

## RESEARCH ARTICLE

# Population differences in multimodal lizard communication are not well explained by habitat or history

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## Abstract

Animals evolve in complex selective regimes, where a suite of different factors can shape signal use. We might predict that more closely related species will exhibit more similar behavior than those more distantly related; however, sometimes signals are shaped more profoundly by the environment or other forces. Lizards in the genus *Sceloporus* communicate with conspecifics with multimodal signals that combine species-typical push-up and headbob displays and chemical signals in the form of femoral gland secretions. Here, we examine behavioral activity and signal use across three closely related populations of the *Sceloporus undulatus* species complex from diverse habitats across the United States, to test the relative roles of habitat and phylogeography in shaping communicative behavior. We filmed undisturbed levels of activity for free-ranging males of *S. consobrinus*, syn. *S. u. erythrocheilus*, in Colorado, *S. undulatus hyacinthinus* in Indiana and *S. u. undulatus* in Georgia, and scored frequency and rates of behavior important for communication. We found that populations differed in their use of communicative signals in a way that deviates from expectations based solely on phylogeographic proximity or habitat, suggesting that plasticity or adaptation to conditions that vary among populations may be especially important. Specifically, canonical discriminant analyses found the largest differences in movement patterns. *Sceloporus u. hyacinthinus* was the most behaviorally different out of the three: males in this population had lower movement rates and particularly low levels of chemosensory behavior while male *S. consobrinus* and *S. u. undulatus* showed similar rates of chemosensory acts and headbob/push-up displays. Phenotypic and environmental variation among closely related populations, in combination with phylogeographic knowledge can help us untangle the processes responsible for the origin and maintenance of organismal diversity in communicative behavior.

## KEYWORDS

behavioral plasticity, chemosensory behavior, habitat-dependent selection, push-up displays, *Sceloporus* lizard, signal

## 1 | INTRODUCTION

Animal communication evolves in complex selective regimes, influenced by evolutionary history and the biotic and abiotic properties of signaling environments. We expect variation across taxa in their use of signaling systems and communicative behavior and can use comparative studies to identify the selective environment and evolutionary processes driving divergence and speciation (Camargo et al., 2010). However, the mechanisms shaping intra-specific phenotypic differentiation are relatively more elusive, since different populations often evolve in very similar landscapes and share the same evolutionary history (Zamudio et al., 2016). Here, we compare the signaling behavior of *Sceloporus* lizards from three phylogeographically distinct populations of the *undulatus* clade to discriminate among some of the most likely forces that shape population differences in communicative behavior, in a species-complex lacking clear diagnostic characters where geographic boundaries and taxonomical relationships are not fully resolved (Leaché & Reeder, 2002).

The biotic and abiotic conditions of habitats can profoundly affect how animals communicate with one another in various contexts, including mating, territorial defense, and antipredation, shaping the structure, type, and timing of communicative behavior (Endler, 1992, 1993). For example, male anole lizards (genus *Anolis*) spend more time headbobbing in denser populations, where intra-sexual competition is higher (Bloch & Irschick, 2006), increase the rate of territorial displays in warmer environments (Ord & Stamps, 2017), and reduce the frequency or amplitude of their headbob displays in habitats with high predation (Simon, 2007; Steinberg et al., 2014). Similarly, túngara frogs (*Engystomops pustulosus*) limit their call rate and complexity in habitats with higher intensity of micropredator attacks (Leavell et al., 2022), and birds adjust the characteristics and timing of their acoustic signals to stand out against the background noise (Brumm & Slabbekoorn, 2005). If habitats have shaped the evolution of communication systems, we might expect individuals from populations that live in different habitats also to use signals differently. Thus, in closed habitats where visual signals may be obscured by poorer visibility (e.g., lower light levels, more visual obstacles), we might expect stronger use of chemical or acoustic signals (but see Hardt & Benedict, 2021) and lower frequency of visual displays, or the use of visual displays that incorporate attention-eliciting elements that enhance the efficiency of long-range communication (Ord et al., 2007; Ord & Stamps, 2008). Conversely, in open habitats we might expect more reliance on visual and less on chemical signals.

In other cases, phylogenetic history may play a more prominent role in shaping communicative behavior (e.g., Chen & Wiens, 2020; Starrett et al., 2022). Phenotypic and genetic divergence are frequently correlated with geographic distance ("isolation by distance," Wright, 1943). Under this scenario, geographically closer populations should be more alike than they are to more distant populations. In túngara frogs, most of the geographic variation in the male advertisement call is predicted by genetic relationships

(Ryan et al., 1996). Similarly, divergence of male nuptial coloration among closely related species of darters (genus *Etheostoma*) is correlated with genetic distance but not with differences in environmental conditions (Martin & Mendelson, 2012). Although phylogenetic history may be especially important in signals undergoing strong stabilizing selection, such as frog distress calls that need to be loud and last long enough to be effective against predators (Forti et al., 2018), it is also a critical predictor of signals that are used in species discrimination (as in woodpecker drumming signals; Garcia et al., 2020) and that are learned (as in the songs of passerine birds; Arato & Fitch, 2021). Studies of intraspecific geographic variation in acoustic communication in birds have offered inconclusive support for isolation by distance (reviewed in Podos & Warren, 2007) and thus whether behavioral differences in signal use across populations match genetic or geographic distances cannot be assumed.

Several processes can lead to deviation from this geographic pattern. Behavioral convergence, for example, makes distantly related species resemble each other more closely than expected, such as Caribbean anoles found in habitats of similar visibility, which convergently evolved similar display behavior (Johnson et al., 2010). Flying lizards (genus *Draco*) and anoles repeatedly converged in the speed and duration of their headbob and dewlap motion displays along common environmental gradients of ambient light and background visual noise (Ord et al., 2021). Communicative displays (behavioral traits) are often more labile than morphological or physiological traits and can exhibit rapid evolutionary change (e.g., Martins et al., 1998; Martins & Lamont, 1998), for example, via local adaptation to habitat (Ord & Martins, 2006). Moreover, signaling is context-dependent and shows plasticity in different environments (Ord et al., 2010), potentially masking other underlying causes of variation. If these and other selective factors are the primary factors shaping evolution of communication systems, then we would expect separate populations to differ from each other, regardless of shared habitat and phylogeographic history.

Lizards in the genus *Sceloporus* are an excellent system for examining the role of habitat and evolutionary history on display behavior. The genus is large and includes several examples of species living in an array of different habitats (Hews & Martins, 2013; Rivera et al., 2020, 2021). Male lizards are territorial and exhibit different behavior to communicate with conspecifics (Hews & Martins, 2013; Ossip-Drahos et al., 2018). First, free-ranging males perform push-up and headbob motions, with or without a conspecific in the immediate vicinity, to broadcast information on individual, sex, and species identity (Carpenter, 1978; Martins, 1993). The motions are often accompanied by body postures that also expose ventrolateral color patches, typically blue, which are often used in male aggressive encounters (Cooper & Burns, 1987; Martins, 1993; Ossip-Klein et al., 2013). A second type of signal consists in the use of chemical secretions, which are produced by glands located on the inner thighs of the hind legs. Chemical secretions are detected via chemosensory behavior linked to

olfaction and/or vomerolfaction and convey similar information as the headbob motions (Martins, 1991; Thompson et al., 2008): sex identity, male competitive ability, and physiological condition (Duvall, 1979; Hews et al., 2011; Martins et al., 2006). Although these signals are used widely across the genus, different species and populations often vary in display structure and use. For example, syntopic populations of two species, *S. virgatus* and *S. jarrovi*, were shown to differ in their basal frequency of chemosensory behavior (Romero-Diaz et al., 2020; Romero-Diaz, Campos, et al., 2021) and three populations of *S. graciosus* differed in the type of body postures and the number of up-and-down motions used to produce the visual display (Martins et al., 1998). A more holistic and informative approach would be to test differences in signal use across the two sensory modalities, among populations occupying different habitat types.

