), the same measurements were taken, but we measured the maximum height of the rock at the highest point directly above the location of the lizard's perch. To compare the rocks where lizards were sighted to other rocks available in the habitat, we took the same measurements on a rock paired to each lizard's original location. Paired rocks were the closest rock in a randomly chosen cardinal or ordinal direction.

We used R v.3.6.1 for data analyses (R Core Team, 2018). We tested for normality in the distribution of lizard mass, SVL, perch height, and distance to closest vegetation using Shapiro-Wilks tests, and then developed a general linear model to describe the relationship between log-SVL, log-mass, and sex. We performed chi-square analyses to compare sex to color variants and paired *t*-tests for habitat comparisons between rocks on which lizards were sighted and those available in the environment (i.e., rock height, closest vegetation). We tested for frequency differences of color morph by sex, tail break by sex, and tail break by color morph using proportion tests. Mann-Whitney tests were used to compare distances to closest vegetation by sex and perch height by color morph and sex.

RESULTS

We assessed phenotypic variation and habitat use in 90 *Liolaemus silvai.* SVL was normally distributed across adults of both sexes (males: n = 54, females: n = 31), but mass was not normally distributed for adult females (Shapiro-Wilks test: W = 0.902, P = 0.008). Adult males were significantly larger in both SVL and mass (Mann-Whitney test: SVL: W = 1315.5, P < 0.001; Mass: W = 1379, P < 0.001; Table 1). Mass increased with SVL at a higher rate for males than for females (Regression: Female log(Mass) = −8.173 + 2.441(log SVL), Male log(Mass) = −10.018 + 2.927(log SVL); *t*-test: Log(SVL) t = 12.804, P < 0.001; Sex t = −2.111, P = 0.038; Log(SVL) * Sex t = 2.225, P = 0.029; Fig. 2).

We observed two main color morphs: orange and yellow. Within our population, 58.9% (n = 53) were orange,

Table 1. Median (range) snout–vent length (SVL) and mass by sex and age class. All possible pairings within SVL and mass were significantly different ($P < 0.001$).

	SVL (mm)	Mass (g)
Females ($n = 31$)	52 (43–68)	4.74 (2.72–9.74)
Males ($n = 54$)	63 (42–76)	7.735 (2.28–14.44)
Juveniles ($n = 5$)	40 (35–41)	2.13 (1.26–2.18)

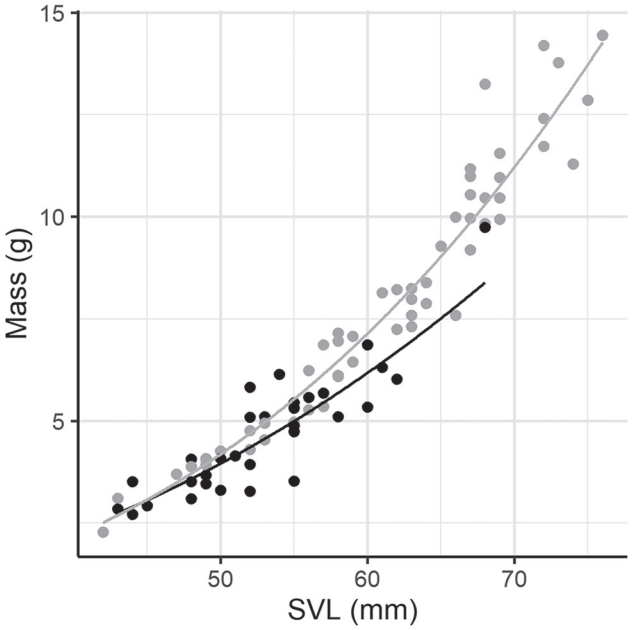

Figure 2. Scatterplot comparing lizard mass and snout–vent length (SVL) between the sexes (gray = males; black = females).

35.6% ($n = 32$) were yellow, and 5.5% ($n = 5$) had no distinct or ambiguous coloration. Color variation was independent of sex (Chi-Square Test: $X^2 = 0.380$, df = 1, $P = 0.538$), but within males a higher proportion (64.81%) were orange (1-sample proportion test: $X^2 = 4.741$, df = 1, $P = 0.029$). More than half the lizards in our population (54.4%; $n = 90$) had ≥1 tail breaks. However, there was no significant difference between sex and tail break frequency (broken tail: females 61.29% (19/31); males 48.15% (26/54); 2-sample proportion test: $X^2 = 1.655$, df = 2, $P = 0.437$). The likelihood of tail breakage was independent of color (2-sample proportion test: $X^2 = 0.295$, df = 2, $P = 0.863$).