Here, we examine differences in the communication behavior of free-ranging males in the absence of immediate receivers from three distinct lizard populations of the Eastern fence lizard (*Sceloporus undulatus* species complex) from diverse habitats across the United States (Figure 1). Based on their phylogeography, we would expect the more distant *S. consobrinus* and *S. u. undulatus* to be the most different from each other, with *S. u. hyacinthinus* being roughly intermediate (Leaché, 2009; Leaché et al., 2016; Rivera et al., 2020) ("phylogeography hypothesis," Figure 1b). Although the three taxa were historically recognized subspecies of "*Sceloporus undulatus*": *S. u. hyacinthinus*, *S. u. undulatus*, and *S. u. erythrocheilus* (Smith et al., 1992), more recent phylogenetic analyses identify four distinct, monophyletic clades within *S. undulatus*, proposed to be separate species that lack diagnostic characters (Leaché & Reeder, 2002). These most recent taxonomic analyses retain *S. u. hyacinthinus* and *S. u. undulatus* as subspecies of *S. undulatus*, but reclassify *S. u. erythrocheilus* as a separate species, *S. consobrinus* (Leaché, 2009; Leaché & Reeder, 2002). *S. consobrinus* (in the western US) and *S. u. undulatus* (southeastern US) are also furthest apart geographically and are separated by populations of *S. u. hyacinthinus* (northeastern US) in central North America. In contrast, from the perspective of habitat, *S. consobrinus* is either a prairie or canyon "ecomorph" (sensu Williams, 1972; similarly large or smaller, more terrestrial animals with dorsal light striping, and less prominent dark cross-barred pattern), and so may be quite different behaviorally from the other two populations, both of which are forest ecomorphs (Leaché & Reeder, 2002; Smith et al., 1992). We expect lizards in the more open habitats to rely more heavily on visual signals, and spend proportionally more time patrolling, whereas we expect those living in more closed habitats to use more chemical behavior and less frequent visual displays. Thus, based on habitat differences alone, we expect male *S. consobrinus* to produce more visual and less chemosensory behavior than do males from the other two populations. Habitats in the north and southeastern US are similarly forested, so we would predict *S. u. hyacinthinus* to be more similar to *S. u. undulatus*, rather than intermediate, as expected based on phylogeography alone ("habitat similarity" hypothesis, Figure 1b). By comparing these three

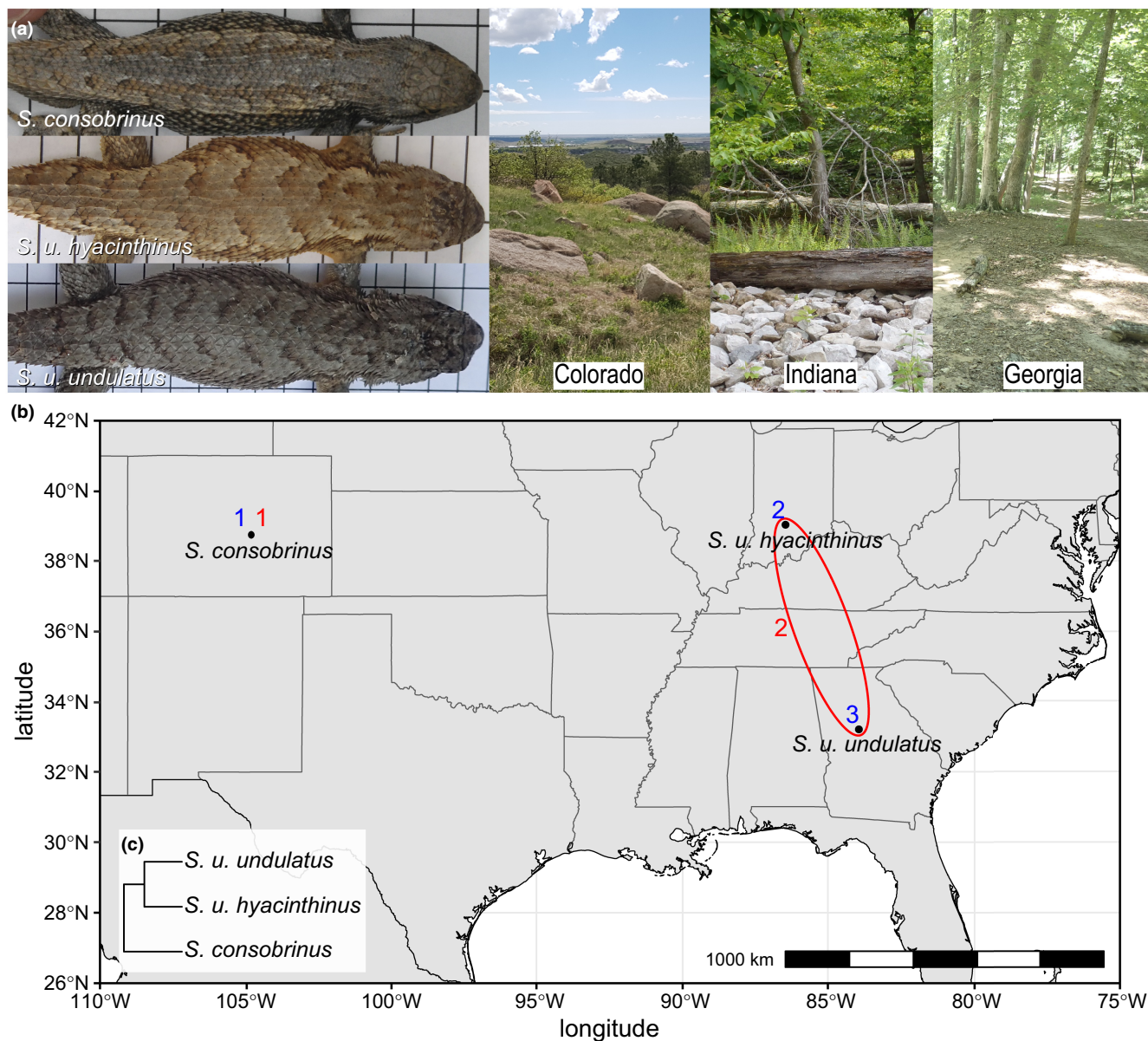
populations, we can thus test the relative importance of phylogeography and habitat in shaping communicative behavior (Zamudio et al., 2016).

## 2 | MATERIALS AND METHODS

### 2.1 | Subjects and procedure

All procedures described here were ethically reviewed and approved by the Arizona State University Institutional Animal Care and Use Committees (protocol #17-1597R RFC#11) and conducted with permission from the Indiana and Georgia Departments of Natural Resources, and Colorado Parks and Wildlife (permits 14-228, 1000729793 and 19HP3336, respectively). Following Martins et al. (2018), we filmed for up to 25 min any free-ranging adult male lizard not in proximity of conspecifics that we spotted while walking through a population to determine rates of undisturbed behavior using Canon Elura 100 and Canon Vixia HF R800 HD camcorders at 30 fps, from a distance of 2–10 m. We avoided approaching a lizard directly or occupying its direct line of sight. We conducted recordings crouched, hiding behind natural obstacles of the surrounding area, and remained still throughout the duration, except when a repositioning of the camera was needed. Duration of trials was highly variable, as subjects often moved out of sight where we could not follow, which ended the trial sooner, but we strived to record each subject uninterrupted for the longest time possible. We filmed *S. consobrinus* at the Cheyenne Mountain State Park in Colorado Springs, Colorado, from May to June of 2019 in a transitional zone between mixed-grass prairie and mesic oak shrubland, spotted with exposed rocks and fractured boulders (Figure 1). We filmed *S. u. hyacinthinus* at the Hoosier National Forest near Bedford, Indiana, from April to July of 2013 in a woody area surrounding an artificial lake (Figure 1). We filmed *S. u. undulatus* at Dauset Trails Nature Center in Jackson, Georgia, from May to July of 2018 in a pine-tree dominated forested area (Figure 1). All data collection occurred during the breeding season of each species. We found males on trees, wood-piles, fallen logs, rocks, and on concrete structures. We filmed all lizards between 09:00 and 17:00 h, and thus hours of high activity. We collected 48 samples of undisturbed behavior from *S. consobrinus* (trials ranged from 2 to 19 min; median = 12 min), 73 samples from *S. u. hyacinthinus* (trials ranged from 1 to 25 min; median = 11 min), and 29 samples from *S. u. undulatus* (trials ranged from 8 to 21 min; median = 11 min). Following a behavioral recording, we attempted to capture the subject lizard to confirm its sex, measure its body size (snout-to-vent length, to the nearest mm) and mark it with non-toxic paint. To prevent re-recordings of unmarked lizards, we covered different areas on different days of sampling and avoided returning to already-covered areas with unmarked lizards. In cases when a lizard evaded capture, sex was confirmed by observation of enlarged tail bases and male-typical territorial behavior.

As environmental temperatures might have a profound effect on any behavioral variable (Gunderson & Leal, 2015), we also downloaded



**FIGURE 1** (a) Dorsal view of a representative adult male and representative habitat for each of the three studied populations of Eastern fence lizard: *Sceloporus consobrinus* in Cheyenne Natural State Park, CO; *S. undulatus hyacinthinus* in Hoosier National Forest, IN; and *S. u. undulatus* in Dauset Trails Nature Center, GA; (b) geographic location of each population and predicted behavioral differentiation based on two alternative hypotheses, namely, the “phylogeographic hypothesis,” in blue, and “habitat similarity,” in red; (c) putative phylogenetic relationships among the three populations. Photos: C. R-D and A. O-D.

Population	DAT (°C)	Precipitation (mm)	Year	Weather station
<i>S. consobrinus</i>	14.1 (7.8–18.6)	0.4 (0–1.27)	2019	38.81°N, 104.69°W
<i>S. u. hyacinthinus</i>	21.0 (11.9–27.2)	3.6 (0–31.7)	2013	39.15°N, 86.62°W
<i>S. u. undulatus</i>	26.0 (23.3–27.5)	2.4 (0–39.6)	2018	33.33°N, 83.70°W

Note: Data taken from weather stations closest to each study site, ranging from 14 to 25 km away. See Supplementary Material (Data S1 and S2) for data on additional years for each population.

**TABLE 1** Mean and range (in parenthesis) daily average temperature (DAT) and precipitation of days in which behavioral observations of lizards were conducted.

weather data from the National Oceanic and Atmospheric Administration's National Weather Service (<https://www.weather.gov/>) for the days and years of filming for the three populations. Daily average

temperature (DAT) and precipitation data were taken from the three weather stations closest to each study site and are reported on Table 1 and the Supplementary Material (Data S1 and S2).



## 2.2 | Scoring

Following Martins et al. (2015) and Martins et al. (2018), we scored frequencies of behavior from video recordings, focusing on visual (headbob/push-up displays with and without display of colorful belly patches ["full-show"]) and chemosensory (tongue-flicks, lip smacks, mouth gapes, chin wipes, and nose taps) behavior. Because chemosensory behavior is also often used in non-social contexts, such as prey detection, and we cannot unequivocally determine the purpose of a chemosensory act from undisturbed behavior, here, "chemosensory behavior" reflects overall chemosensory reliance across tasks, rather than chemosensory reliance in social communication only. Nonetheless, all else being equal, we expect more chemically reliant populations to use more chemosensory behavior in social contexts as well. As a measure of total activity, we summed all behavioral acts performed during recordings, including body adjustments (i.e., small motions of the head or limbs), small movements (<10cm, which is a conservative equivalent to moving less than 1 snout-to-vent length away; "moves"), large movements (>10cm; "travel"), chemosensory acts, visual displays, and other uncommon behavior such as shudder displays, tail wags, and prey capture. To calculate rates of behavior, we divided these behavioral counts by the total duration of the trial (i.e. the total time the lizard was visible on camera) and extrapolated to 1 h (e.g., Campos et al., 2020; Martins et al., 2018).

## 2.3 | Statistical analyses

To test to what extent different populations of *Sceloporus* within the *undulatus* clade can be distinguished from one another using behavioral observations, we conducted a canonical discriminant analysis (CDA). This analysis allowed us to examine further which behavior best distinguishes among populations, and the relationships between different behavioral traits for each population. We excluded full-shows, due to low count, and small movements, which showed multicollinearity (assessed via correlation matrix) with large movements, from this analysis. We also fit one-way ANOVAs followed by Tukey's HSD tests to test for population differences in body size, total activity, headbob/push-up displays, and chemosensory behavior. To test for differences in habitat weather across populations and years, we performed two generalized linear models using either "DAT" or precipitation probability (with precipitation coded as a binomial variable [0/1] and a logit link function), as the response variable and the factors: population, year, and their interaction as explanatory variables. We conducted pairwise comparisons of factor levels after a significant interaction effect using the "testInteractions" function and adjusted *p*-values for multiple comparisons. In all tests, we applied a significance level of  $\alpha = .05$ . We examined the residuals to confirm that the data conformed to the usual assumptions of linear regression. In cases where it failed, we log-transformed all the response variables (i.e., headbob, adjustment, moves, and chem in CDA) or conducted non-parametric analyses (Kruskal-Wallis

test) to confirm the results. We performed all statistics using the base package of R (v. 4.1.0; R Development Core Team, 2018) and the packages phia (De Rosario-Martínez et al., 2015) and candisc (Friendly & Fox, 2021).

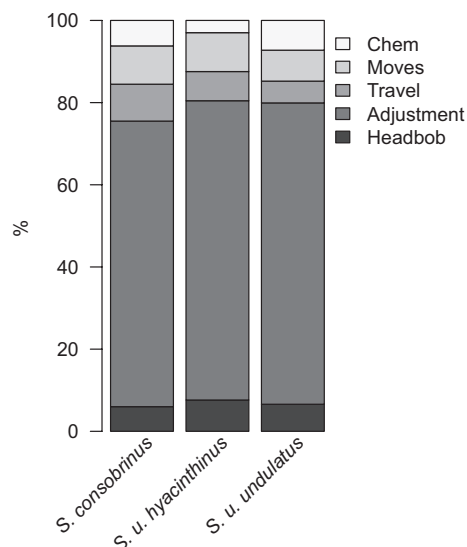
## 3 | RESULTS

### 3.1 | Population ecomorph

Snout-to-vent length was on average ( $\pm$ SE)  $62 \pm 0.8$ ,  $62 \pm 0.9$ , and  $60 \pm 1.0$  mm in *S. consobrinus* ( $n=37$ ), *S. u. hyacinthinus* ( $n=30$ ) and *S. u. undulatus* ( $n=22$ ), respectively, and overall ranged from 48 to 73 mm. We found no significant differences in male body size across populations (ANOVA:  $F_{2,86} = 0.93$ ,  $p = .40$ ); however, adult male dorsal pattern matched ecomorph descriptions made by Smith et al. (1992) and Leaché and Reeder (2002). Males of both *S. u. hyacinthinus* and *S. u. undulatus* were often in trees (showed scansorial habits) and carried the complete or almost complete cross-barred dorsal pattern typical of the forest ecomorph, while *S. consobrinus* males were predominantly on rocks (saxicolous) and showed a greyish dark dorsum, with undefined dorsolateral light stripes and less prominent crossbars, which are more typical of the canyon ecomorph (Figure 1).

### 3.2 | Relationships between populations and behavior

Males of all three populations spent most of their time basking, and thus the most common behavioral act was a slight head or limb adjustment ("Adjustment," Figure 2), followed by small and large movements ("Moves" and "Travel," respectively, Figure 2). Frequencies of headbob displays were on par with previous observations of undisturbed behavior in *Sceloporus* lizards (e.g., Romero-Díaz, Pruett, et al., 2021) and highly aggressive behavior (e.g., headbobs with display of color patches) was rare. CDA revealed that the populations differed significantly in their behavioral means collectively (MANOVA:  $F_{4,145} = 17.49$ ,  $p < .001$ ). In canonical space, the separation of the populations' means is two-dimensional (Figure 3). Canonical axis 1 (90.1% of the population effect;  $F_{8,288} = 8.97$ ,  $p < .001$ ) is largely attributable to large movements and, to a lesser degree, body adjustments, although all variables except headbob/push-up displays contributed positively (Table 2). *S. u. hyacinthinus* males scored lower than did *S. consobrinus* and *S. u. undulatus* males on all measures of this first canonical axis. Canonical axis 2 (9.9% of between-population mean difference;  $F_{3,144} = 2.55$ ,  $p = .057$ ) marginally separated *S. consobrinus* and *S. u. hyacinthinus* from *S. u. undulatus*. Chemosensory acts and headbobs were the clearest measures of this dimension, while travel strongly contributed in the opposite direction (Table 2). Chemosensory acts and visual displays were very similarly correlated with both canonical dimensions.