For lizards initially observed on rocks ($n = 74$), median rock height was 31 cm (2–310 cm), with a median perch height of 29.5 cm (1–170 cm). Most lizards perched on rocks that were in contact with vegetation so that median distance to closest vegetation was 0 cm (0–458 cm). Comparisons of maximum height between rocks available in the habitat and rocks on which lizards were observed did not differ significantly ($n = 49$; Paired t-test: $t = 0.884$, df = 48, $P = 0.381$). However, lizards used rocks that were closer to vegetation than random rocks available in the environment (Paired t-test: $t = -2.385$, df = 49, $P = 0.021$). The distance to closest vegetation did not vary by sex (Mann-Whitney test: $W = 578.5$, $P = 0.901$), and perch height did not differ significantly between color morphs or by sex (color: Mann-Whitney test: $W = 661.55$, $P = 0.204$; sex: Mann-Whitney test: $W = 584.5$, $P = 0.967$).

In addition, we observed instances of different *Liolaemus silvai* individuals eating the leaves and flowers of *Nolana* cf. *crassulifolia* (Solanaceae; four observations) and flowers of *Frankenia chilensis* (Frankeniaceae; one observation; Fig. S1).

DISCUSSION

Liolaemus silvai exhibits male-larger sexual size dimorphism. Sexual size dimorphism in lizards is not uncommon and has been reported frequently in other *Liolaemus* species (Ibarguengoytia and Cussac, 1999; Rocha, 1999; Block et al., 2012; Troncoso-Palacios et al., 2015). Although reported previously with a small sample size ($n = 10$; Troncoso-Palacios et al., 2015), our findings provide a more robust characterization of sexual size dimorphism in *L. silvai.* In terms of sexual dimorphism in color, the orange and yellow color morphs were both common in our population, and although more males than females tended to be orange, color morph was independent of sex. Nevertheless, the higher frequency of orange males could indicate the significance of color in *L. silvai* social organization and behavior. For example, color can play an important role in male dominance displays (Cooper and Greenberg, 1992; Sinervo and Lively, 1996; Martin and Lopez, 2009). Darkness or intensity of orange color has also been associated with testosterone levels in lizards (Edgren, 1959; Cooper and Clarke, 1982; Cooper et al., 1987; Cox et al., 2005), which can affect social position and display behavior (Marler and Moore, 1989; Sinervo et al., 2000). There have been a few intraspecies descriptions of color variation and preliminary studies of social behavior in a few *Liolaemus* species, but they are not definitive, and any possible link between coloration, social behavior, and dominance rank merits further investigation (Halloy et al., 2007; Labra et al., 2007; Quinteros et al., 2008; Troncoso-Palacios et al., 2015).

Our finding of no difference in tail break frequency between the sexes contradicts the idea that sexual variation in behavior might cause differences in tail injury (Parker and Pianka, 1973; Vitt et al., 1974; Schoener and Schoener, 1980). In populations with high, usually male–male, competition for mates, the sex competing for mates has a higher risk of injury from direct fights or reduced fitness as a result of defending a resource (Sinervo et al., 2000). When tail breaks were compared among 12 *Liolaemus* species, excluding *L. silvai,* frequencies ranged from 23.8–77.2%, which is within the range we found for *L. silvai* (54%). *Liolaemus* is a large genus; variation in tail break frequency could result from differences in predation or escape efficiency (Jaksic and Fuentes, 1980; Medel et al., 1988). In *Crotaphytus* Holbrook, 1842 and *Ctenophorus* Fitzinger, 1843 lizards, more conspicuously colored individuals face increased predation risk (Stuart-Fox et al., 2003; Macedonia et al., 2004). The lack of a difference in color-based tail break frequency in our population indicates that predation risk might not vary with color, an idea worth testing experimentally.

Understanding a species' habitat use provides insights into its ecology, physiology, social structure, required resources, and, ultimately, behavior. For recently discovered or data insufficient species, information on habitat use is critical to making informed decisions about their conservation (Vega et al., 2000; Block et al., 2012). We examined habitat use by comparing rock height and distance to closest vegetation between rocks where lizards perched and randomly chosen rocks available in the habitat. Although rock height did not differ, independently of sex, *Liolaemus silvai* tended to occur on rocks closer to vegetation than random rocks in the habitat. Additionally, one of the most common plants adjacent to rocks used as perches by *L. silvai* was *Nolana* cf. *crassulifolia,* a succulent-leaved plant that we saw *L. silvai* consuming (Fig. S1). Rocks proximate to the plant might be chosen preferably owing to the shelter, food, water or combination of features they provide, perhaps even as a form of secondary defense (Block et al., 2012). Experimental studies are needed to determine the specific role played by plants adjacent to perching rocks for *L. silvai.*

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ONLINE SUPPORTING INFORMATION

The following Supporting Information is available for this article online:

Figure S1. The plants that *Liolaemus silvai* were observed consuming: **(A)** *Nolana* cf. *crassulifolia* (Solanaceae), and **(B)** *Frankenia chilensis* (Frankeniaceae).