**FIGURE 2** Relative proportion of observed behavioral acts in adult male *Sceloporus consobrinus*, *S. u. hyacinthinus*, and *S. u. undulatus*. “Headbob” consists of the number of headbob or push-up displays (series of up-and-down motions) without display of blue belly color. “Adjustment,” “Travel,” and “Moves,” refer to small body or limb adjustments, large movements where the distance travelled is greater than 10cm, and small movements with travelled distance less than 10 cm, respectively. ‘Chem’ refers to the number of chemosensory acts (tongue-flicks, lip-smacks, mouth gaping, jaw rubs and nose taps). “Full-shows” are not included due to low count.

### 3.3 | Population differences in behavior and weather

In general, rates of behavior for different activities did not trade-off, with the most active populations also exhibiting the highest rates for each type of behavior. Male *S. consobrinus* and *S. u. undulatus* performed more than twice as many behavioral acts as did male *S. u. hyacinthinus* (Figure 4a), such that there was a significant effect of population on the rate of total activity (ANOVA:  $F_{2,147}=30.09$ ,  $p<.001$ ). Male *S. consobrinus* and *S. u. undulatus* also produced more than twice as many visual displays and a greater number of chemosensory behavior compared to male *S. u. hyacinthinus*, leading to a significant effect of population on the rate of headbob displays (Figure 4b;  $F_{2,147}=4.92$ ,  $p=.008$ ) and chemosensory acts (Figure 4c;  $F_{2,147}=13.81$ ,  $p<.001$ ), respectively.

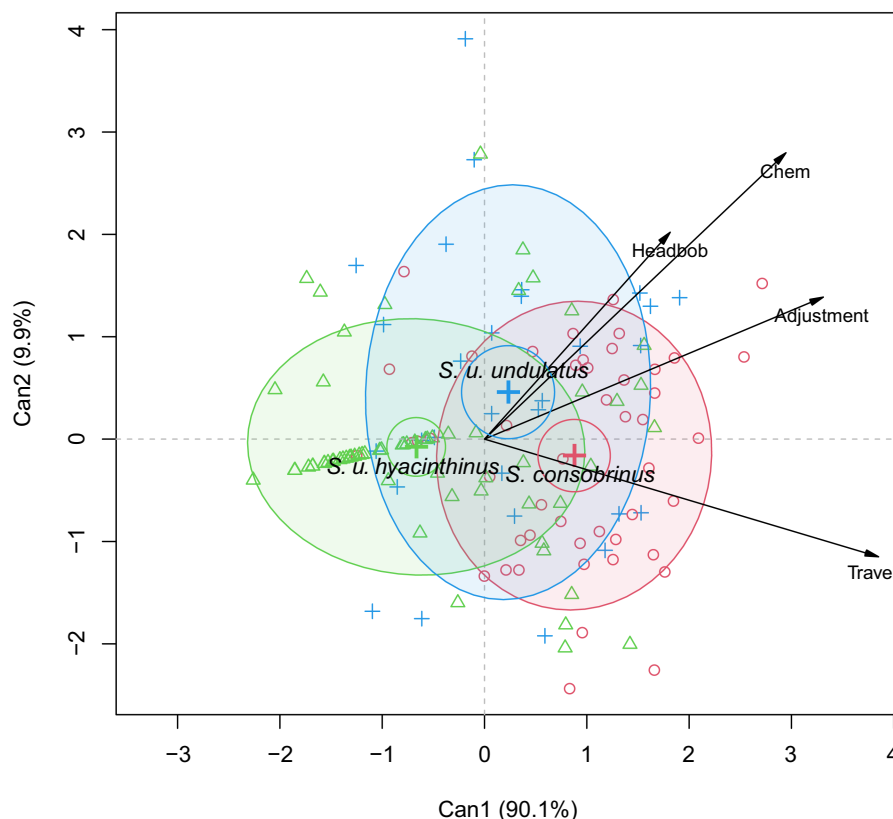
Ambient temperature differed among populations but was largely stable within populations across years, with very few exceptions, leading to a significant interaction between population and year (Figure 5; population $\times$ year:  $F_{4,193}=3.34$ ,  $p=.010$ ). Post hoc comparisons revealed that in Colorado, DATs were significantly lower in 2019 compared to 2013 ( $F_{1,193}=10.11$ ,  $p=.015$ ) and marginally lower in 2019 compared to 2018 ( $F_{1,193}=7.55$ ,  $p=.052$ ). In Indiana, 2018 tended to be warmer than 2013, but not than 2019 (2013 vs. 2018:  $F_{1,193}=7.23$ ,  $p=.054$ ). *S. u. undulatus* consistently experienced the highest DATs, followed by *S. u. hyacinthinus*, followed by *S. consobrinus*, which experienced the lowest temperatures

(Figure 5). Precipitation was infrequent (24% of days), and the probability of precipitation did not differ across years nor populations (all  $X<7.4$ , all  $p>.11$ ). Overall, weather was more similar between the *S. u. undulatus* and *S. u. hyacinthinus* populations in Georgia and Indiana, respectively, than between any of these two and *S. consobrinus* in Colorado.

## 4 | DISCUSSION

We found more similarities between the more distant male *S. consobrinus* (living in open rocky habitats in Colorado) and forest-dwelling *S. u. undulatus* (in Georgia) than between males of either population and male *S. u. hyacinthinus* (in Indiana), such that neither habitat nor phylogeography accurately predicted behavioral differences. The primary difference among the three populations was that *S. u. hyacinthinus* males were considerably less active and used less communicative behavior than did males of the other two populations. Based on both habitat and phylogeny, we predicted similar undisturbed behavior between male *S. u. hyacinthinus* and *S. u. undulatus*. These two subspecies are both forest ecomorphs, occurring primarily in pine and hardwood forests, they exhibit a more arboreal lifestyle that differs substantially from the more terrestrial canyon ecomorph, *S. consobrinus* (Smith et al., 1992) (Figure 1), and experience more similar thermal environments (Table 1). *S. u. hyacinthinus* and *S. u. undulatus* also cluster together in the Eastern clade of the *S. undulatus* species complex, and are closer to each other geographically (Leaché & Reeder, 2002). This also agrees with a more general pattern found across the genus, where closely related species have similar morphology and tend to occur in close geographic proximity (Rivera et al., 2021). More specifically, we expected the behavior of *S. u. hyacinthinus* males to be roughly intermediate to that of males from the other two populations, based on geographic distances, and more similar to that of *S. u. undulatus* based on habitat. Instead, we found that male *S. u. hyacinthinus* were the most behaviorally different of the three. In addition, male body size varied considerably and was similar across populations, suggesting that it is not a reliable diagnostic character for the distinction of populations nor predicting behavioral differences.

Although closed and open habitat distinction did not clearly explain observed differences in our study, habitat may still contribute to explaining why male lizards from some populations had higher rates of visual displays and overall behavior than others. Closed, forested, habitats pose a special challenge to visual signalers, and are associated with the evolution of elaborate ornaments (Ord et al., 2015) and colors (Fleishman et al., 2022; Mitchem et al., 2018) that enhance conspicuousness. In territorial animals, habitat topography can also directly impact activity. Male lizards significantly increase the frequency of territorial patrolling and aggressive visual displays for hours following encounters with male competitors (Moore, 1987). Also, male collared lizards (*Crotaphytus collaris*) court more females when living in open than in closed habitats (Baird & York, 2021) and male green anoles spend more time performing visual displays and



**FIGURE 3** Canonical discriminant plot for the multivariate analysis of variance (MANOVA) of population on behavioral data. Scores on the two canonical dimensions are plotted, together with 68% data ellipses for each group (*S. consobrinus*, *S. u. hyacinthinus*, and *S. u. undulatus*). The contributions of each behavior to differences in population means are shown by the direction and relative length of the variable vectors. Variable definitions are as in Figure 2.

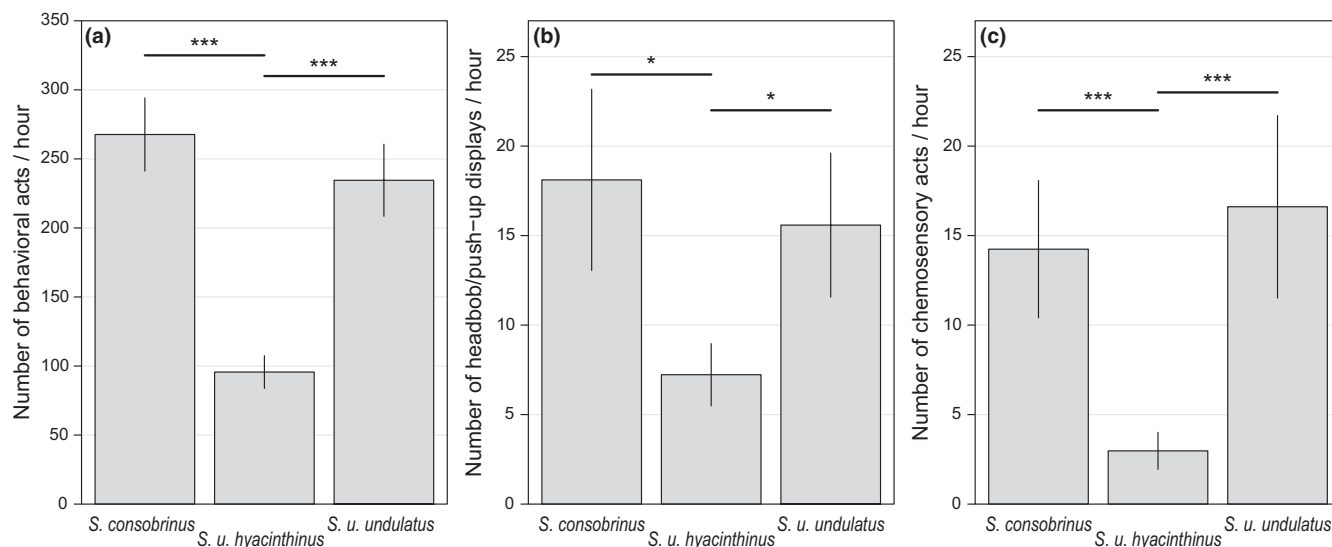
**TABLE 2** Standardized canonical coefficients and structure correlations for two canonical variables summarizing between-class variation in population behavior across *S. consobrinus*, *S. u. hyacinthinus*, and *S. u. undulatus*.

Behavioral trait	Standardized canonical coefficients		Structure correlations	
	Canonical axis 1	Canonical axis 2	Canonical axis 1	Canonical axis 2
Headbobs	−0.323	0.659	0.402	0.448
Adjustments	0.464	0.109	0.734	0.307
Travel	0.764	−0.841	0.854	−0.255
Chemosensory acts	0.318	0.648	0.653	0.620

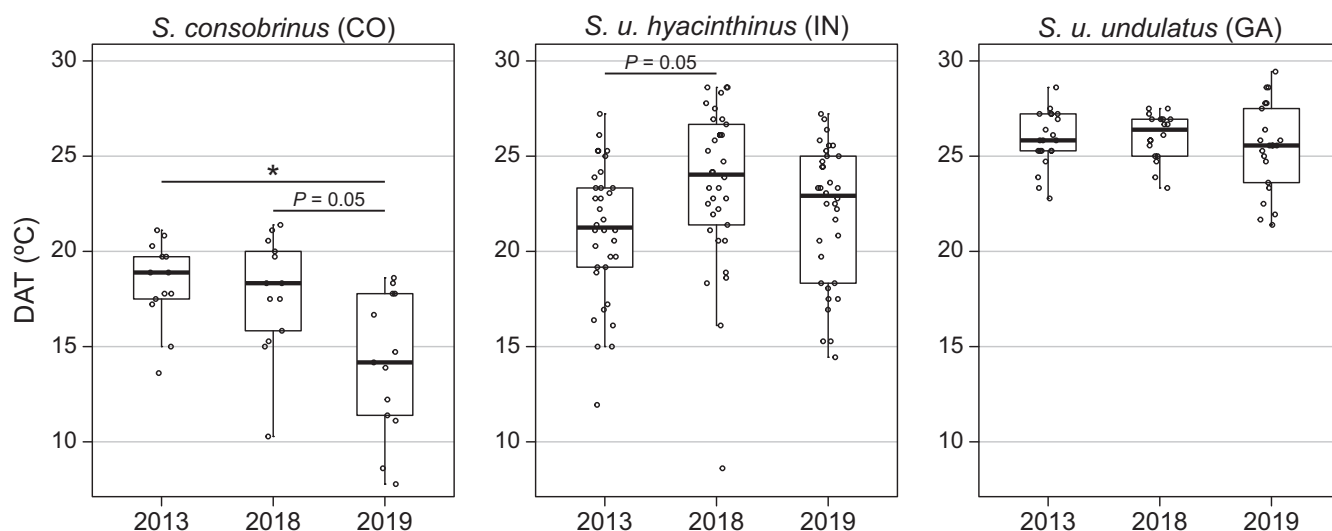
patrolling their territories when living in habitats with clumped vegetation and higher visibility (McMillan & Irschick, 2010). In line with these studies, here we found that lizards in the canyon ecomorph, *S. consobrinus*, which live in a habitat characterized by large boulders with few visual obstructions (Figure 1), also had the highest frequency of visual displays and total activity, suggesting that direct and inadvertent receivers may also importantly influence broadcasting behavior. We need additional studies to determine whether male *Sceloporus* lizards living in closed, forest habitats (e.g., *S. u. hyacinthinus* and *S. u. undulatus*) are also experiencing different levels of intra-sexual competition or are in closer proximity to each other.

Although lizard body temperature can have profound effects on activity and performance, it seems unlikely that population differences in ambient temperatures in our study were responsible for observed

behavioral differences. For example, DATs were consistently and comparatively the lowest in Colorado, where activity rates of lizards were qualitatively the highest. *S. undulatus* select body temperatures in the range of 32–34°C, a preference that seems to be conserved across populations (Angilletta, 2001; Angilletta et al., 2002); however, locomotor performance is maximal at body temperatures ranging from 25 to 38°C, a much wider range (Angilletta et al., 2002). Because we only sampled during hours of high lizard activity on mostly clear-sky days, it is likely that the fine-scale range of operative temperatures overlapped the species' broad optimal temperature range for activity, allowing us to film unconstrained behavior (Gunderson & Leal, 2015). For example, substrate temperatures of random available perches (e.g. rocks, tree trunks, the ground, logs) on the same days and times of filming *S. consobrinus* ranged from 12.8 to 45.1°C with a mean of 30.05°C



**FIGURE 4** Behavioral differences among male lizards from three populations of *Sceloporus undulatus*. Mean rate of (a) total activity, (b) headbob/push-up displays, and (c) chemosensory acts per hour  $\pm 1$  standard error are shown. Asterisks indicate significant differences, as determined by Tukey's HSD test (\* $p < .05$ , \*\* $p < .01$ , \*\*\* $p < .001$ ).



**FIGURE 5** Mean daily average temperature (DAT) during days of filming in the years 2013, 2018 and 2019 differed among populations of Eastern fence lizards but were mostly stable within populations across years, with few exceptions (marked by an asterisk: \* $p < .05$ ). Shown are boxplots for each population and year with each data point representing a day of sampling.

( $n = 138$ ; C.R.-D., unpublished data), providing lizards ample opportunities to quickly achieve optimal temperatures.

Behavioral differences between the two forest-habitat lizard populations may be related to the balance of visual and chemical behavior. Intriguingly, male *S. u. undulatus* had the highest rate of chemosensory behavior, such that this population was the only one of the three in which lizards produced more chemosensory than visual behavior (Figure 4b,c). Male *Sceloporus* lizards are attracted to conspecific scent marks (Campos et al., 2017), and comparatively more chemically oriented species may thus move more. Higher activity levels may also reflect a need to refresh chemical signals more often, as these are also passively deposited in the environment as

lizards move, because the scent marks of more-active *Sceloporus* lizard species are less smelly, containing fewer aldehydes (Campos et al., 2020). Male *S. consobrinus* were also very active, suggesting that there may be other reasons that encourage (or discourage) movement. For example, different rates of movement could also reflect differences in predation pressure (Refsnider et al., 2015). In particular, snake predators use chemical cues to select ambush sites or track prey (Clark, 2004), and a comparatively higher snake presence may thus favor lizard inactivity, which decreases an individual's risk of predation. Although we did not assess population density nor predation pressure in our study sites, we observed larger variance in *S. consobrinus* and *S. u. undulatus* behavior than in *S. u. hyacinthinus*,



perhaps as a result of relaxation of selection pressures (e.g., less predation), and these hypotheses warrant further study.

Population differences in communication behavior can offer important insights into evolutionary processes. Male sagebrush lizards (*S. graciosus*) produce visual displays that can be used to distinguish populations (Martins et al., 1998), with male approach and female avoidance being the most likely mechanisms of population-level recognition (Bissell & Martins, 2006). Response behavior can also differ, as in collared lizards (Baird et al., 1997) and chuckwallas (Kwiatkowski & Sullivan, 2002), which vary in their preferences for, and aggressive responses to, brightly colored as opposed to dull conspecifics in the context of intra- and inter-sexual selection. Habitats and climate can also play an important role in shaping population differences in communicative behavior, as in the motion signals of Australian agamid lizards (Ramos & Peters, 2017) and chemical signals of Iberian wall lizards (Martín et al., 2015). In both cases, signals varied in ways that emphasize efficacy of transmission in the local environment, either by increasing movement speed in noisier (i.e. higher plant motion speed) environments, or by adjusting the volatility of chemical secretions to local humidity and temperature conditions. Our results are more similar to those found for visual displays of Australian jacky dragons (Barquero et al., 2015) or distress calls of Chilean weeping lizards (Labra et al., 2021), in which differences in signaling behavior are not fully explained by either genetic relationships or habitat, suggesting that interpopulation variation is the result of behavioral plasticity and different selective pressures in each population.

In summary, we found behavioral differences among three populations of *Sceloporus undulatus* that are not easily explained by habitat or phylogenetic history alone. Both phenotypic plasticity and local adaptation can have marked effects on the morphology, performance, and behavior of animals, producing geographic variation among populations (Zamudio et al., 2016). As we have seen, closely related taxa can use signals very differently when faced with different environments, making more distant populations appear more behaviorally similar to each other than more closely related populations. Phenotypic and environmental variation within species, in combination with phylogeographic knowledge is crucial to determine the processes responsible for the origin and maintenance of organismal diversity in communicative behavior.

## AUTHOR CONTRIBUTIONS

**Cristina Romero-Diaz:** Conceptualization; data curation; methodology; investigation; formal analysis; writing – original draft; writing – review and editing; project administration; visualization; supervision; validation. **Bryce R. Wetherell:** Investigation; formal analysis; writing – original draft. **Danielle Ury:** Investigation. **Mikayla Reuter:** Investigation. **Jake A. Pruett:** Investigation; writing – review and editing; resources. **Emília P. Martins:** Conceptualization; writing – review and editing; funding acquisition; project administration; methodology; resources. **Alison G. Ossip-Drahos:** Investigation; funding acquisition; data curation; conceptualization; methodology; project administration; resources; writing – review and editing; supervision.

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## CONFLICT OF INTEREST STATEMENT

The authors confirm that there is no conflict of interest.

## DATA AVAILABILITY STATEMENT

The datasets generated during and/or analyzed during the current study are available in the Supplementary Material (Data S1 and S2).

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## REFERENCES

- Angilletta, M. J. (2001). Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). *Ecology*, 82(11), 3044–3056. <https://doi.org/10.2307/2679833>
- Angilletta, M. J., Hill, T., & Robson, M. A. (2002). Is physiological performance optimized by thermoregulatory behavior?: A case study of the eastern fence lizard, *Sceloporus undulatus*. *Journal of Thermal Biology*, 27(3), 199–204. [https://doi.org/10.1016/S0306-4565\(01\)00084-5](https://doi.org/10.1016/S0306-4565(01)00084-5)
- Arato, J., & Fitch, W. T. (2021). Phylogenetic signal in the vocalizations of vocal learning and vocal non-learning birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376(1836), 20200241.
- Baird, T. A., Fox, S. F., & McCoy, J. K. (1997). Population differences in the roles of size and coloration in intra- and intersexual selection in the collared lizard, *Crotaphytus collaris*: Influence of habitat and social organization. *Behavioral Ecology*, 8(5), 506–517. <https://doi.org/10.1093/beheco/8.5.506>
- Baird, T. A., & York, J. R. (2021). A decade of sexual selection studies reveals patterns and processes of fitness variation in male collared lizards. *Animal Behaviour*, 180, 37–49. <https://doi.org/10.1016/j.anbehav.2021.07.021>
- Barquero, M. D., Peters, R., & Whiting, M. J. (2015). Geographic variation in aggressive signalling behaviour of the Jacky dragon. *Behavioral Ecology and Sociobiology*, 69(9), 1501–1510. <https://doi.org/10.1007/s00265-015-1962-5>
- Bissell, A. N., & Martins, E. P. (2006). Male approach and female avoidance as mechanisms of population discrimination in sagebrush lizards. *Behavioral Ecology and Sociobiology*, 60(5), 655–662. <https://doi.org/10.1007/s00265-006-0209-x>
- Bloch, N., & Irschick, D. J. (2006). An analysis of inter-population divergence in visual display behavior of the Green Anole Lizard (*Anolis carolinensis*). *Ethology*, 112(4), 370–378. <https://doi.org/10.1111/j.1439-0310.2006.01162.x>
- Brumm, H., & Slabbekoorn, H. (2005). Acoustic communication in noise. *Advances in the Study of Behavior*, 35, 151–209.
- Camargo, A., Sinervo, B., & Sites, J. W. (2010). Lizards as model organisms for linking phylogeographic and speciation studies. *Molecular Ecology*, 19(16), 3250–3270. <https://doi.org/10.1111/j.1365-294X.2010.04722.x>
- Campos, S. M., Pruett, J. A., Soini, H. A., Zúñiga-Vega, J. J., Goldberg, J. K., Vital-García, C., Hews, D. K., Novotny, M. V., & Martins, E. P. (2020). Volatile fatty acid and aldehyde abundances evolve

- with behavior and habitat temperature in *Sceloporus* lizards. *Behavioral Ecology*, 31(4), 978–991. <https://doi.org/10.1093/beheco/araa044>
- Campos, S. M., Strauss, C., & Martins, E. P. (2017). In space and time: Territorial animals are attracted to conspecific chemical cues. *Ethology*, 123(2), 136–144. <https://doi.org/10.1111/eth.12582>
- Carpenter, C. C. (1978). *Comparative display behavior in the genus Sceloporus (Iguanidae)*. Milwaukee Public Museum.
- Chen, Z., & Wiens, J. J. (2020). The origins of acoustic communication in vertebrates. *Nature Communications*, 11(1), 369. <https://doi.org/10.1038/s41467-020-14356-3>
- Clark, R. W. (2004). Timber rattlesnakes (*Crotalus horridus*) use chemical cues to select ambush sites. *Journal of Chemical Ecology*, 30(3), 607–617. <https://doi.org/10.1023/b:joec.0000018632.27010.1e>
- Cooper, W. E., Jr., & Burns, N. (1987). Social significance of ventrolateral coloration in the fence lizard, *Sceloporus undulatus*. *Animal Behaviour*, 35, 526–532. [https://doi.org/10.1016/s0003-3472\(87\)80277-4](https://doi.org/10.1016/s0003-3472(87)80277-4)
- De Rosario-Martínez, H., Fox, J., & R Core Team. (2015). *Analysing interactions of fitted models*. <https://cran.r-project.org/web/packages/phia/index.html>. <https://cran.r-project.org/web/packages/phia/vignettes/phia.pdf>
- Duvall, D. (1979). Western fence lizard (*Sceloporus occidentalis*) chemical signals. I. Conspecific discriminations and release of a species-typical visual display. *Journal of Experimental Zoology*, 210(2), 321–325. <https://doi.org/10.1002/jez.1402100215>
- Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *The American Naturalist*, 139, S125–S153. <https://doi.org/10.1086/285308>
- Endler, J. A. (1993). The color of light in forests and its implications. *Ecological Monographs*, 63(1), 1–27. <https://doi.org/10.2307/2937121>
- Fleishman, L. J., Perez-Martínez, C. A., & Leal, M. (2022). Can sensory drive explain the evolution of visual signal diversity in terrestrial species? A test with *Anolis* lizards.
- Forti, L. R., Zornosa-Torres, C., Márquez, R., & Toledo, L. F. (2018). Ancestral state, phylogenetic signal and convergence among anuran distress calls. *Zoologischer Anzeiger*, 274, 1–5. <https://doi.org/10.1016/j.jcz.2018.02.004>
- Friendly, M., & Fox, J. (2021). *Candisc: Visualizing generalized canonical discriminant and canonical correlation analysis*. R package version 0.8-6. <http://CRAN.R-project.org/package=candisc>
- García, M., Theunissen, F., Sèbe, F., Clavel, J., Ravignani, A., Marin-Cudraz, T., Fuchs, J., & Mathevon, N. (2020). Evolution of communication signals and information during species radiation. *Nature Communications*, 11(1), 4970. <https://doi.org/10.1038/s41467-020-18772-3>
- Gunderson, A. R., & Leal, M. (2015). Patterns of thermal constraint on ectotherm activity. *The American Naturalist*, 185(5), 653–664. <https://doi.org/10.1086/680849>
- Hardt, B., & Benedict, L. (2021). Can you hear me now? A review of signal transmission and experimental evidence for the acoustic adaptation hypothesis. *Bioacoustics*, 30(6), 716–742. <https://doi.org/10.1080/09524622.2020.1858448>
- Hews, D. K., Date, P., Hara, E., & Castellano, M. (2011). Field presentation of male secretions alters social display in *Sceloporus virgatus* but not *S. undulatus* lizards. *Behavioral Ecology and Sociobiology*, 65(7), 1403–1410. <https://doi.org/10.1007/s00265-011-1150-1>
- Hews, D. K., & Martins, E. P. (2013). Visual and chemical signals of social communication: Providing the link to habitat and environment. In W. Lutterschmidt (Ed.), *Reptiles in research: Investigations of ecology, physiology and behavior from desert to sea* (pp. 111–141). Nova Publishers.
- Johnson, M. A., Revell, L. J., & Losos, J. B. (2010). Behavioral convergence and adaptive radiation: Effects of habitat use on territorial behavior in *Anolis* lizards. *Evolution*, 64(4), 1151–1159. <https://doi.org/10.1111/j.1558-5646.2009.00881.x>
- Kwiatkowski, M. A., & Sullivan, B. K. (2002). Geographic variation in sexual selection among populations of an Iguanid lizard, *Sauromalus obesus* (=ater). *Evolution*, 56(10), 2039–2051. <https://doi.org/10.1111/j.0014-3820.2002.tb00130.x>
- Labra, A., Reyes-Olivares, C., Moreno-Gómez, F. N., Velásquez, N. A., Penna, M., Delano, P. H., & Narins, P. M. (2021). Geographic variation in the matching between call characteristics and tympanic sensitivity in the Weeping lizard. *Ecology and Evolution*, 11(24), 18633–18650. <https://doi.org/10.1002/ece3.8469>
- Leaché, A. D. (2009). Species tree discordance traces to phylogeographic clade boundaries in north American fence lizards (*Sceloporus*). *Systematic Biology*, 58(6), 547–559. <https://doi.org/10.1093/sysbio/syp057>
- Leaché, A. D., Banbury, B. L., Linkem, C. W., & Nieto-Montes de Oca, A. (2016). Phylogenomics of a rapid radiation: Is chromosomal evolution linked to increased diversification in North American spiny lizards (genus *Sceloporus*)? *BMC Evolutionary Biology*, 16(1), 63. <https://doi.org/10.1186/s12862-016-0628-x>
- Leaché, A. D., & Reeder, T. W. (2002). Molecular systematics of the Eastern Fence Lizard (*Sceloporus undulatus*): A comparison of parsimony, likelihood, and Bayesian approaches. *Systematic Biology*, 51(1), 44–68. <https://doi.org/10.1080/106351502753475871>
- Leavell, B. C., Beaty, L. E., McNickle, G. G., & Bernal, X. E. (2022). Eavesdropping micropredators as dynamic limiters of sexual signal elaboration and intrasexual competition. *The American Naturalist*, 199(5), 653–665. <https://doi.org/10.1086/718967>
- Martín, J., Ortega, J., & López, P. (2015). Interpopulational variations in sexual chemical signals of Iberian Wall Lizards may allow maximizing signal efficiency under different climatic conditions. *PLoS One*, 10(6), e0131492. <https://doi.org/10.1371/journal.pone.0131492>
- Martin, M. D., & Mendelson, T. C. (2012). Signal divergence is correlated with genetic distance and not environmental differences in Darters (Percidae: *Etheostoma*). *Evolutionary Biology*, 39(2), 231–241. <https://doi.org/10.1007/s11692-012-9179-2>
- Martins, E. P. (1991). Individual and sex-differences in the use of the push-up display by the sagebrush lizard, *Sceloporus graciosus*. *Animal Behaviour*, 41, 403–416. [https://doi.org/10.1016/s0003-3472\(05\)80841-3](https://doi.org/10.1016/s0003-3472(05)80841-3)
- Martins, E. P. (1993). A comparative study of the evolution of *Sceloporus* push-up displays. *American Naturalist*, 142(6), 994–1018. <https://doi.org/10.1086/285585>
- Martins, E. P., Bissell, A. N., & Morgan, K. K. (1998). Population differences in a lizard communicative display: Evidence for rapid change in structure and function. *Animal Behaviour*, 56(5), 1113–1119. <https://doi.org/10.1006/anbe.1998.0872>
- Martins, E. P., & Lamont, J. (1998). Estimating ancestral states of a communicative display: A comparative study of *Cycluracrock* iguanas. *Animal Behaviour*, 55(6), 1685–1706. <https://doi.org/10.1006/anbe.1997.0722>
- Martins, E. P., Ord, T. J., Slaven, J., Wright, J. L., & Housworth, E. A. (2006). Individual, sexual, seasonal, and temporal variation in the amount of sagebrush lizard scent marks. *Journal of Chemical Ecology*, 32(4), 881–893. <https://doi.org/10.1007/s10886-006-9029-8>
- Martins, E. P., Ossip-Drahos, A. G., Vital García, C., Zúñiga-Vega, J. J., Campos, S. M., & Hews, D. K. (2018). Trade-offs between visual and chemical behavioral responses. *Behavioral Ecology and Sociobiology*, 72(12), 189. <https://doi.org/10.1007/s00265-018-2617-0>
- Martins, E. P., Ossip-Klein, A. G., Zuniga-Vega, J. J., García, C. V., Campos, S. M., & Hews, D. K. (2015). Evolving from static to dynamic signals: Evolutionary compensation between two communicative signals. *Animal Behaviour*, 102, 223–229. <https://doi.org/10.1016/j.anbehav.2015.01.028>
- McMillan, D. M., & Irschick, D. J. (2010). Experimental test of predation and competition pressures on the Green Anole (*Anolis carolinensis*) in varying structural habitats. *Journal of Herpetology*, 44(2), 272–278, 277.
- Mitchem, L. D., Stanis, S., Sutton, N. M., Turner, Z., & Fuller, R. C. (2018). The pervasive effects of lighting environments on sensory drive in bluefin killifish: An investigation into male/male competition, female choice, and predation. *Current Zoology*, 64(4), 499–512. <https://doi.org/10.1093/cz/zoy038>

- Moore, M. C. (1987). Circulating steroid hormones during rapid aggressive responses of territorial male mountain spiny lizards, *Sceloporus jarrovi*. *Hormones and Behavior*, 21(4), 511–521. [https://doi.org/10.1016/0018-506X\(87\)90009-2](https://doi.org/10.1016/0018-506X(87)90009-2)
- Ord, T. J., Klomp, D. A., Garcia-Porta, J., & Hagman, M. (2015). Repeated evolution of exaggerated dewlaps and other throat morphology in lizards. *Journal of Evolutionary Biology*, 28(11), 1948–1964. <https://doi.org/10.1111/jeb.12709>
- Ord, T. J., Klomp, D. A., Summers, T. C., Diesmos, A., Ahmad, N., & Das, I. (2021). Deep-time convergent evolution in animal communication presented by shared adaptations for coping with noise in lizards and other animals. *Ecology Letters*, 24(9), 1750–1761. <https://doi.org/10.1111/ele.13773>
- Ord, T. J., Losos, J. B., & Stamps, J. A. (2010). Adaptation and plasticity of animal communication in fluctuating environments. *Evolution*, 64(11), 3134–3148. <https://doi.org/10.1111/j.1558-5646.2010.01056.x>
- Ord, T. J., & Martins, E. P. (2006). Tracing the origins of signal diversity in anole lizards: Phylogenetic approaches to inferring the evolution of complex behaviour. *Animal Behaviour*, 71(6), 1411–1429. <https://doi.org/10.1016/j.anbehav.2005.12.003>
- Ord, T. J., Peters, R. A., Clucas, B., & Stamps, J. A. (2007). Lizards speed up visual displays in noisy motion habitats. *Proceedings of the Royal Society B: Biological Sciences*, 274(1613), 1057–1062. <https://doi.org/10.1098/rspb.2006.0263>
- Ord, T. J., & Stamps, J. A. (2008). Alert signals enhance animal communication in “noisy” environments. *Proceedings of the National Academy of Sciences of the United States of America*, 105(48), 18830–18835. <https://doi.org/10.1073/pnas.0807657105>
- Ord, T. J., & Stamps, J. A. (2017). Why does the rate of signal production in ectotherms vary with temperature? *Behavioral Ecology*, 28(5), 1272–1282. <https://doi.org/10.1093/beheco/axx089>
- Ossip-Draho, A. G., Berry, N. J., King, C. M., & Martins, E. P. (2018). Information-gathering as a response to manipulated signals in the eastern fence lizard, *Sceloporus undulatus*. *Ethology*, 124(9), 684–690. <https://doi.org/10.1111/eth.12801>
- Ossip-Klein, A. G., Fuentes-González, J. A., Hews, D. K., & Martins, E. P. (2013). Information content is more important than sensory system or physical distance in guiding the long-term evolutionary relationships between signaling modalities in *Sceloporus* lizards. *Behavioral Ecology and Sociobiology*, 67(9), 1513–1522. <https://doi.org/10.1007/s00265-013-1535-4>
- Podos, J., & Warren, P. S. (2007). The evolution of geographic variation in birdsong. *Advances in the Study of Behavior*, 37, 403–458.
- R Development Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing <http://www.R-project.org>
- Ramos, J. A., & Peters, R. A. (2017). Habitat-dependent variation in motion signal structure between allopatric populations of lizards. *Animal Behaviour*, 126, 69–78. <https://doi.org/10.1016/j.anbehav.2017.01.022>
- Refsnider, J. M., Des Roches, S., & Rosenblum, E. B. (2015). Evidence for ecological release over a fine spatial scale in a lizard from the White Sands formation. *Oikos*, 124(12), 1624–1631. <https://doi.org/10.1111/oik.02406>
- Rivera, J. A., Lawing, A. M., & Martins, E. P. (2020). Reconstructing historical shifts in suitable habitat of *Sceloporus* lineages using phylogenetic niche modelling. *Journal of Biogeography*, 47(10), 2117–2128. <https://doi.org/10.1111/jbi.13915>
- Rivera, J. A., Rich, H. N., Lawing, A. M., Rosenberg, M. S., & Martins, E. P. (2021). Occurrence data uncover patterns of allopatric divergence and interspecies interactions in the evolutionary history of *Sceloporus* lizards. *Ecology and Evolution*, 11(6), 2796–2813. <https://doi.org/10.1002/ece3.7237>
- Romero-Diaz, C., Campos, S. M., Herrmann, M. A., Lewis, K. N., Williams, D. R., Soini, H. A., Novotny, M. V., Hews, D. K., & Martins, E. P. (2020). Structural identification, synthesis and biological activity of two volatile cyclic dipeptides in a terrestrial vertebrate. *Scientific Reports*, 10(1), 4303. <https://doi.org/10.1038/s41598-020-61312-8>
- Romero-Diaz, C., Campos, S. M., Herrmann, M. A., Soini, H. A., Novotny, M. V., Hews, D. K., & Martins, E. P. (2021). Composition and compound proportions affect the response to complex chemical signals in a spiny lizard. *Behavioral Ecology and Sociobiology*, 75, 42. <https://doi.org/10.1007/s00265-021-02987-5>
- Romero-Diaz, C., Pruett, J. A., Campos, S. M., Ossip-Draho, A. G., Zúñiga-Vega, J. J., Vital-García, C., Hews, D. K., & Martins, E. P. (2021). Evolutionary loss of a signaling color is linked to increased response to conspecific chemicals. *Proceedings of the Royal Society B*, 288, 20210256. <https://doi.org/10.1098/rspb.2021.0256>
- Ryan, M. J., Rand, A. S., & Weigt, L. A. (1996). Allozyme and advertisement call variation in the túngara frog, *Physalaemus pustulosus*. *Evolution*, 50(6), 2435–2453. <https://doi.org/10.1111/j.1558-5646.1996.tb03630.x>
- Simon, V. B. (2007). Not all signals are equal: Male Brown Anole Lizards (*Anolis sagrei*) selectively decrease pushup frequency following a simulated predatory attack. *Ethology*, 113(8), 793–801. <https://doi.org/10.1111/j.1439-0310.2007.01379.x>
- Smith, H. M., Bell, E. L., Applegarth, J. S., & Chiszar, D. (1992). Adaptive convergence in the lizard superspecies *Sceloporus undulatus*. *Bulletin of the Maryland Herpetological Society*, 28, 123–149.
- Starrett, J., McGinley, R. H., Hebets, E. A., & Bond, J. E. (2022). Phylogeny and secondary sexual trait evolution in *Schizocosa* wolf spiders (Araneae, Lycosidae) shows evidence for multiple gains and losses of ornamentation and species delimitation uncertainty. *Molecular Phylogenetics and Evolution*, 169, 107397. <https://doi.org/10.1016/j.ympev.2022.107397>
- Steinberg, D. S., Losos, J. B., Schoener, T. W., Spiller, D. A., Kolbe, J. J., & Leal, M. (2014). Predation-associated modulation of movement-based signals by a Bahamian lizard. *Proceedings of the National Academy of Sciences of the United States of America*, 111(25), 9187–9192. <https://doi.org/10.1073/pnas.1407190111>
- Thompson, J. T., Bissell, A. N., & Martins, E. P. (2008). Inhibitory interactions between multimodal behavioural responses may influence the evolution of complex signals. *Animal Behaviour*, 76(1), 113–121. <https://doi.org/10.1016/j.anbehav.2007.12.015>
- Williams, E. E. (1972). The origin of faunas. Evolution of lizard congeners in a complex Island fauna: A trial analysis. In T. Dobzhansky, M. K. Hecht, & W. C. Steere (Eds.), *Evolutionary biology* (Vol. 6, pp. 47–89). Springer US.
- Wright, S. (1943). Isolation by distance. *Genetics*, 28(2), 114–138.
- Zamudio, K. R., Bell, R. C., & Mason, N. A. (2016). Phenotypes in phylogeography: Species' traits, environmental variation, and vertebrate diversification. *Proceedings of the National Academy of Sciences of the United States of America*, 113(29), 8041–8048. <https://doi.org/10.1073/pnas.1602237113>

## SUPPORTING INFORMATION

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